Sensitivity Increasing of Auditory Receptors due to Stochasticity of their Reactions

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SUMMARY

A model of the auditory nerve fiber was object of this research. In the model known connection of a fiber's spontaneous activity with their threshold, adaptation, reproduction of a sound's amplitude modulations, as well as with their I/O characteristic, was reproduced. (The spontaneous activity is the fiber's feature to generate a spike, if a stimulus (useful sound signal) is absent. The fiber's I/O characteristic represents dependence of average firing rates on a tone's level; the tone has specific frequency, named the characteristic frequency). Two examples showed how auditory nerve fibers restore and even increase their sensitivity to the analysis of temporal and amplitude changes of stimuli, if stimuli were mixed with a band-pass noise. Stimuli were pairs of identical pulses with moderate intensity levels in the first example and sine-amplitude-modulated signals with subthreshold intensity levels in the second example. Sensitivity increasing had arisen due to stochastic reactions of set of auditory nerve fibers in the first example and due to the phenomenon of a stochastic resonance, which had shown this set in the second one.

1.0 INTRODUCTION

The sensor information is perceived by animal's special modified nervous cells - receptors. The sensor receptors carry out primary coding of a stimulus, at that they transform their energy in sequence of action potentials (spikes). Auditory receptors are inner hair cells, which simultaneously innervate a number of neurons (single units) of the spiral ganglion or auditory nerve fibers. The given work reveals some features of primary coding of the sounds in noise at the peripheral auditory system.

Sensitivity of auditory receptors to temporal and amplitude changes of the sounds arises from a divergence of the excitation, from a fiber's spontaneous activity (SA), from a fiber's adaptation. (The divergence appears because one receptor is connected with several auditory nerve fibers. The spontaneous activity (SA) is ability of the fiber to generate spike without stimulation. The adaptation is decrease of the fiber's average firing rate during the action of long stimulus.)

As well as all nervous cells, single units of the spiral ganglion (auditory nerve fibers) are inertial. The generation of the spike arises at the time's moment, when the receptor's potential exceeds some unit's threshold. After spike generation the fiber has the refractoriness period (or the recovery period of the fiber's excitability), being continued some milliseconds. The generation of the subsequent spike is possible after ending of the refractoriness period. Therefore, properties of one fiber (or the single unit) can't explain auditory temporal analysis, being lasted some tens of microseconds. But such analysis is possible [Bel'kovich 1976]. The analysis is provided with reaction of a set of auditory nerve fibers with stochastic reactions, because the spontaneous activity exists in each of the fiber. Reactions of the set of fibers compensate the inertial property of one fiber. Let's stimulus will be pair of identical pulses with levels

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corresponding to the fiber's reaction threshold and an interval between pulses is smaller the refractoriness period. There is no doubt that on account of fiber's stochastic reactions, the part of the fiber’s set will have replied on the first pulse and the residuary part - on the second pulse. As the auditory nerve fibers with low threshold have the highest SA [Winter 1990], the approximately equal number of excited fibers will encode each of the pair’s pulses at any time moment. Therefore the temporal structure of pair will be reproduced in total reaction of fiber's set [Bibikov 1986; Rimskaya-Korsakova 1989, 2003, 2004].

If the level of the pair's pulses is increased, then both the synchronization of reaction of fiber's set with the first pulse and the masking of the second pulse by the first one will be increased. Nevertheless if the pair of pulses are mixed with a band-pass noise, then the synchronization of reaction of fiber's set with the first pulse will be decreased, but the number of the fibers, which may respond to the second pulse, will be increased.

Properties of one fiber also can't explain auditory features of the temporal and amplitude analysis of sounds with subthreshold levels. It is known that fibers with lower thresholds and with higher SA have the steeper I/O characteristic [Winter 1990]. (The fiber's I/O characteristic represents dependence of the average firing rate on the level of the tone with the characteristic frequency.) At moderate and high levels of sounds, such fibers adapt [Frisina 2001] and synchronize the reactions with the envelope of the sine-amplitude-modulated sound (SAMS) more poorly, than fibers with high thresholds, with low SA and with flat I/O characteristics [Rhode 1994]. Simulating experiment has shown [Rimskaya-Korsakova 2003] that synchronization of the fiber's reaction with the envelope of the moderate level's SAMS is explained of the fiber's adaptation properties, but not of the fiber's nonlinear I/O characteristic. However the nonlinear I/O characteristic creates good conditions for synchronization of fiber's reaction with the envelope of the SAMS with threshold and subthreshold levels. Such sounds do not evoke fiber's adaptation. There is a phenomenon of a stochastic resonance in the fibers with high SA and steep I/O characteristic [Rimskaya-Korsakova 2004]. The stochastic resonance is a feature of nonlinear systems, output characteristic of which is the Poisson sequence of events [Bezrukov 1998]. Due to a stochastic resonance nonlinear systems find out subthreshold signals, if they are mixed with a weak noise. As reactions of real sensor receptors represent such Poisson sequence of events, the role of a stochastic resonance at the periphery of the auditory is now being investigated widely [Tougaard 2002; Ward 2002].

