Echolocation in Noctuidae (Lepidoptera)*

D. N. LAPSHIN, M. V. FEDOROVA, and R. D. ZHANTIYEV

Moscow State University, Moscow

Abstract. The adaptive significance of ultrasonic clicks in flight of noctuid moths was studied. Three series of experiments were performed. In the first one the ability of moths to discriminate between their own clicks and their echo was studied (Fig. 1). The results have shown that noctuids can distinguish between their own signals and artificial echo-like stimuli following the clicks with delay of 0.2 ms (Fig. 3). In the second series of tests we examined the capability of flying moths glued to a thin wire to avoid artificial obstacles in complete darkness (Fig. 2). We recorded me number of contacts with two types of comer reflectors. One of the reflectors had the coefficient of ultrasound reflection at frequencies above 40 kHz, twice as high as another one. Moths with intact auditory organs were found to be more capable of avoiding collisions with obstacles of higher ultrasound reflection (Fig. 4). Perforation of the tympanic membrane resulted in loss of ability to discriminate between two types of reflectors. In the third series of experiments the correlation between length of periods of sound emission and number of moths calling with two types of spherical reflectors was studied. Flying moths emitting sound were able to avoid obstacles having higher ultrasound reflection, while during flight without clicks the number of contacts with both types of reflectors was approximately equal (Fig. 5). These results suggest that some noctuid moths can use echolocation for orientation in flight.

Key words: Lepidoptera; Noctuidae; echolocation.

Many species of Noctuidae during flight may produce ultrasound impulses (clicks) in the rhythm of wing movements. The function of these signals has been discussed in the literature (Roeder and Treat, 1957; Kay, 1969; Agee, 1971, Zhantiev et al., 1993). However, until now, evidence confirming any role of these sounds in the behavior of the moths has been lacking. Analysis of features of the clicks and behavioral situations in which they are emitted suggests that they are not a mean intraspecific or interspecific communication but may be used for spatial orientation at low light intensity, in other words for echolocation. Study of this problem is the major aim of this work.

The proposition that Noctuidae are capable of echolocation was first suggested by Roeder and Treat (1957). These researchers established that the maximal distance at which the tympanic organs of *Prodenia eridania* reacted to clicks of other individuals was 20 cm. A similar value was obtained after calculations of the maximal distance of communication founded on the intensity of clicks of Noctuidae and sensitivity of their hearing organs to similar stimuli (Zhantiev et al., 1993).

The radius of sensitivity of an echolocation system with similar parameters of emission-receptory track, taking into account me coefficient of reflection from natural obstacles (mean value 0.5), is 5 cm. Sound passes over this distance twice during a total time of 0.3 ms.

^{*}Originally published in Zoologicheskiy zhumal. Vol. 72, No. 9,1993, pp. 93-104.

A powerful acoustic strike appearing as a result of the emission of the insect's own acoustic impulse is probably followed by the returning reflected signal. For normal work of an echolocation system it is necessary that hearing organs of Noctuidae could receive a weak reflection from the obstacle signal with minimal delay after the insect's own click. Therefore, our first task was to investigate the reaction of noctuid moths to short ultrasonic stimuli mimicking the echo produced by a moth's impulses at a distance of 3-5 cm.

Our next task was to check the capability of moths to locate surrounding objects by using ultrasonic probing signals. In designing such experiments it was necessary to remember that during flight an insect creates disturbance of the surrounding air in the form of alternating vortices (Brodskiy, 1988). These vortices would interact with objects near the moth and become distorted. At short distances the moth senses such changes with its mechanical receptors rather than using echolocation. To exclude possible effects of aerodynamic air disturbances in ethological experiments we used two types of angle reflectors as alternative obstacles having different coefficients of reflection of ultrasonic waves and insignificant differences in their acoustic properties at frequencies of wing strokes of a flying moth. According to our working hypothesis noctuids using echolocation must touch obstacles poorly reflecting the ultrasound more frequently, and with absence of echolocation the number of contacts with various types of reflectors would be approximately the same.

