INTENSITY VARIATIONS OF EMITTED PULSES BY DOLPHIN COULD BE AN ADAPTIVE MECHANISM PROVIDING AUDITORY PERIPHERAL ENCODING OF RECEIVED ECHO SIGNALS

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1 INTRODUCTION

The dolphin auditory system is known to be capable of analyzing the fine frequency and temporal structure of short high-frequency echo-signals [1, 2]. The analysis can be explained by using the principle of volley [3]. According to the principle, the auditory peripheral encoding of sounds is determined by the collective action of a set of synchronously excited auditory nerve fibers. This encoding is efficient when the sensitivity of the majority of the fibers corresponds to the level of the synaptic potential evoked by the echo-signals [4]. If the echo signals were long, the correspondence is achieved as a result of auditory adaptation. This adaptation develops during certain period of time and adjusts the sensitivity of the fibers to the synaptic potential [5]. But what mechanism of auditory adaptation to short signal is? Dolphins identify an object by analyzing one short echo-signal but in the echolocation they use wide range of intensity of the emitted pulses [6, 7]. A hypothesis that intensity variation of the emitted pulses may be an adaptive mechanism serving for the adjustment of the intensity of echo-signals to the fiber sensitivity, which is appeared under the ambient noise effect is examined in this report with simulation [7] and psychoacoustical researches [8].

2 THE SUMULATION RESEARCH

The auditory peripheral encoding of sounds is completed by spikes reactions of the auditory nerve fibers (ANF). The encoding properties depend on both properties of arising synaptic potentials and properties of changes in postspikes excitability of ANF: the refractoriness and the adaptation. If stimuli have duration smaller, than duration of the ANF recovery process, they should be encoded without losses in the set of ANF, because of excitation divergence of the receptor cell on the set of ANF (the principle of volleys). We will demonstrate the encoding has its specific character. Also we will define conditions, in which the common reaction of the set of ANF had reflected fine temporal structure of short stimuli and at the same time had not undergone the influence of refractoriness and the adaptation of the separate fibers.

2.1 The modified double pulse’s method

Changes in ANF postspikes excitability can be estimated by the responses recovery functions, receiving by the double pulse's method [9,10] The double pulse’s method estimates the recovery process as dependence of relative amplitudes of the second-pulse response P2/P1 on inter-pulse intervals T, where P1 and P2 are probabilities of reaction occurrence to the first and second pulses The recovery process is estimated the more precisely, than higher characteristic frequency of a fiber.

We can modify the double pulse’s method [7,11], if it is determined that the reaction of one fiber on multiple stimulus presentation corresponds to the common reaction of the set of ANF on one stimulus presentation. The second-pulse response in the set of ANF can be formed only two ways. The first way, named stochastic, is based upon spontaneous activity (SA). It provides occurrence of response to the second pulse in those fibers, which have not yet reacted to the first one. The second way, named deterministic, is based upon recovery process. It provides occurrence of response in fibers, which have already reacted to the first pulse and which have the lowered sensitivity after spikes generation to the first pulse. The contributions of the ways into the recovery function estimate the probabilities Ps2 and Pd2, given that the second-pulse response occurs under condition of absence or occurrence of the first-pulse response, respectively. As P2=Ps2+Pd2, where Ps2 and Pd2 are the stochastic and deterministic component of the second-pulse response. The stochastic component of the recovery function Ps2/P1(T) depends on the properties of the arisen synaptic potentials. In case of recalculation the probability Ps2 in the conditional probability is capable to evaluate the synaptic process. The deterministic component Pd2/P1(T) of the recovery function reproduces process of postspikes excitability [12] and corresponds the known hazard function [13]

2.2 The model of auditory nerve fibers

Researches were carried out on a models of ANF (MANF). MANF performs the following transformations of the input signal X(t) [7,11,14]:

1. Band-pass filtration (the central frequency of the filter sets characteristic frequency (CF) of a fiber);
2. Compression and detecting of a signal;
3. Formation of synaptic noises and spontaneous activity (SA);
4. Low-frequency filtration of synaptic noise with a time constant equal 0,2 ms (the output function G(t));
5. Transformation of synaptic potentials G(t) in sequence of spikes ΣPi by comparison G(t) with threshold H(t);
6. Change in time of H(t) after spikes generation. Threshold function H(t) represents the refractoriness and the adaptation.