The given work considers two mechanisms of the sensitivity increasing of peripheral coding of the temporal and amplitude changes of the sound, when sound is summarized with a noise. The set of fibers participates in such coding, but the each fiber has stochastic reactions and the each fiber adapt their reaction.

2.0 THE MODEL OF THE AUDITORY NERVE FIBER

2.1 Description of the model

Researches are made on the phenomenological model of the auditory nerve fiber [Bibikov 1986; 1987 Rimskaya-Korsakova 1989, 2003, 2004]. In the model following transformations of signal X(t) have been consistently carried out:

- Band-pass filtration (Output function is Y(t));
- Compression and detection (Output function is R(t));
- Formation of synaptic noise in the form of random normal process (Output function is S(t));
- Low-frequency filtration (Output function is G(t));
- Transformation of synaptic potentials in sequence of spikes (Temporal sequence of spikes is P_i);

- Temporal changes of the threshold of the neuron's model after spike's generation (Threshold function is H(t)).

In the fiber's model the impulse response of the basilar membrane Y(t) is formed by convolution of the input signal X(t) with the impulse characteristic of the filter of the basilar membrane h(t):

$$Y(t) = \int h(t - t') \, X(t') \, dt' \quad ; \quad (1)$$

$$h(t) = (\omega t)^{\beta} e^{-\alpha(\omega t)} \sin(\omega t) \quad ; \quad (2)$$

where: t is time, ω is the central frequency of the filter of the basilar membrane. The central frequency of the filter corresponds to characteristic frequency of the fiber's model. α and β are constants. The central frequency of the filter corresponds to characteristic frequency of model of auditory nerve fiber.

The nonlinear transformation of a signal, which reproduces the stage of mechanoreception, is often conveyed by the sigmoid function

$$R(t) = R_{max} \cdot \left\{ \frac{2.0}{1.0 + e^{(Dis - Y(t))/Slope}} - 1.0; \right\} \quad ; \quad (3)$$

where: parameter R_{max} is the maximum synaptic potential; parameter Dis determines the displacement; parameter Dis is always equal 0,05 and parameter Slope determines the steepness of function R(t).

It was assumed that the mechanism of formation of the synaptic potential from the receptor potentials is related to the mechanism responsible for the appearance of SA [Rimskaya-Korsakova 2003, 2004]. Therefore, in the model of auditory nerve fiber the slope of the sigmoid function (parameter Slope in Eq.(3)) depends on the level SA as well as the slope of the I/O characteristic of real fibers depends on the level of SA [Winter 1990].

The synaptic potential is formed at the following stage of transformations. At first, the random process S(t) is created. The mean and a root-mean-square deviation of S(t) are proportional to the detected function R(t). The root-mean-square deviation of the random process is increased by a quantity ξ to reproduce SA. If the signal is absent (X(t) = 0), then the synaptic noise S(t) has a zero mean and root-mean-square deviation proportional to ξ. Formation of the synaptic potential G(t) has been terminated by integrating S(t):

$$G(t) = \int e^{-t/\tau} S(t) dt \quad ; \quad (4)$$

where: τ is a time constant, equal to 0,2 ms. Eq. (4) takes into account the inertial properties of the signal transformation at the mechanoreceptor stage and (or) at the membrane of the spiral ganglion neuron.

The synaptic potential G(t) is compared of with the time-dependent threshold H(t) at the stage of the transformation of the synaptic potential into the spike's train (a firing rate of the auditory nerve fiber). If G(t) exceeds H(t), the spike is generated by the neuron's model. Each spike stimulates a temporal threshold increase. Within a time interval, being equal to the sum of the periods of absolute and relative refractoriness, the threshold has been reduced up to initial level H_o. At the stage of the relative refractoriness, the threshold H(t) has fast and slow components [Bibikov 1987], each of which may increase by remainder of this components, being preceded to spikes generation. The temporal change of threshold H(t) after spike's generation has the form:

