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RESPONSES OF THE TYMPANIC ORGANS OF CUTWORM MOTH (Amphipyra perflua: NOCTUIDAE) TO ULTRASOUND IMPULSES

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A comparative analysis of the responses of the tympanic organs of cutworm moths to single and paired acoustic clicks was carried out. Discharges of A1 receptors produced in response to single stimuli at a frequency of 25 Hz consisted of no more than four spikes, and the latent period of the response initially decreased with increasing stimulus amplitude, and then increased at levels of greater than 10 dB, in which conditions the threshold was altered. The sensitivity of the receptors was increased by a minimum of 3 dB when the stimulus consisted of paired clicks separated by an interval of 0.l5-1 msec. The temporal resolution of the tympanic organ was 4-5 msec. These results are considered from the point of view of echolocation as a means of orientation in the noctuid moth..

Moths of the family Noctuidae can emit short ultrasound clicks while flying [1, 8,12]. Behavioral studies have shown that noctuid moths flying in the dark can avoid collisions with obstacles only by emitting sound signals [3]. These results led to the suggestion that during the dark part of the day the moths can use impulse echolocation to determine their spatial orientation.

In order to understand the operation of the echolocation system of moths it is important to obtain physiological data on the sensitivity and temporal resolution of their auditory organs using short stimuli which imitate probe signals. Some of the properties of the receptor apparatus which limit the general capacity of the echolocating system include:

- the threshold sensitivity, which defines the maximum radius of action and reliability of obstacle detection;
- temporal resolution, which is needed for separating the probe impulse itself and its subsequent echo. In its turn, the echo signal can have a complex temporal structure, resulting from reflection of echoes from objects positioned at different distances from the locator system. The ability to resolve individual components of such a signal determines the linear resolution of the system in terms of spatial depth,
- the dynamic range and precision of measuring the amplitude of the incoming signal. In noctuid moths, the direction of an incoming sound is determined from binaural differences [10, 13], i.e., on the basis of amplitude analysis, and consequently, both of these receptor properties depend on the limiting angular resolution of the echolocation system.

Initial evaluations of the threshold sensitivity of the tympanic organs of two species of noctuid moth to short acoustic signals were published by Zhantiev et al. [1], who obtained values of 61 dB for Barathra brassicae and 65 dB for Agrotis segetum. For stimuli consisting of paired impulses separated by short intervals of time (0.6-3 msec), the thresholds were some 3-4 dB lower [2]. This effect can be explained in terms of temporal summation at the level of the A1 auditory receptor. The same report included initial data on the temporal resolution of the tympanic organ of noctuid moths (4 msec) for short clicks with amplitudes close to the threshold. The conclusions agreed with previously published data [17], based on results obtained by stimulating the tympanic organ with amplitude-modulated sound. However, the question of the effect of the amplitude of the incoming signal on the temporal resolution of the receptors remains open.

The aim of the present investigation was to study the responses of the peripheral auditory system of noctuid moths to impulse signals resembling the moths' own clicks, and to assess the perception of paired clicks separated by intervals of 0.15-10 msec.

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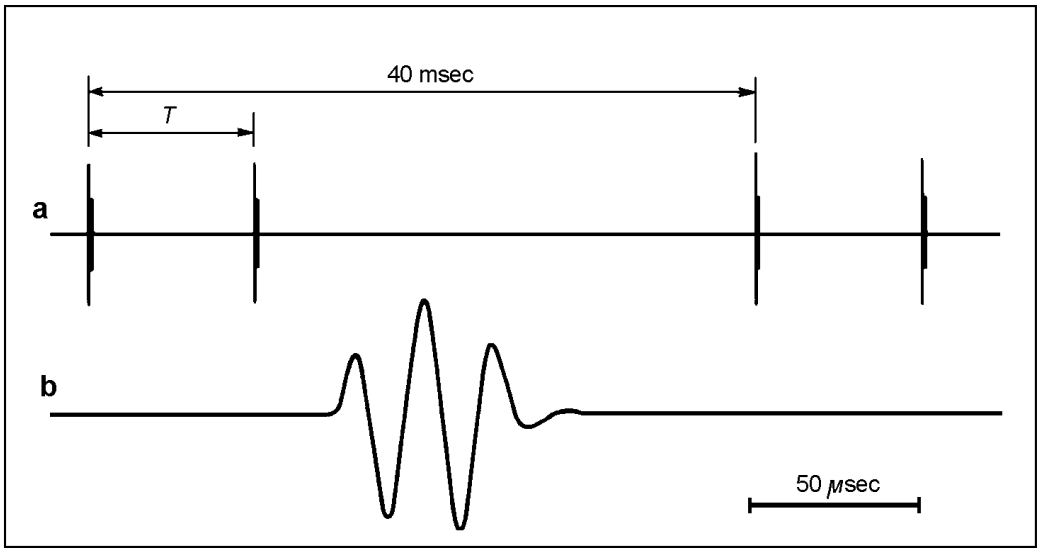

Fig. 1. Stimulating signal: (a) temporal relationships in a double stimulus, (b) oscillogram of a single click.