Parameters of MANF were chosen so that the models reproduced known relationship of the ANF physiological properties with different SA [14]. The CF of MANF was 10 kHz. Stimuli were broadband noises and double pulses with 10 kHz spectrum maximum. The pulse duration was 0,75 ms. The inter-pulses interval varied from 1,5 to 55 ms.

2.3 Results

Figure 1 demonstrates the reactions of several stages of MANF, received in reply to double pulses. The stimulus spectrum maximum X(t) and the CF of MANF (10 kHz) were on the order more than the high-frequency limit of the low-frequency filter (1 kHz), which takes into account integrating properties of the receptor cells, and so the synaptic potentials G(t) are smoothed. At high stimuli intensity the refractoriness resists the reproduction of fine temporal structure of double pulses, i.e. the second- pulse response is less, than the first.

Figure 2 shows that the probabilities of pulses and noise reactions (P1, P2, P0) and the amplitudes of the second-pulse response (P2/P1, Ps2/P1, Pd2/P1) depend on interval T and stimuli intensities. All of them were received in MANF with low SA. At first we examined the responses arisen without noise. If stimuli intensities are near a threshold of fibers reaction (13 dB), the probabilities P1 and P2 are small but they are identical at any interval T. The deterministic component of the second-pulse response is absent (Pd2/P1=0). So reaction to the second pulses is formed only by the stochastic way, (P2/P1=Ps2/P1), as a result fibers reproduce fine temporal structure of double pulses at any interval T.

The probability P1 grows up to a maximum, and stochastic component Ps2/P1 decrease down to a minimum with increasing of stimuli intensity (15 and 20 dB). When the interval T is about 1,5-2 ms, the probability P2 is minimal too and it is defined by SA. Thus, the fibers reaction synchronizes strongly with the first pulse, and a number of fibers answering to the second pulse is miminal so far. Both the probability P2 and the deterministic component Pd2 increase with the interval T.

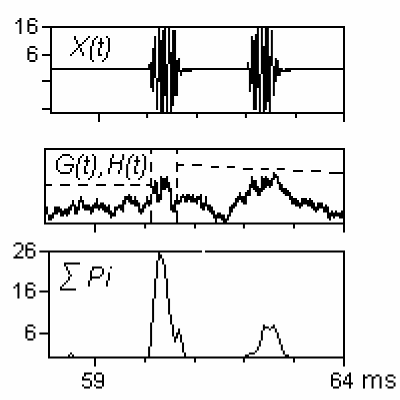

Figure 1. Model synaptic potentials G(t), threshold functions H(t) and poststimulus histogram, arisen on double pulses X(t) with 2 ms interval. On abscise: time in ms, on ordinate: amplitudes of reactions. ∑Pi is spikes sum, arisen on 100 presentation of pair.