In the concluding series of experiments we studied the influence of clicks on the capability of noctuid moths to distinguish obstacles in darkness differently reflecting ultrasounds.

MATERIALS AND METHODS

In laboratory experiments we used noctuid moths caught using light of a mercury-fluorescent bulb in the vicinity of Moscow. In experiments on the reaction of moths to echo-like stimuli, behavioral responses were obtained from the following species, *Xestia c-nigrum* and *Agrotis segetum* (2 \bigcirc s of each). In experiments connected with the investigation of the capability of moths to avoid obstacles we used 166 specimens of noctuids of both sexes belonging to 23 species: *Agrotis segetum* Schiff., *Aplecta nebulosa* Hufn., *Apamea fucosa* Frr., *Amphipyra perflua* F., *Archanara sparganii* Esp., *Autographa gamma* L., *A. pulchrina* Haw., *Catocala nupta* L., *Cerastis rubricosa* F., *Cosmia fulvago* L., *Crino satura* Schiff., *Diachrysia chrysitis* L., *Eurois occulta* L., *Hypena proboscidalis* L., *Hydraecia micacea* Esp., *Ipimorpha subtusa* F., *Mythimna turca* L., *Phragmitiphila typhae* Thnbg., *Plusia festucae* L., *Scoliopteryx libatrix* L., *Tholera popularis* F., Xestia baja F., and X. c-nigrum L.

Among moths tested 69 flew poorly under laboratory conditions, and therefore data of only 97 experiments were used.

A model of the device used to investigate reactions of moths to echo-like stimuli is shown in Fig. 1. An experimental insect was held with beeswax on a thin tin wire mechanically connected with a curtain controlling a light beam in the phototransmitter. An electric signal from its exit came to an S8-13 memorizing oscillograph. This system allowed recording shifts of the moth from the horizontal plane when it attempted to maneuver. Photoresistance used in the ultrasound generating device was plugged into the bridge model in such a manner that when the moth moved toward the source of the sound or away from it the light beam on the screen of the oscillograph moved accordingly upward or downward. To record clicks of the moth we used a condenser microphone (RFT MK301 and preamplifier RFT MV201) placed 2 cm above the insect. The electric signal of the click was transmitted from an RFT 00023 microphone amplifier to the electronic generator, which generated a short impulse 50 ms after recording the moth's signal by the microphone. This impulse could trigger controlled generator of the artificial click (made in the laboratory) and connected with the condenser of the radiation device (RFT MK 201). The latter was placed beside the moth 3 cm from its longitudinal axis. The total signal delay time (including the time of distribution of sound waves from the mom to the microphone and from the generating device to the moth) was approximately 0.2 ms.



Fig. 1. Diagram of the experimental setup for study of reaction of moth to repeated short acoustic clicks (echo-like stimuli): M - microphone, MA - microphone amplifier, G - generator of short acoustic impulses, CS – condenser speaker, PR - photorecorder of mechanical movements. Insert: solid line shows trajectory of moth's flight, turn downward indicates movement of moth away from source of sound. Dots above this line indicate moth's own clicks and dots below the line indicate echo-mimicking stimuli.



Fig. 2. Diagram of the experimental setup for study of echolocation capabilities of noctuid moths; W - obstacles well reflecting ultrasounds; V - obstacles poorly reflecting acoustic impulses in direction of source of sound.

The intensity of echo-like stimulus near the tympanic organ of the moth was 74 and 71 dB SPL at the frequencies constituting the artificial click 30 and 50 kHz, respectively; the duration was equal to 2 periods of carrying signal. For visualizing moments of generation of ultrasound impulses by the moth and generator on the screen of the oscillograph simultaneously with their appearance, bright dots were formed above and below the oscillogram according to the movement of the insect in relation to the emission device.

To determine echolocation capabilities of noctuid moths we used a carousel type of device (Fig. 2). To secure conclusive interpretation of results we conducted experiments in complete darkness. Moths were held with beeswax to a fine wire 40 cm long, which allowed them to fly. m the plane of movement of the insects about a circle of 40 cm diameter six obstacles of two types were placed: either angular reflectors (first series of experiments), or spherical obstacles (second series of experiments). Length of the wire holding the moths was chosen in order to allow insects to alight on any available reflector, but not to allow it to fly below the level of reflectors.