MATERIALS AND METHODS

The noctuid moth *Amphipyra perflua* F. was used. Insects were trapped using mercury luminescence lamps in the surroundings of Moscow in August, 1994. The thorax was opened laterally as described by Lechtenberg [9]. The activity of neurons in the tympanal nerve was measured using an extracellular tungsten electrode. After amplification, electrophysiological responses were recorded on magnetic tape. A total of 12 individuals of both sexes were used.

Preparations were stimulated with single or paired short acoustic signals imitating the moths' own clicks (frequency 46 kHz, duration 50 μsec) (Fig. 1). Signals were produced using a G3-56A generator fitted with a device-for converting a continuous sine wave signal into short impulses with the desired properties. The sound source was a condenser probe with non-linear amplitude-frequency characteristics of +5 dB over the frequency range 15-90 kHz. This was calibrated using an RFT-00023 apparatus with an MK301 microphone (¼ inch) set to measure peak acoustic pressure amplitudes (in dB). A pressure of 0.00002 Pa was taken as 0 dB SPL.

Single and paired stimuli were repeated in all experiments at the same frequency, with intervals of 40 msec. The intervals between individual impulses in paired stimuli were varied from 0.15 to 10 msec.

Preparations were exposed to sequences of 100 stimuli with a fixed set of properties. Experiments were performed in laboratory conditions, at a temperature of 18-20°C. Data recorded on magnetic tape were subsequently analysed by computer.

RESULTS

Responses to Single Impulses. The tympanal nerve of noctuid moths includes afferent fibers from two auditory receptor cells, A1 and A2, and from a B cell, which is thought to be a proprioceptor [18]. In general, the B cell shows regular spontaneous activity which is not affected by sound stimuli and is easily recognized among tympanal nerve responses, as its spikes have an amplitude greater than that of the bursts from the auditory receptors [11]. The latter have similar frequency characteristics, but differ in terms of dynamic range: responses of the A1 cell to tonal stimuli have a threshold some 20 dB lower than that of the A2 cell [15]. In our studies, the electrophysiological response of the tympanic organ to stimulation with short clicks did not include spikes from the A2 receptor and the impulses which were recorded were taken to be responses of the A1 receptor.

At the beginning of each experiment, the sensitivity threshold of the A1 receptor of the tympanic organ was determined using single clicks. The threshold was defined as a probability of 0.8 of obtaining a spike in response to the threshold stimulus. The threshold (Th) value was Th = 61±1 dB.

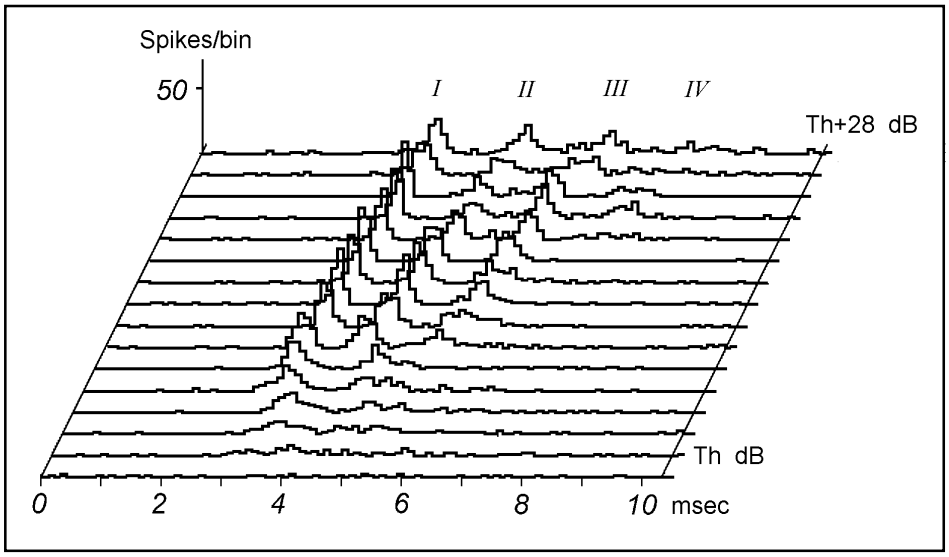

Fig. 2. Post-stimulus histograms of A1 receptor responses to single impulse stimuli. The horizontal axis shows the time elapsed from the moment of stimulus presentation; the vertical axis shows the number of spikes in a single detection channel (spikes/bin); the tilted axis shows the relative amplitude of the stimulus from Th - 2 to Th + 28 dB. Th is the threshold amplitude (61 dB SPL). The resolution step is 0.1 msec/bin.

Studies of the effects of stimulus amplitude on the responses of the tympanic organ were carried out by increasing the signal level in discrete steps of 2 dB, starting from a subthreshold value of Th-2 dB (i.e., 2 dB below threshold). The results of such an experiment are shown as a family of post-stimulus histograms in Fig. 2.

Depending on the stimulus amplitude, the A1 receptor could respond to each acoustic impulse with one or several (up to four) spikes (Fig. 3). Spikes were numbered according to their positions on the time scale relative to the stimulating click; that is, if a receptor burst started for example 6.5 msec after the stimulus (in the zone 11 peak of Fig. 2), this was considered to be the second burst regardless of whether or not an earlier spike had been obtained.