$$H(t) = H_o + H_f \cdot e^{-\frac{t-\tau_a}{\tau_f} + \Omega \cdot \mathrm{Sign}(\tau_a - t)} + H_s \cdot e^{-\frac{t-\tau_a}{\tau_s} + \Omega \cdot \mathrm{Sign}(\tau_a - t)} \quad ; \qquad (5)$$

where: H_{of}; H_{os}; H_f; H_s are the constant and varying values of the fast and slow component of the neuron threshold at the stage of the relative refractoriness; $H_f = H_{of} + dH_f$; $H_s = H_{os} + dH_s$; dH_f и dH_s are the remainders of each of the threshold components at the instant preceding the spike generation; τ_a is the period of absolute refractoriness; τ_f и τ_s are the time constants of two threshold components at the stage of relative refractoriness; Ω is a constant, that determines the threshold value at the stage of absolute refractoriness; Sign is a function; $\mathrm{Sign}(t) = 1$, if $t < 0$; and $\mathrm{Sign}(t) = 0$, if $t > 0$.

Threshold function H(t) given above allows one to preset different properties of adaptation and refractoriness in the auditory nerve fiber. The refractoriness is the neuron excitability changes after the spike's generation, and adaptation is the reduction of the average firing rate of the neuron during the action of a long stimulus.

The adequacy of the model to the biological prototype was verified by comparing model's responses with responses of real auditory nerve fibers [Rimskaya-Korsakova 1989, 2003, 2004].

2.2 Parameters of the model

The central frequency of the basilar membrane filter is 10 kHz, threshold H_o – 0.02, the period absolute refractoriness τ_a – 0.5 ms. The parameter ξ determines SA. The parameter Slope presets the steepness of function R(t). Parameters ξ, τ_f, τ_s, H_{of}/H_o, H_{os}/H_o specify properties of adaptation and refractoriness. Parameters are chosen so, when the parameter ξ less, then the parameter Slope more, and then parameters τ_f, τ_s, H_{of}/H_o, H_{os}/H_o less. The parameter R_{max} is established so that the maximal firing rate of fiber’s models does not exceed 380-400 pps (pulse per sec). The chosen values of parameters will be given below.

2.3 Stimulation of the model

Stimuli are the pair of identical pulses with moderate intensity levels in the first example and the sine-amplitude-modulated signals (SAMS) with subthreshold intensity levels in the second example. Duration of a single pulse is 0,5 ms long. The maximum of the pulse’s spectrum is equal 10 kHz. The intervals between pulses are chosen in range 1 – 80 ms. The carrier frequency of the SAMS is equal 10 kHz, the modulation frequency – 100 Hz, the modulation's depth – 20 %. The SAMS duration is 100 ms. Stimuli are operated without noise or mixed with band-pass noise.

2.4 Output characteristics of the model

Statistic properties of firing reactions of fiber's models were estimated as well as in electrophysiological experiments.

If stimuli were pairs of pulses, dependencies of relative amplitudes of reactions to second pulse N2/N1 on intervals between pulses were estimated. N1 and N2 were the sums of spikes, which had arisen in reply to the first and second pulses in equal time intervals.

There are only two mechanisms of formation of reaction to the second pulse in the set of the excited auditory nerve fibers. The first mechanism, named "stochastic", provides occurrence of reaction in those fibers, which have not reacted to the first pulse. The stochastic reaction of each fiber of this set is its basis due to SA. The second mechanism, named "repeated", provides occurrence of reactions in fibers, which already answered, because the fiber's threshold has gone down after the arisen spike in reply to the first pulse. The deterministic reaction of each fiber of this set is its basis due to refractoriness.

Relative amplitudes of reactions to the second pulse, being received separately for stochastic and repeated mechanisms, were calculated on the basis of relation Ns2/N1 and Nr2/N1. Ns2 and Nr2 were the sums of spikes, arisen on the second pulse under conditions of absence and occurrence of reaction to the first pulse accordingly. Dependencies of relations Ns2/N1 and Nr2/N1 on intervals between pulses of pairs were estimated too.

The post-stimulus time histogram, determining the probability of firing for fiber's model before, during and after stimulus's presentation, was received. The dependence of fiber's average firing rate M on the stimulus level (I/O characteristics) during the stimulus presentation was received.

Dependences the synchronization coefficient K on the level of the SAMS were estimated. For this purpose the phase histogram, which determines the probability of firing, corresponding to a given phase of the SAMS, was received. For the phase histogram, the synchronization coefficient K was calculated. Quantity of K characterized the degree of reproduction of modulations in the response of the fiber's model. If K=0, then the density of spikes distribution over the modulation period was constant, and if K=1, then all spikes were localized on one step of the phase histogram.