Each angular reflector was made of 3 plates 30 mm in diameter. In the type W reflector all 3 plates were in mutually perpendicular planes, and in type V plates were at an 80° angle to each other. Acoustic properties of such systems in the ultrasonic range were different, the type W reflector reflected acoustic waves at a reflection coefficient K = 0.5 at a frequency of 45 kHz, and type V reflected acoustic waves in a direction away from the source, except directions perpendicular to the surface of its own plates (K = 0.25). In relation to the low-frequency waves formed by the flying insect reflectors of both types did not differ significantly, because their size was considerably less than the wave length.

The spherical obstacles that we used also had different acoustic properties. As an obstacle to reflecting ultrasounds relatively well (type *S*) we used plastic balls 4 cm in diameter, covered with metallic mesh. The reflection coefficient of such balls (K= 0.4 at 3 cm from its surface) depended little on the angle of the direct acoustic wave and therefore a moth could sense these obstacles independently of the angle of its flight. Spherical obstacles of type *R* were net-like spherical structures of the same diameter and actually did not reflect acoustic waves (K = 0.05).

Each reflector used in the experiments was connected with an individual preliminary amplifier with high entrance resistance (3 MOm). Through the tethering wire insects received a potential of 5 V. When any part of the insect's body touched the reflectors on exits of preliminary amplifiers an electric impulse was emitted. These signals were electrically summarized by 3-2 channels and after additional amplification and transformation were recorded in the 2-channel microphone.

In experiments with spherical reflectors, besides recording number of touches of obstacles by the moth, sounds produced by moths during the flight were also recorded. For this purpose we placed an acoustic locator with a parabolic reflector 1.5 m from the center of the device. Signals recorded by this device, after transformation, were recorded on a tape recorder along with information on the touching of obstacles by the moth.

Experiments were conducted in the laboratory at 18-22° temperature.

Statistics, m experiments investigating the capability of moths to avoid collisions with obstacles we recorded separately the number of contacts of the insect with each type of obstacle. The significance of differences between values obtained for each individual was evaluated with χ^2 criterion. The total number of contacts with reflectors varied widely and depended primarily on the general duration of flight. The mean number of contacts in one experiment was 58; distribution of this value among all experiments was close to Maxwell's distribution. Because the significance of experimental data was in the comparison of reactions

of moths to obstacles with different coefficients of reflection of acoustic waves, in later treatments we used the parameter $T = \ln (P_v/P_w)$, or $T = \ln (P_v/P_s)$. where $P_v (P_r)$ is the number of contacts with obstacles with low coefficient of reflection, $P_w (P_s)$ is number of contacts with obstacles with good reflection of ultrasounds. Evaluation of significance of differences among distributions of values of T was based on Student and Fisher criteria (Lakin, 1990).

RESULTS

Reactions of noctuid moths to echo-like stimuli. Stimuli-mimicking echoes of moth's signals were offered only after the insect showed stable emission of clicks for 1-2 s. The character of behavioral reactions to the echo-like signals varied in different individuals. Examples are shown in Fig. 3. It should be noted that the emission of a moth's own clicks did not have any effect on the maneuvering of the insect. Changes in the character of flight on both oscillograms coincided with the moment of the beginning of the stimulation with echo-like signals. In Fig. 3A the movement of the moth from the source of the sound (negative phonotaxis) began immediately after the first impulse stimulus was offered. Further stimulation led to a change of the type of maneuvering, displayed in chaotic movement of an insect in a horizontal plane.

Figure 3B shows another type of response. The first offer of the echo-like signal caused termination of generation of the mote's own clicks, but did not affect the insect's flight. Continuation of the stimulation after the moth had resumed generation of sounds was followed by a change in its flight activity. In this case amplitude of shifts in a horizontal plane decreased, which probably was associated with the beginning of more even and rapid flight. Termination of the stimulation led to the restoration of the original flight activity.