At the threshold level, it was not possible to distinguish the first and second spikes in responses because of the high level of dispersion of bursts on the time scale (Fig. 2). In the amplitude range Th + 2 to Th + 6 dB, the position of the first spike in the response increased in stability. The probability of obtaining the first (p1) and second (p2) spikes showed no significant variation over this range (Fig. 4).

Figure 5 curve *a* shows the mean statistical relationship between the number of impulses in a receptor burst and the stimulus level (coefficient R); there is an initial rapid increase in the response, reflecting the parallel increase in p1 and p2 as the amplitude of the stimulus signal increased.

A third spike appeared in the receptor response from a stimulus amplitude of Th + 6 dB. The probability of its appearance (p3 on Fig. 4) increased sharply over the range Th + 8 to Th + 10 dB. At higher amplitudes, the slope of the curve for p3 showed a sharp decrease, indicating that the transition from a two- to a three-impulse response occurred over a range of only 2-3 dB. The increase in coefficient R in zone III of curve a (Fig. 5) is determined by the corresponding increase in p3.

Further increases in the amplitude of the signal, to Th + 16 dB, were not accompanied by any significant changes in the discharges from receptor A1. At signal levels of greater than Th + 16 dB, responses from this cell could include a fourth spike, though the probability of its appearance was no greater than 0.6 even when the curve for p4 had reached a horizontal plateau at Th + 22 dB and greater (Fig. 4).

Figure 5 curve b shows the relationship between changes in the mean value of the latent period of the first spike and the amplitude of the stimulus. Over the range Th + 2 to Th + 10 dB, the latent period decreased from 4.2 to 3.3 msec as the amplitude increased; at higher levels, there was a reversal in the trend of this change: this sequence of changes in the latent period occurred in all insects studied. The error of the mean depended primarily on variations in the position of the electrode on the tympanal nerve in different experiments.

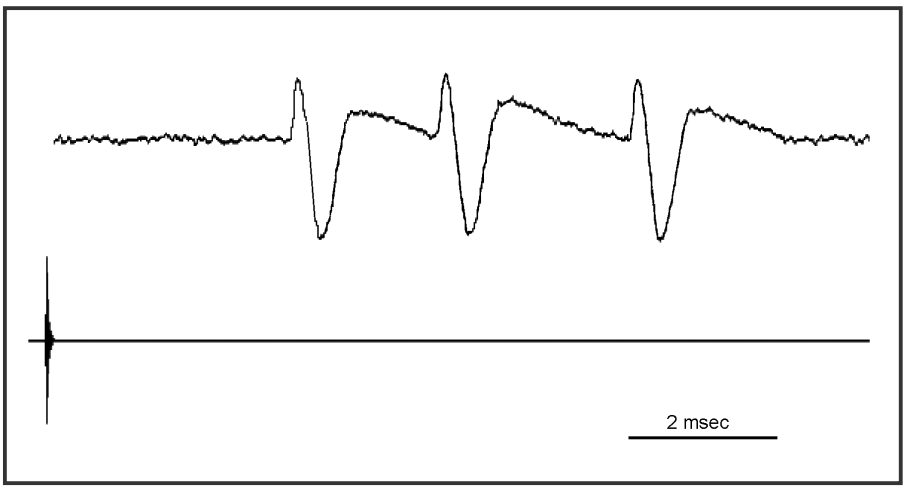

Fig. 3. The electrophysiological response of the A1 receptor to a single-impulse stimulus with a peak amplitude of 75 dB SPL.

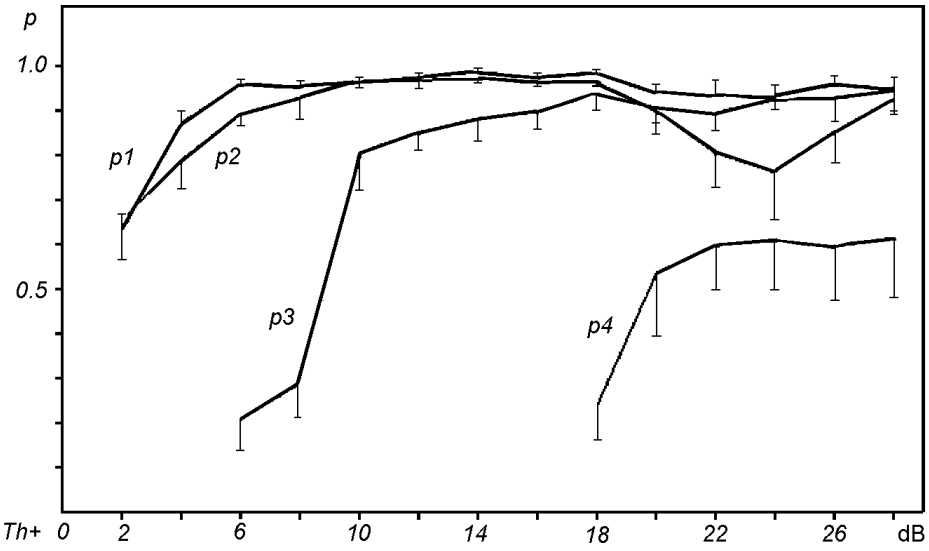

Fig. 4. Graphs showing the probability with which sequential spikes appear in response to stimuli of different amplitude. Numbers are the number of the spike in the electrophysiological burst. Bars show mean errors.