Besides, it was estimated the dependence of the fundamental component of the Fourier transformation of the phase histogram K1 on the noise level, for the case of a stimulus in the form of an additive mixture of SAMS and noise: K1=2M*K. The quantity K1 allows one to estimate the modulation of the instantaneous firing rate of the fiber. This measure takes into account the average firing rate in addition to K and could be treated as a power characteristic of the fiber's model on the modulation frequency [Kim 1990].

3.0 RESPONSES OF THE MODEL OF THE AUDITORY NERVE FIBER

3.1 Responses of the model on the pairs of pulses

Let's consider reactions of the model of the auditory nerve fiber, parameters of which are given in Table 1, on the pairs of identical pulses.

Table 1: Parameters of the model of auditory nerve fiber; stimuli are pairs of identical pulses

SA, pps	R_{max}	Slope	τ_f, mc	H_{of} / H_o	τ_s, ms	H_{os} / H_o
55	0,06	0,1	5	0,7	20	0,1

The fiber's I/O characteristics, received in reply to a single pulse and tone, are displayed on Figure 1. The steepness of the I/O characteristic is set by parameter Slope of function R (t). The average firing rate achieves a level of saturation, which equals 800 pps in reply to the short pulse, and 200 pps in reply to the tone. The average firing rate has decreased due to adaptation in the second case.

Dependencies of relative amplitudes of reactions to the second pulse on intervals between pulses are displayed on Figure 2. Levels of pulses correspond to different sites of the I/O characteristic (Figure 1). If levels of pulses are close to the threshold of fiber’s model (Figure 2, the top row), relative amplitudes of reactions to the second pulse do not practically depend on intervals as they were formed only due to the stochastic mechanism.

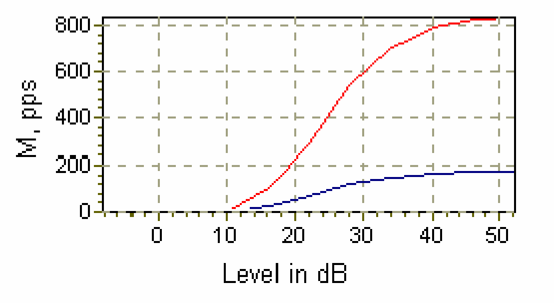

Figure 1: Dependence of average firing rate of the model of the auditory nerve fibers on the stimulus's level. The curve of red color shows reaction to the short pulse, the curve of blue color - on the tone with duration of 100 ms and with frequency 10 kHz.