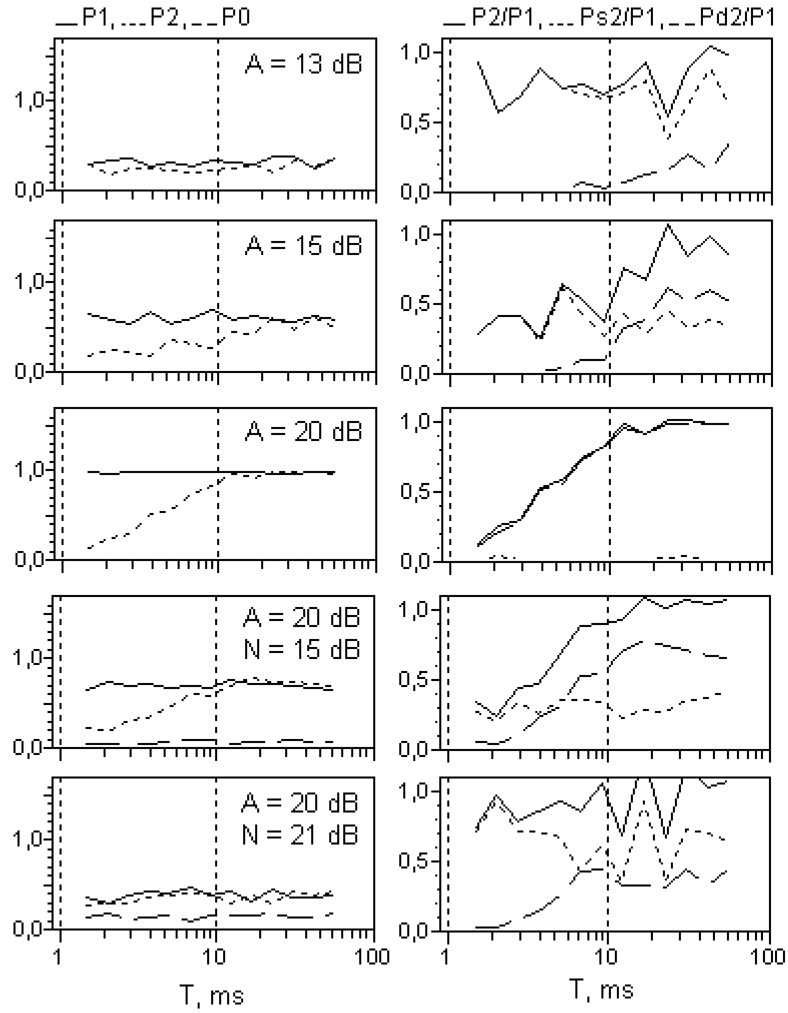

Figure 2. Dependences of the probabilities of pulses and noise reactions (P1, P2, P0) and the amplitudes of the second-pulse response (P2/P1, Ps2/P1, Pd2/P1) on the interval T. Parametres: pulses' intesities (A) and noise level (N) in dB. On abscise: interval T in ms, on ordinate: value of probabilities and relative amplitudes of the second-pulse response.

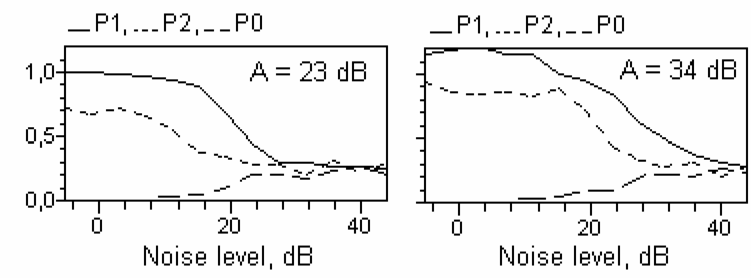

Figure 3. Dependences of the probabilities of pulses and noise reactions (P1, P2, P0) on the noise level. Interval T is 5 ms. Parametres: pulses' intesities (A) in dB. On abscise: noise level in dB, on ordinate: probabilities P1,P2,P0.

When stimuli intensity is the greatest, the amplitudes P2/P1 are defined by its deterministic components Pd2/P1 (P2/P1=Pd2/P1), so the fine temporal structure of double pulses is not reproduced.

So, it is shown (figure. 2) that the second pulse of the double pulses or fine temporal structure of short stimulus is reproduced in the reactions of the set of ANF at small intensity, when contribution of the stochastic component into second pulse reaction is greatest. For making this reproduction for stimuli different intensity, it is necessary to raise the contribution of the stochastic component, for example, by addition signal with noise. Noise desynchronizes the first pulse responses, and it also creates conditions for detection of the second pulse. Addition of noise decreases the probability (P1 and P2) and increases the stochastic component. At certain noise level (21 dB) and when both pulses easily define in the reaction of the set of ANF, there is a situation at which values of the recovery function achieves one at any intervals T. Noise decreases the ANF absolute sensitivity, but noise increases the ANF differential sensitivity to the fine temporal structure of short stimuli.