Responses to Paired Stimuli. The temporal resolution of the A1 receptor was studied over three of stimulus sound pressures (Th + 0) to (Th + 2). (Th + 6) to (Th + 8), and (Th + 14) to (Th + 16) dB. Using single stimuli, these intensities elicited 1, 2, and 3 spikes respectively (empty histogram bars, Fig. 6a-c). Stimulation with paired clicks with an interval of T = 0.15-1 msec increased the number of peaks on post-stimulus histograms by one in all cases. Changes in the interval T over this range had no significant effect on the temporal structure of the electrophysiological response. Increases in the number of spikes in receptor bursts under these stimulation conditions apparently resulted from temporal summation of the responses to the two stimuli. A similar response could be obtained from the A1 cell by stimulating the tympanic organ with single clicks of high amplitude (+3 to 6 dB).

At low stimulus levels (Th + 0) to (Th + 2) dB with intervals of T = 1-3 msec, post-stimulus histograms of the auditory receptor responses showed increases in the dispersion of the latent periods of spikes (Fig. 6a).

This suggests that this effect results from superimposition onto the rhythm of receptor bursts of the rhythm resulting from repeated clicks in a paired stimulus, which is of similar magnitude.

At T periods of greater than 3 msec, responses on post-stimulus histograms were separated into two distinct groups, separated by an interval (*D*) which increased with increases in *T*. At *T* periods of greater than 5 msec, the relationship between the magnitudes of *D* and *T* approached the linear (Fig. 6a, Fig. 7a).

In order to confirm that the receptor responded sequentially to each stimulus click at levels of (Th + 0) to (Th + 2) dB, A1 responses were analysed for spikes forming synchronously with the stimulus pair. Such spikes were found to account for a little more than half of all spikes (Fig. 8), i.e., the receptor responded sequentially to both acoustic impulses in a paired stimulus in only half of the presentations. At signal levels close to the threshold, the probability of this event decreased with increases in the interval *T*.

At stimulus amplitudes within the range (Th + 6) to (Th + 8) dB, electrophysiological responses to paired clicks changed with the interval between them as follows: at $T = 3$ msec, the dispersion of the third histogram peak increased (Fig. 6b), and a fourth peak appeared at $T = 4$ msec; this peak became clearer in responses to pairs of clicks separated by $T > 5$ msec.

A1 receptor responses to separate clicks followed a similar pattern at stimulus levels greater than (Th + 14) dB. The main differences were in the changing form of the fourth peak: at these higher intensities, the fourth peak was clear at all values of *T* (Fig. 6c).

Fig. 7b, c shows averaged plots of changes in the interval between the first and third peaks on post-stimulus histograms with increases in *T*. The low dispersion of the peaks at high stimulus levels allowed the natures of changes in the period *D* to be studied over the range $2 < T < 4$ msec. The temporal resolution of the auditory receptor clearly showed little dependence on the signal amplitude, and averaged 4 msec (corresponding to the elbow in the graph).

DISCUSSION

Increases in the sensitivity of the receptor apparatus are meaningful as long as the sound level at the entry point is no greater than the threshold. At greater levels of sensitivity, noise creates a constant background excitation of the receptors, which reduces the real dynamic range of the auditory system as a whole. Touching of the rear wings at the upper point of their range of movement creates a sound of 62 dB in the cutworm moth Agrotis segetum; these impulses have a wide spectrum (up to 125 kHz) whose peak is around 46 ± 9 kHz [19]. Since the spectrum of the moth's own signals is similar to that of the stimuli used [1], the sensitivity thresholds for this species of cutworm moth for impulse signals (65 dB SPL) [1] is comparable to the amplitude of flight sounds (62 dB SPL). This small difference, of 3 dB, suggests that the threshold sensitivity of the cutworm moth tympanic organ is determined by the level of external noise and cannot be significantly reduced. By analogy, the sensitivity threshold of *A. perflua* (61 ± 1 dB SPL) is presumably also determined by external noises. This may explain the low level of individual variation in threshold values.

The curve in Fig. 5a shows that the upper limit of the dynamic range of the A1 receptor can be taken as Th + 20 dB. Response saturation occurred at values greater than this. Within the dynamic range of 20 dB (the lower limit being defined by the threshold value), up to four impulses can be expected in the response of the receptor to single stimuli, i.e., amplitude is encoded into five levels (including 0). However, the actual number of levels is clearly lower, because of the low (less than 0.6) probability that the fourth spike will be produced.

The process of a single action of the echolocation system involves ingress into the tympanic organ of sequential acoustic clicks emitted by the noctuid moth and the echo signal, which generally consists of several impulses which are delayed relative to the insect's own signal to extents proportional to the distances of the objects being ranged.