Fig. 3. Reactions of noctuid moths to echo-like stimuli: A - negative phonotaxis (*X. c-nigrum*), B - change of flight of *A. segetum*. Continuous lines show shifts of moths in horizontal plane. Dots above these lines indicate moth's own clicks, and dots below the lines indicate impulse echo-mimicking stimuli 0.2 ms after moth's signals. Fluctuations of lines correspond to individual wing strokes. Arrow indicates moment of ending stimulation. Time mark, 200 ms.



Fig. 4. Histogram of distribution of results of experiments for study of echolocation capabilities of noctuid moths. $T = \ln (P_v/P_w)$, where P_v indicates number of contacts of obstacles reflecting ultrasounds, and P_w is the same for obstacles well reflecting ultrasonic waves.

Therefore, noctuid moths were capable of distinguishing their own signals from artificial echo-like stimuli followed by a delay of 0.2 ms, which proves the possibility of their sensing acoustic signals reflected from close objects.

Investigation of capabilities of noctuid moths of avoiding collisions with angular reflectors. Histogram of distribution of results of tests of 35 specimens of various species is shown in Fig. 4. In area "0" on the horizontal axis, results of those experiments in which the number of contacts with reflectors of both types was approximately equal $(P_v = P_w)$ are shown. Results of experiments, in which moths mostly touched reflectors V are to the right of "0" while negative values of T correspond to those experiments in which contacts with obstacles of type W relatively well reflecting sounds were predominant. Analysis of results obtained allows distinction on histogram of 3 groups designated as P1, P2, and P3. The latter is characterized by large values of the coefficient T ($T \ge 0.7$: $P_v/P_w > 2$). In 3 experiments differences in the number of contacts with different type reflectors were significant according to the χ^2 criterion (*C. fulvago*, T = 0.7; A. pulchrina, T = 1.2; E. occulta, T = 1.5). Evidently these moths distinguished obstacles with different acoustic properties, and the predominance of contacts with poorly reflecting ultrasound sounds was not accidental, P > 97%. In other experiments, the total number of contacts was not sufficient for significant evaluations of this criterion. Therefore we should note that with an increase of efficiency of the echolocation system the probability of collision of the moth with reflectors of both types should decline. Therefore, it was impossible to obtain large initial numbers in all experiments. This fact considerably determined the specificity of treatment of obtained results.

Repeated testing of noctuid moths under the same conditions, but after damage of their tympanic membranes showed that as a result of this operation moths lose their ability to sense differences between alternative reflectors, and also that the total number of collisions with obstacles during the same period of time increased. Thus, *C. satura* normally touched type *V* reflectors more often ($T=1: P_v/P_w = 2.7$), and after damage to its tympanic membranes the number of contacts with both types of obstacles became approximately the same ($T = 0: P_v/P_w = 1$). The total number of contacts in this case doubled. The latter fact may indicate that an intact moth is capable to some extent of sensing an echo from type *V* obstacles having a lower than *W* coefficient of reflection.

The P2 group includes results of those experiments in which contacts with type V reflectors were also predominant, but not as much as in the P3 group. At first glance it may be supposed that moths of the P2 group possess a lower sensitivity to echolocation system, but other causes are also possible. Analysis of records of experiments proves that frequency of contact of the moth with different types of obstacles may



Fig. 5. Fragment of record of experiment with *A. perflua on* study of the moth during flight with simultaneous recording of generation of ultrasounds (upper line). On lower line, vertical lines mark moments of contact with respective reflector. During active emission of clicks moth touched obstacles *S* well reflecting sound less frequently. Mark time 10 s.

vary considerably in the course of the experiment. For example, in one experiment *C. nupta* during the first 100 s of flight touched *V* and *W* reflectors with equal frequency $(P_v/P_w = 1)$, and during the next 180 s it touched *V* twice as often as *W*. Similar unequal frequency in the number of contacts was observed also in some other experiments with group P2. It is most likely that the cause of this phenomenon may be in constant generation of acoustic clicks by the moth. Evidently, moths using echolocation are capable of sensing obstacles only during generation of ultrasonic signals, and during its flight without clicks frequency of contacts with reflectors would have a random character and would not depend on their acoustic properties.