This issue confirms the figure 3, which dependences of the probabilities of pulses and noise reactions (P1, P2, P0) on the noise level are shown on. Probability P0 increases and probabilities P1, P2 decreases with rising of noise level. If noise level is low, P1 is higher than P2. These all probabilities (P1, P2, P0) are equal at certain noise level. For each stimulus intensity there is a definite noise level when P1, P2 и P0 are equal. The fine temporal structure of short stimulus is displayed without losses in reaction of the set of ANF, if intensity is near signal-detection threshold in noise.

So, if the contribution of the stochastic component exceeds the contribution of the deterministic one, the refractoriness of each auditory fiber doesn't influence on encoding of the short stimuli in the set of ANF. The conditions practically always exist in the ANF with high SA (reactions of MANF are not shown). But there are the same conditions in the ANF with low SA only in case of stimuli representing in isolation or in noise and their intensities are near the signal-detection threshold (figure 2,3).

2.4 Discussion and conclusions

Reactions of MANF was supposed to be the same as reactions of real ANF, because the model parameters were chosen in case of coincidence between both reactions, received in response to tones or modulated signals [14]. If stimulus is double pulses, the model and real recovery functions do the same. When the stimuli intensities are near a threshold of ANF, the model (fig. 2) and the real [9] recovery functions may be equal to one at any intervals. At high stimuli intensities the model (fig. 2) and the real [10] ANF restore the second-pulse response in 20-30 ms.

In case of the composition of short pulse and noise and when noise increases the real neuron reaction of cochlear nuclei caused by short pulse is down, and the reaction caused by noise is up [15]. These reactions are equal in about 30 dB. Such reactions are reproduced in MANF reations (figure 3).

Investigating of the recovery function and its two components are detected complex conditions, in which (1) the principle of volleys is realized, (2) the reactions of the set of ANF don't depend on the refractoriness properties of separate fibers, and (3) the fine temporal structure of short stimulus are reproduced without losses. The conditions appear, when the stimulus is showed in isolation or in noise and when stimuli intensity approaches the signal-detection threshold.

3 THE PSYCHOACOUSTICAL RESEARCH

In psychoacoustical experiment we decided to define conditions, when it is try a statement, that for the certain intensity of short stimuli it is possible to find out the certain noise level when recognition of stimulus is better in noise, than without noise. We also assumed that reproduction of the fine temporal structure of short stimuli on the periphery improves the auditory discrimination.

The auditory facilitation of intensity discrimination of short stimuli in noise was detected [16 -20]. If noise was absent, the dependence of intensity discrimination thresholds (IDT) on intensity revealed local deterioration at average intensities. The local deterioration increased, if the spectral bandwidth of stimuli corresponded to the auditory critical bandwidth formed on the maximum frequency of a stimulus spectrum [19, 20] (i.e. the listeners are able to use temporal stimuli characteristics and not spectral one). However, if stimulus was a mix of pulses and noise, local deterioration disappeared [17, 18].

The question on the reasons of abnormal behavior of IDT in silence and the reasons of its disappearance in noise has remained debatable yet. So, it was solved to reproduce experiments [16 -17] with some new conditions to check up a hypothesis about a role of the stochastic and deterministic reactions in intensity discrimination.

3.1 Method

Researches were carried out in the soundproof chamber of N. N. Andreyev Acoustics Institute. Stimuli were reproduced in headphones simultaneously on both ears. The modernized computer complex stimulus generation, data recording and control of experiment have been used. Intensity discrimination thresholds (IDT) were measured using an adaptive two-interval two-alternative forced choice technique.

Stimuli to be detected or discriminated were Gaussian-windowed sinusoid and band noise. Spectral maxima of stimuli and noise were 4 kHz. The bandwidth of noise was equal 1000 Hz

Three listeners with normal hearing participated in measurements. Listeners were given 4 h practices on the task before data collection began. Individual results of listeners have been average. Audibility thresholds of stimuli and noise were measured.