Calculations based on comparisons of the expected amplitudes of reflected clicks and the sensitivity of the auditory organs of moths to these signals have demonstrated that the range of the cutworm moth echolocation system is 10 cm [1]. After reflection, the emitted sound signal returns to the moth after an interval of 600 μsec. Our measurements show that the temporal resolution of the A1 receptor is 0.4 msec. so that separate perception of the direct and reflected signals is impossible at the level of the tympanic organ. Nonetheless, cutworm moths can sense echo-like stimuli following with small delays relative to their own signals [3]; the physiological mechanisms involved in the simultaneous action on the tympanic organ of two impulses - the probe click and the echo - should therefore be assessed.

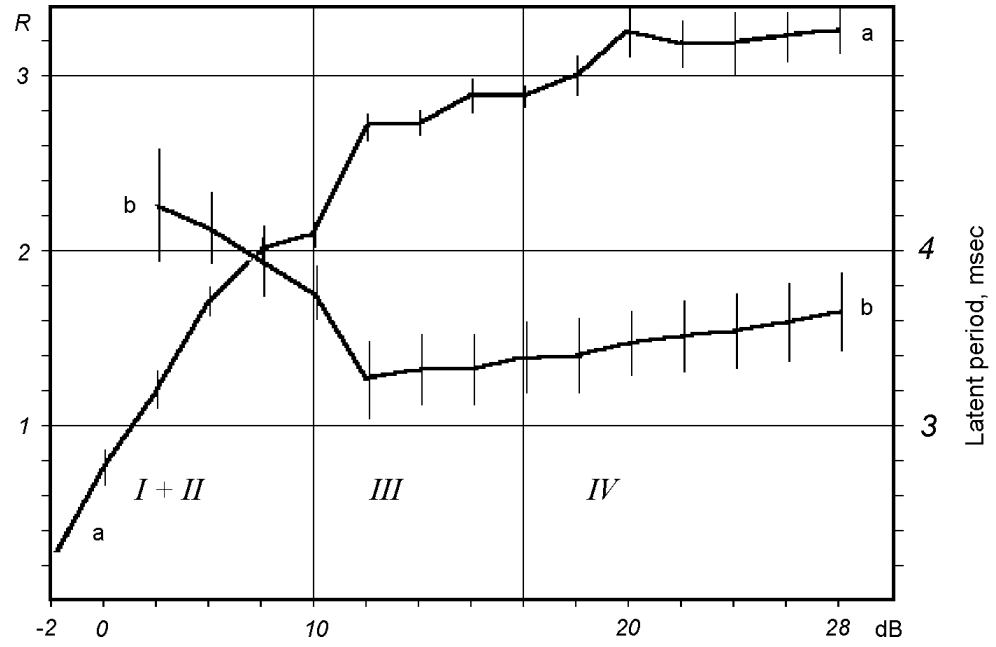

Fig. 5. The relationship between the coefficient *R* and the amplitude of the stimulus (a) and plot of changes in the latent period of the first spike in bursts from the A1-cell (b). Zones *I* + *II*, *III* and *IV* denote regions of rapid increases in the probabilities for, respectively, the first, second, third, and fourth spikes in electrophysiological responses. Bars show mean errors.

An approximate evaluation of the amplitude of the insect's own signal at the entrance of the tympanic organ can be made, assuming that the moth's thorax operates as a spherical emitter characterized by a hyperbolic relationship between acoustic pressure and distance [5]. Using this assumption, the amplitude of the signal acting on the tympanic membrane can be expressed by:

$$P=P_0+20 \lg(A/R) \text{ dB}, \quad (1)$$

where P_0 = 76-94 dB, i.e., the measured acoustic pressure of the noctuid 's own signals at a distance A = 20 mm, and R = 3 mm, i.e., the average radius of curvature of the moth's thorax. At P_0 = 76 dB SPL, the amplitude of the sound acting on the membrane is P = 92.5 dB SPL, or P = Th + 31.5 dB; at P_0 = 94 dB SPL, the value of P = 110.5 dB SPL, or P = Th + 49.5 dB.

Allowing for dispersion of the wave and losses due to reflection from obstacles leads to the expectation that the amplitude of the echo at the entrance of the tympanic organ will be an order of magnitude less than that of the emitted impulse (measured at distance A from the moth) [1], and is 56-74 dB SPL ((Th - 5) to (Th + 13) dB). The lower limit is below the threshold by 5 dB, and such signals will not be perceived. Thus, the expected dynamic range of echo perception lies within the limits Th - (Th + 13) dB. At the entrance of the tympanic organ, the amplitude of emitted acoustic impulse can exceed the reflected impulse by 31-36 dB (35-63 - fold). At such a large ratio of emitted to reflected signals, the electrophysiological response will be determined only by the moth's own first acoustic impulse, and addition of the echo cannot elicit an additional spike in the discharge from the receptor by the mechanism of temporal summation. Thus, the question of the mechanism of perception of acoustic signals, following each other with small delays relative to the insect's own click, remains unanswered.

It may be suggested that the A1 receptor does not respond to strong mechanical stimulation such as the insect's own signal, or mat the response to this type of stimulus is significantly weaker.

Apparently, the generator potential arising in the A1 cell in response to a high-amplitude acoustic stimulus has a duration comparable with the total duration of a single burst (volley), i.e., several milliseconds, so the depression of the response of A1 to the insect's own signal should be associated primarily with blockade of the process involved in generating the receptor potential at the moment of emission of the click. This hypothesis overcomes the basic contradiction, though it requires the receptor membrane to have special properties.