The P1 group includes results of experiments in which moths touched reflectors of both types with approximately equal frequency. Despite the fact that in all these experiments values of *T* were close to zero, frequencies of contacts with obstacles differed significantly in different individuals. A considerable number of experimental moths during me first 300 s of flight contacted obstacles 50-70 times, whereas some individuals of *A. gamma, S. libatrix,* and other species during the same time made 10-30 contacts. It seems likely that noctuids touching obstacles frequently did not use echolocation during the experiment. Quite the opposite, in moths with low frequency of contacts it may be supposed that there was such a capability of the echolocation system that they avoided collisions with reflectors of both types.

Influence of the emission of ultrasounds on the capability of noctuid moths to navigate in space. In this series of experiments angular reflectors were substituted by spherical obstacles of two types different in their acoustic properties in the whole range of wavelengths. Using the acoustic locator permitted tracing changes of the emission of ultrasounds by moths during relatively small intervals of time and to find changes in the behavior of experimental insects. When an experimental moth did not click during flight, it was possible to evaluate its capability of sensing an approaching obstacle because of the distortion of air vortices produced by each wing stroke, because the mesh balls, unlike plastic balls, used in these experiments created insignificant aerodynamic resistance. The model of the entire device and its size in this series of experiments remained unchanged.



Fig. 6. Distribution of results of ethologic experiments on generation of echolocation capabilities of noctuid moths taking into account their emission of ultrasounds: A - experiments in which moths did not produce ultrasounds; B -experiments in which clicks of moths were recorded; C - results of experiments of group B, but by segments of time when ultrasound emission did not take place; D - same by segments of time with active ultrasound emission.

The total number of moths of both sexes was 106. Among them, 44 moths flew poorly under laboratory conditions and therefore we used data of 62 experiments only. Simultaneous recording of moth clicks and contacts with ball obstacles showed that during the emission of sound moths less often touch obstacles that reflect ultrasound well (Fig. 5). After sound emission was terminated, the number of contacts with obstacles of both types became approximately the same.

Taking into account the absence or presence of ultrasound click generation during the experiment results of all experiments were divided into 2 groups and in each group histograms of distribution of coefficient T were assembled (Fig. 6).

The histogram in Fig. 6A is based on data of 26 experiments with moths which did not click during the experiment. Maximum of distribution occurs at point T = 0; in other words there was no preference between contacts with either type of obstacle. This group included those species in which earlier ultrasonic clicks were recorded, for example, *H. micacea, A. perflua, E. occulta,* etc.

Group B (Fig. 6B) includes results of 35 experiments in which active emission of ultrasonic signals was recorded. In this group the distribution differs from that described above, it is characterized by a shift in the direction of positive values of T, in other words, in these experiments moths more often touched obstacles not reflecting sounds.

Because in experimental moths emission usually took place during certain intervals of time, this gave us an opportunity to find differences in the behavior of moths between periods when they produced or did not produce sounds, which resulted in our experimental recordings. On basis of number of contacts we calculated coefficient T rounded to 0.1 and whether clicks were absent; the result was included in the histogram of group B, while clicks were produced in group D. Parts of experiments in which occasional clicks were not used.

The distribution of group B did not differ from that of group A (Fig. 6); in other words, if sound emission was absent, experimental moths did differentiate between the two types of reflectors.

The distribution D (Fig. 6D) is of more complex structure and consists of several groups. First of all, results with T > 0.5 should be considered. In these experiments moths distinguished well the two types of obstacles. Five results with F=0 and T = 0.1 were obtained from moths, emission of clicks of which did not affect their behavior. The group with T < 0.3 is especially interesting. In these experiments moths actively approach obstacles reflecting sounds well. Some individuals of this group changed their behavior during the experiment, during one period avoiding contacts with *S* reflectors (usually at the beginning of the experiment) and during another period tending to contact them. In the latter case moths touched the *S* reflector more often (T < 0). This phenomenon was especially typical of Plusiinae; in 2 specimens of *D. chrysitis* and *P. festucae* the behavior changed during one experiment. It may be supposed mat during the experiment motivation in these moths changed; in other words, as a result of exhaustion they attempted to alight on the detected object.