3.2 Results

At first IDT have been determined for stimuli presented in isolation. Dependences IDT on intensity have been received for stimuli with different spectral bandwidth. Thresholds were determined in dB above the audibility threshold (figure 4). The local deterioration of IDT was detected in range of 20-40 dB. The size of local deterioration and its value depend on stimuli spectral bandwidth. They were maximal at bandwidths of 1000 and 200 Hz. In this case duration of the ANF reactions caused by stimuli was less than the recovery period of separate fibers [10] and spectral bandwidth corresponded auditory critical band. The local deterioration decreases if spectral bandwidth is expanded up to 5000 Hz or narrowed up to 40 Hz.

The data on the intensity discrimination in noise are submitted on figure 5. Dependences of IDT on noise level have been received for stimuli with the bandwidth equal to the critical bandwidth, i.e. 1000 Hz. For stimuli of certain intensities, which have the highest IDT without noise, it is possible to reveal the certain noise levels when IDTs are less in noise, than without noise. The stimuli intensities have to be near signal-detection threshold in noise.

The effect of auditory facilitation of intensity discrimination appears on average intensities. The magnitude of facilitation is defined as a difference between IDT received when stimuli presented in isolation and the least IDT received in noise near the signal-detection threshold. The signal-detection threshold is marked by a symbol on the absciss axis of figure 5.

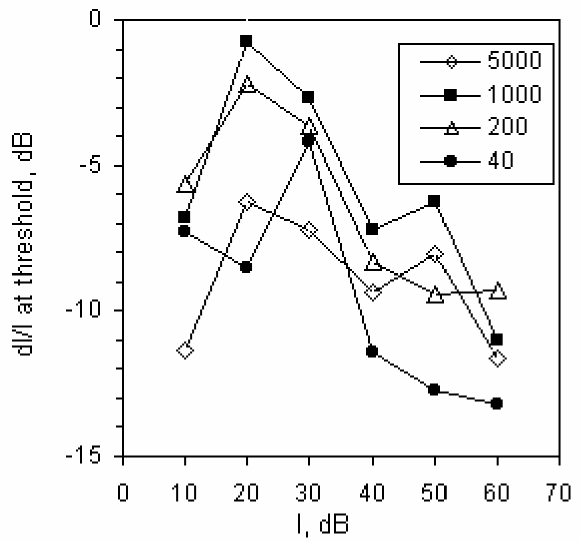

Figure 4. Dependences of the intensity discrimination thresholds (IDT) of short stimuli on intensity. Parameters: stimuli bandwidth in Hz. On abscise: intensity I in dB above the audibility thresholds, on ordinate: dI/I in dB, where dI - threshold increment of intensity

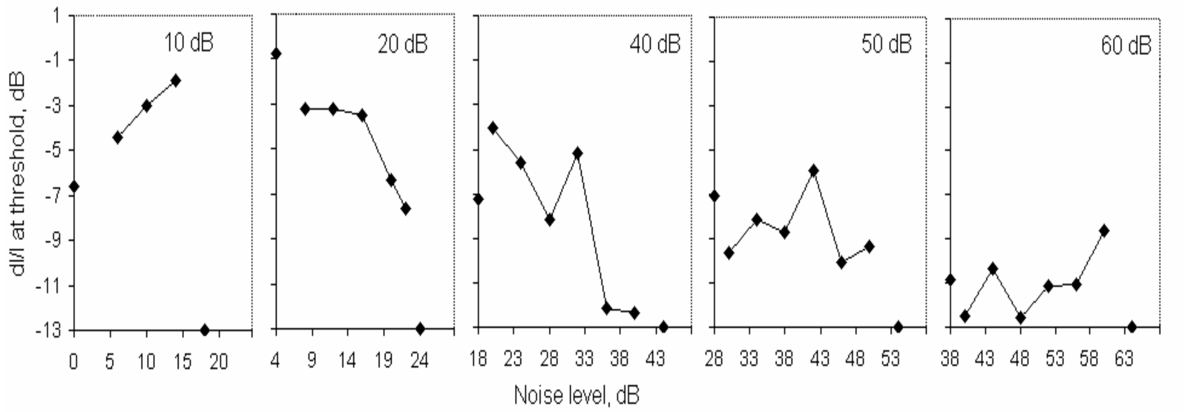

Figure 5. Dependences of the intensity discrimination thresholds (IDT) of short stimuli on noise level. Parameters: stimuli intensity in dB above the audibility thresholds. On abscise: noise level N in dB, also above the audibility thresholds, on ordinate: dI/I in dB, where dI - threshold increment of intensity. Symbols on abscise mark the noise levels at which the listeners can't detect the stimulus with minimal intensity. Symbols on ordinate mark IDTs without noise.