An additional effect should be considered in relation to the processes by which acoustic signals interact at the entrance of the tympanic organ. A strong acoustic blow elicits the corresponding perturbation of the tympanic membrane, in which the vibrations settle down after the stimulus ends. Perception of the echo requires the amplitude of these vibrations at the time of echo arrival to be no greater than the response elicited by the signal of interest.

We will assume that the tympanic membrane is a linear system which can undergo deformations whose amplitude is proportional to the sound pressure level. After the end of the external stimulus, vibrations die down exponentially with a time constant τ. The quenching time of the membrane (t) can be determined if the initial (110.5 dB SPL) and final sound pressure levels are known; taking the threshold as Th = 61 dB SPL, this is given by:

$$t = \tau(P\text{-Th})/[20 \lg(e)], \quad (2)$$

where e = 2.71828.

Studies of the mechanical responses of the membrane to clicks were carried out using a laser vibrometer as described by Schiolten et al. [14]. Their data indicate that τ = 61 μsec. The quenching time constant can also be determined using audiograms. In this case, the resonance frequency F_0 and the quality factor Q are read directly from a graph [4]. The time constant is calculated according to:

$$\tau = Q/(\pi F_0) \text{ sec}. \quad (3)$$

At Q = 2 and F_0 = 20 kHz [4], τ = 32 μsec.

The shape of tympanic organ audiograms simultaneously reflects the amplitude-frequency characteristics of the mechanical structures of the tympanic organ, which include the chordotonal sensilla and ligament as well as the tympanic membrane [7]. This explains the large divergence in quality factors: Q = 4.8 in [14] and Q = 2 in [4]. Since the time constant is proportional to Q, the value of τ in the first case will also be greater. Substituting τ = 61 μsec into equation (2) gives a quenching time t = 350 μsec, τ = 32 μsec gives t = 182 μsec.

Since vibrations of the membrane provide the input signal for the A1 cell, the minimum period of insensitivity of this receptor to incoming impulses must be determined by the magnitude of t. Behavioural studies have shown that moths can perceive echo-like stimuli 200 μsec after emitting a click [3], suggesting that the process of quenching of the receptor response to the insect's own signal must be essentially complete by this time, that is, t < 200 μsec. The period of receptor insensitivity (182-200 μsec) determines the minimum distance (D_m) for detection of an obstacle: D_m = 3-3.3 cm.

Studies of the response of the tympanic organ to paired stimuli separated by 0.15-1 msec have demonstrated that the response of the A1 cell is equivalent to the action of a single high-amplitude (+3 dB, min.) signal. This result can be explained in terms of temporal summation at the level of the auditory receptor. In real situations, sequences of acoustic impulses would be expected to arrive at the entrance of the tympanic organ with small (0.15-0.3 msec) intervals between them, when the probe signal is reflected from obstacles with complex surface shapes, such as leaves, the bark of large trees, undergrowth plant stems, and so on. It should be noted that a 3 dB increase in the amplitude of the incoming signal allows the maximum distance limit of the echolocation system to be increased 1.4-fold, or allows an increase in the precision with which nearby obstacles are detected.

The ability to perceive two objects separately when they are located at different distances from the insect's body depends on the temporal resolution (4 msec) and the sensitivity of the echolocator. The corresponding distance between two obstacles at different distances in the same direction, for which the tympanic organ can separately perceive reflections, is 67 cm. This value is greater than the calculated radius of action of the noctuid's echolocation system, even in conditions ideal for reflection [1]. This indicates that noctuid moths can detect only the closest obstacles, which give echoes with amplitudes greater than the t tympanic organ sensitivity threshold.

Moths determine the direction from which a sound arrives by using binaural amplitude differences. Each auditory organ has a direction diagram whose maximum is oriented at an angle of 90-110° to the longitudinal axis of the insect's body [13]; binaural differences reach 20 dB [10]. This is greater than the actual dynamic range (13 dB), and the angular resolution of the auditory system will be determined by the latter value.

The data obtained here allow the angle, relative to the longitudinal axis of the moth's body, at which a source of acoustic impulses of amplitude Th + 13 dB must be located in order to change the number of spikes in a receptor burst by one.