In both series of experiments values of *T* greater than 0.4 were obtained in specimens of the following species: *A. nebulosa, A. perflua, A. gamma, A. pulchrina, C. nupta, C. fulvago, C. satura, D. chrysitis, E. occulta, H. micacea, I. subtusa. M. turca, and P. festucae.*

All results described indicate the ability of moths to use ultrasonic signals for orientation in space. On the basis of analysis of behavior of moths without sound emission it may be concluded that the studied moths are not capable of sensing objects situated close to them by means of aerodynamic distortions during flight.

Approximately 1/3 of all tested individuals did indicate active locomotory activity in complete darkness, but they began to fly as soon as weak light (5 lx) was turned on. In moths flying in the dark, emission of clicks was observed irregularly and often began after the first collision with an obstacle. Weak light usually stimulated click emission.

DISCUSSION

The capability of moths to react to echo-like stimulus from closely situated objects, to distinguish obstacles with different coefficients of reflection, and to avoid collisions with obstacles during click emission proves the possibility of use by these insects of echolocation for orientation in space.

It is necessary to take into account technical difficulties that could have influenced the moth's behavior in the process of the experiment and make the interpretation of results difficult. Among them is the necessity for complete darkness in the experiment, in other words to create conditions that never occur naturally. This was necessary to exclude effects of visual stimuli on the behavior of the insects. The absence of natural lighting completely depressed flight activity in about 1/3 of the tested moths (a similar effect, but in all moths without exception, was caused by covering their eyes) and probably was a major cause of unstable sound emission. This indicates a close association between visual and echolocation systems of orientation. Probably under natural conditions they complement each other under poor lighting conditions during flight among vegetation while foraging, ovipositing, or landing on a chosen object.

Second, in the course of the experiment it was difficult to separate attempts of moths to avoid obstacles from their attempts to land on them. In the first case insects using echolocation should be expected rarely to contact obstacles that well reflect ultrasound (T > 0), and in the second case, quite the opposite, being attracted by "acoustically bright" obstacles (T < 0). It is quite possible that such a controversial behavior of moths resulted in the decline of significant differences in values of T in some experiments.

Obstacles reflecting ultrasounds relatively well (W and S) in general did not have high reflection coefficients in the close area, and differences in the reflecting properties of alternate obstacles were not great, especially in the first series of ethologic experiments. Both these factors could also lower me estimates of efficiency of the echolocation system of moths. In order to determine acoustic properties of objects with which the moth actually is dealing under natural conditions, we measured reflection coefficients of fresh leaves. It appeared that the angle between the direction to the sound generator and plane of the leaf, and its shape as well, are most important for intensity of reflected ultrasonic impulse. Leaves always have a somewhat curved surface, as a result of which they may concentrate the acoustic energy by a concave surface. Efficiency of this phenomenon remains at distances similar to the radius of the curve. As a result the integral coefficient of reflection at frequencies of 40-50 kHz from a concave surface of a leaf may exceed 1, and from the opposite side on the average may be 0.4-0.6. Therefore actual distance of the detecting of natural obstacles may be twice as great as calculated.