The average data is shown the magnitude of facilitation decreases if intensities increase from 20 to 50 dB. The magnitude reaches 7 dB at intensity 20 dB; 5,1 dB at 40 dB; 3 dB at 50 dB. The maximal magnitude in individual measurement reaches 10-11 dB at 20 and 40 dB. However, the facilitation disappears for the lowest (10 dB) and the highest (60 dB) intensity.

3.3 Discussion and conclusions

For an explanation of the results we will take into account a divergence of excitation of one inner hair cell on the set of ANF with different SA and different thresholds [21]. The thresholds dispersion is known to reach 8 dB [22] or 20 dB [23].

What are the possible reasons of the local deterioration of IDT if the stimuli spectral bandwidth corresponds to the auditory critical bandwidth? According to the simulation research, the stochastic component of reaction of the set of ANF provides reproduction of fine temporal structures of short stimuli on the auditory system periphery. The auditory system discriminates stimuli with low intensities successfully because it has enough stochastic components, which belong to ANF with high SA and low thresholds (reactions of MANF with high SA are not shown).

Growth of intensity (about 20-30 dB) is followed by increase of number of fibers with low SA and high thresholds. In that time ANF with high SA run up to saturation state and can not participate in intensity discrimination. The contribution of the stochastic components in the fibers reaction depends on intensity. Intensity growth evokes the following process: 1) amplification of influence of the recovery process in ANF with low SA; 2) increase of the deterministic component of peripheral reactions; and 3) reduce of the stochastic component. All of these processes impoverish and shorten the temporal stimulus description on the periphery. Probably, therefore IDTs are made the worse. The further increase of intensity (higher than 30 dB) leads to extension of the basilar membrane impulse responses and involving in peripheral reaction of ANF with close characteristic frequencies. These processes enrich the peripheral description of stimulus again, and then IDTs reduce [19]. It is also shown on figure 4: IDTs reduce due to extension of stimuli spectrum or stimuli duration.

If short stimuli of average intensities mix with noise, the stochastic component of reaction of the set of ANF increases. The peripheral temporal description of stimuli will be restored and that is why auditory discrimination will be improved. External noise is capable to create the conditions in which little changes of intensity of short stimulus can be found out by the auditory system.

Thus, the hypothesis about a role of external noise in improvement of short stimulus discrimination is confirmed.

4 GENERAL DISCUSSION

There are bases to believe, that the hypothesis declared in the work title has the confirmation because there is a coincidence of the simulation and psychoacoustical data. The coincidence is that for the certain intensity of a short pulse there is a certain noise level close to a signal-detection threshold, when the fine temporal structure of short pulses is effectively reproduced by model of the set of ANF or is effectively discriminated by the listeners. (One can find the correlation between the properties of auditory discrimination and properties of auditory peripheral encoding, when the peripheral description of sound is poor and when listeners solve a threshold task [24]).

The mechanism of auditory adaptation to short stimuli was assumed to find out itself in results of known [16-19] and carried out psychoacoustical researches. An on-set synchronous reaction of the set of ANF dramatic influences on the peripheral description of stimuli whose duration is smaller, than the ANF recovery period, and whose band is closed to the critical band. The on-set reaction can be de-synchronized by external noise.

The role of the stochastic and deterministic reactions in peripheral description is more, than the stimuli frequency is higher, that is why the researches are relevant for animals with high-frequency hearing. The auditory adaptation mechanism to short stimuli should be investigated at dolphins in special researches. They should touch on a subject about temporal mechanisms of the auditory analysis of the high frequency echo - signals, about the dolphin auditory critical bandwidth, etc.

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