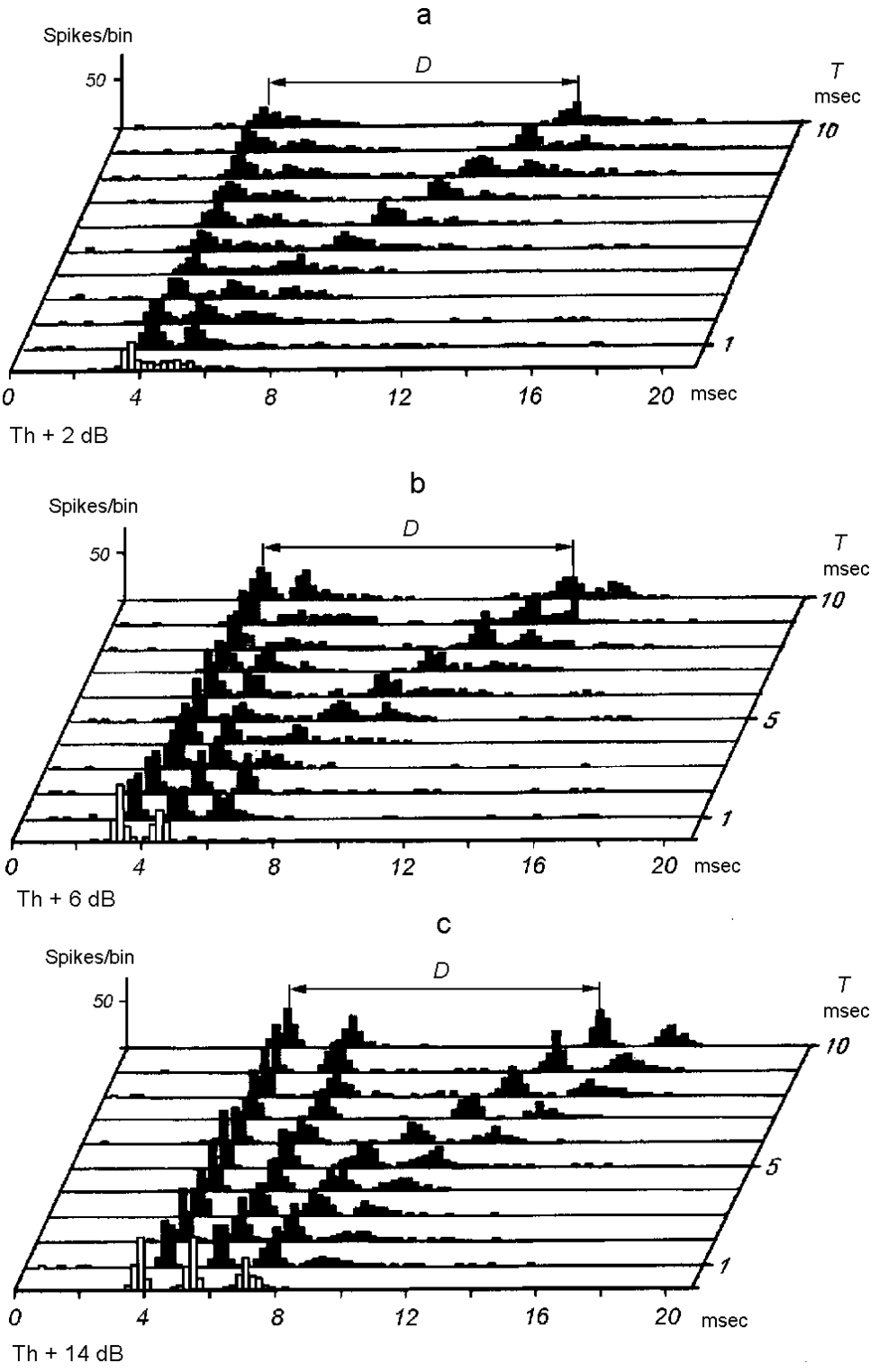

Fig. 6. Post-stimulus histograms of A1 receptor responses to paired stimuli of different amplitude: (a) Th + 2; (b) Th + 6; (c) Th + 14 dB. Empty columns indicate post-stimulus histograms for single stimuli (control). The horizontal axis shows the time period from the moment of action of the first click in a paired stimulus; the vertical axis shows the number of spikes in a single detection channel (spikes/bin); the inclined axis shows the interval between the first and second clicks In the stimulus (*T*), in msec. *D* is the interval between the separate responses of the A1 receptor. The resolution step was 0.2 msec/bin.

TABLE 1. Values of Coefficient *R* at Different Visualization Angles

Angle φ, °	-90	-60	-42	-26	-13	0	13	26	42	60	90
R (spikes per stimulus) of the ipsilateral tympanic organ	0	0	1	1.7	2	2.1	2.4	2.7	2.7	2.7	2.8
R (spikes per stimulus) of the contralateral tympanic organ	2.8	2.7	2.7	2.7	2.4	2.1	2	1.7	1	0	0