Therefore averaged data may not reflect the actual picture, because values of amplitudes of clicks are very scattered. We recorded amplitudes of clicks in many individuals of moths with level of 85 dB and once with 94 dB SPL (Zhantiev et al., 1993). Kay (1969) recorded 96 dB SPL. The threshold sensitivity of tympanic organs of noctuid moths also varies considerably. The minimal threshold of sensitivity to impulse stimuli we recorded in electrophysiologic experiments was 55 dB SPL. Also, at present there are no data on reactions of tympanic organs of noctuids to actual reflecting signals. Such data would be very beneficial to the understanding of the process of sensing of echo of a moth's own click. However, obtaining them is very difficult technically. In addition it should be mentioned that all data concerning levels of radiation and sensitivity were obtained from different individuals of moths, whereas the echolocation transmitter and receiver were located in one organism. Nevertheless, comparison of obtained values proves that maximal sensitivity of the echolocation system of noctuid moths is primarily designed to find objects within immediate proximity (3-30 cm) to the flying insect. In this case it complements vision under poor lighting conditions and supplies information necessary to avoid collisions or for landing. The type of acoustic probing of space discussed here may be classified as an impulse-locationary system.

So far there are no data indicating that noctuid moths using such a method of location may overestimate distance to objects surrounding it by measuring the delay of the return signal. Because temporal resolution of the temporal organ is 2.5 s (Surlykke et al., 1987), it may be supposed that moths do not measure the distance to the obstacle by such a method, but rather react to the first reflected impulse of sufficient amplitude. Taking into account the simplicity of structure of their hearing organs, it seems likely that these insects use exactly such a simplified type of echolocation. It is also possible that they determine distance by evaluation of relative angle change of the located object. However, available data are still not sufficient for actual discussion of this problem.

The problem of the mechanism of sensing of acoustic signals so far remains open. Electrophysiologic data indicate that at small time intervals (0.2-0.3 ms) between two stimuli their separate sensing is impossible. Facts obtained in ecological experiments nevertheless indicate the opposite. Therefore, reaction of tympanic organs of noctuid moths to their own clicks has important peculiarities, in other words, the receptor Al probably does not respond to strong mechanical impact, or its reaction is considerably weakened. At least two hypotheses explaining this phenomenon may be proposed:

1) a reciprocal suppression of hearing receptors exists, which results in the suppression of the potential of action of Al -cell at the moment of emission of a moth's click (this proposition is indirectly confirmed by data of Suga (1961), Perez and Coro (1985), and Coro and Perez (1990);

2) a strong mechanical strike spread over the cuticle at the moment of emission of a moth's own click does not create a generator potential of the hearing receptor as a result of specific blockage of its membranous canals.

REFERENCES

AGEE, H. R. 1971. Ultrasound produced by wings of adults of *Heliothis zea*. J. Ins. Physiol. 17(7): 1267-1273.

BRODSKJY, A. K. 1988. Mekhanika Poleta Nasekomykh i Evolutsiya ikh Krylovogo Aparata. [In Russ.: Mechanics of Flight of Insects and Evolution of Wing Apparatus]. Leningr. Univ. Press : 1-208.

CORO, F., and C. BOCK. 1990. Ultrastructure of the tympanic organ in an arctiid moth. Seventh Internati. Meeting on Insect Sound and Vibration. Piran : 1-12.

KAY, R. E. 1969. Acoustic signaling and its possible relationships to assembling and navigation in the moth *Heliothis zea*. J. Ins. Physiol. 15 : 989-1001.

LAKIN, G. F. 1990. Biometriya. [In Russ.: Biometry]. Vyssh. Shk., Moscow: 1-352.

PEREZ, M., and F. CORO. 1985. Physiological characteristics of the tympanic organ in noctuid moths. J. Compar. Physiol. 156: 689-696.

ROEDER, K. D., and A. E. TREAT. 1957. Ultrasonic reception by the tympanic organ of noctuid moths. J. Exp. Zool. 134 : 127-158.

SUGA, N. 1961. Functional organization of two tympanic neurons in noctuid moths. Japan. J. Physiol. 11: 666-667.

SURLYKKE, A., O. N. LARSEN, and A. MICHELSEN. 1987. Temporal coding in the auditory receptor of the moth ear. J. Compar. Physiol. 162 : 367-374.

ZHANTIEV. P. D., D. N. LAPSHIN, and M. V. FYODOROVA, 1993. Emission and reception of ultrasounds in Noctuidae. [In Russ.]. Zool. Zh. 72 (3) : 76-85.