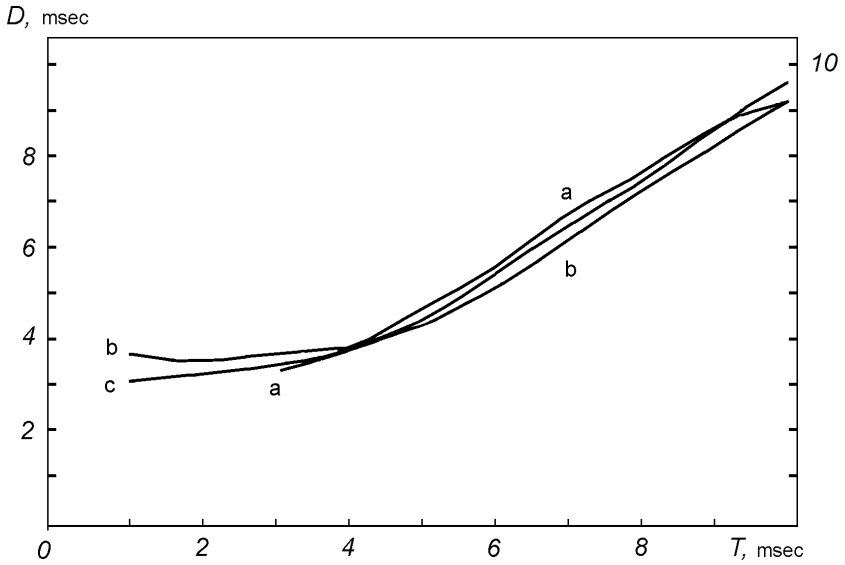

Fig. 7. Averaged plot of changes in the intervals between the fust and second spikes in the A1 receptor response (vertical axis) at a paired stimulus amplitude of Th + 0 dB (a), and between the first and third spikes at amplitudes of Th + 6 dB (b) and Th + 14 dB (c). The horizontal axis shows the interval between clicks in the double stimulus.

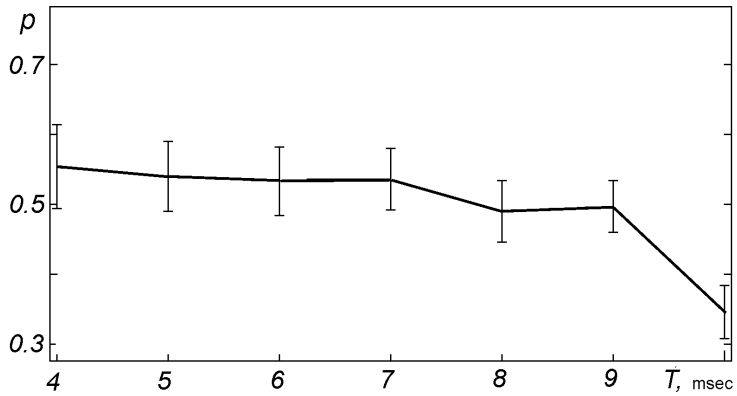

Fig. 8. The probability that an A1 receptor response will occur to each click in a double stimulus with difference values of the interval *T*. The stimulus amplitude was Th + 0 dB. Bars show mean errors.

Direction diagrams for the tympanic organs are presented as cardioids [4, 5] whose axes are oriented perpendicular to the insect's body. The signal level at the entrance of the ipsilateral tympanic organ is:

$$P_i = 20 \lg\{[1 + E \sin \varphi]/(1 + E)\} + Th + 13 \text{ dB}. \quad (4)$$

Similarly, the signal level at the entrance of the contralateral tympanic organ is:

$$P_k = 20 \lg\{[1 - E \sin \varphi]/(1 + E)\} + Th + 13 \text{ dB}, \quad (5)$$

where φ is the angle between the longitudinal axis of the insect and the direction of the sound source (the visualization angle), E is a parameter determined experimentally - at a binaural difference of 20 dB [10], E = 0.818. Values of coefficient *R*, calculated from equations (4) and (5) using the graph in Fig. 5a, are shown in Table 1.

Calculated values for coefficient *R* for the ipsi- and contralateral tympanic organs depend on the visualization angle of the sound source φ.

The expected magnitude of the response to a single spike is within the range over which the angle φ can change: 60° - 42° = 18° (*R* = 1), 42° - 13° = 29° (*R* = 2), and 26° - (-13)° = 39° (*R* = 2.7). At $|\varphi|$ = 60-90°, binaural differences are virtually independent of the visualization angle - this is a result of the initial limit of dynamic range (13 dB). Thus, the minimum range of the visualization angle, within which the number of spikes in a burst changes by one, is 18°. This value is the angular resolution of the auditory system in moths in the horizontal plane.

Impulse echolocation in noctuid moths consists of a sequence of separate acts of probing surrounding space; the rapid movement of the moth relative to surrounding obstacles results in very significant changes in the acoustic information arriving at the entrances of the tympanic organs from probe signal to probe signal. For this reason it is difficult (though in some cases possible) to compensate for errors in ceding the signal amplitude (which result from the probability of a signal being represented in the receptor response (*pl, p2, p3*)) by repeated probing. Since the contralateral tympanic organ also shows inaccuracy, the direction of an incoming echo can only be determined with a particular level of precision, which also depends on the distance to the obstacle, its geometric shape, the coefficient of reflection, and so on. Inaccuracy in the responses from auditory receptors will have the greatest effect on identifying the direction of a sound source at small visualization angles (φ < 26°), when the expected binaural difference in the bursts from the auditory receptors is no more than one (Table 1).

Theoretically, moths could evaluate the distance to the object being ranged using the delay time of the echo relative to the click itself. This time will be summed with the latent period of the first spike in the tympanic organ response. Over the range Th + 0 to Th + 10, the latent period decreases monotonically (Fig. 5, b). Since closer objects will, on average, give stronger echoes, the delay in the acoustic signal and changes in the latent period could act in the same direction with changes in distance to the obstacle. However, considering the large number of other factors affecting the level of the reflected signal, it is likely that the primary function of the echolocation system is to provide simultaneous detection of obstacles and crude identification of their positions (right, left, straight ahead). This information may be sufficient for moths to select their next move correctly.

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