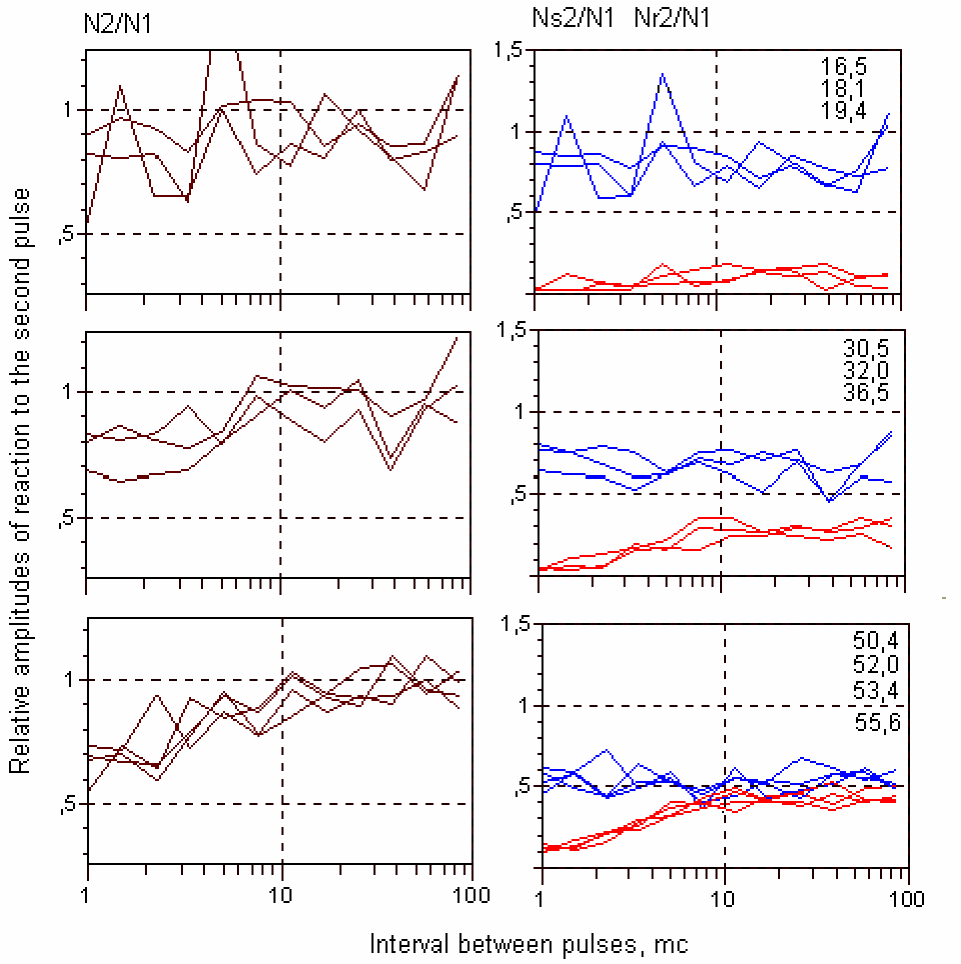

Figure 2: Dependencies of relative amplitudes of reactions to the second pulse on intervals between pulses. Levels of pulses are specified as parameters. Changes of relative amplitudes of reactions to the second pulse (Ns2/N1), generated by the stochastic mechanism, are shown by blue curves; changes of amplitudes Nr2/N1, generated by the repeated mechanism, - red curves; changes of amplitudes N2/N1, generated by two mechanisms, - lilac curves.

Relative amplitudes of reactions to the second pulse, received at pulse's levels corresponding to the middle part of the I/O characteristic, are displayed in the middle row of Figure 2. Amplitudes Ns2/N1 have decreased, but have remained not dependent on intervals between pulses, as reactions to the second pulse have been generated by the stochastic mechanism. Dependence on an interval has appeared for amplitudes Nr2/N1, being generated by the repeated mechanism, and for amplitudes N2/N1, being generated by two mechanisms. These relative amplitudes were restored up to unit through 7-9 ms.

The further increase of the pulse's level (figure 2, the bottom row) reduces up to the minimum the relative amplitude Ns2/N1 of reaction to the second pulse, generated by the stochastic mechanism. This minimum is defined by SA. The relative amplitude N2/N1, generated by two mechanisms, is restored up to unit approximately through 20 ms. Thus, the reaction, arising on the first pulse in the set of excited auditory nerve fibers, masks the reaction, arising on the second one, when amplitudes of pulses have moderate and high levels and intervals between pulses are less, than the period of refractoriness (less 20 ms). But such masking can be reduced, if the pairs of pulses are mixed with a broad-pass noise.

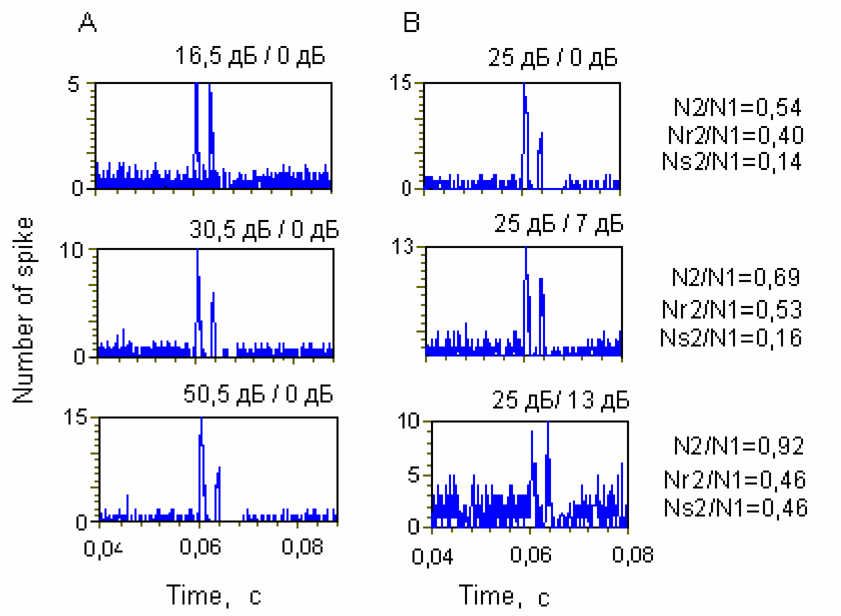

Figure 3: Fragments of post-stimulus histograms of reactions of the model of the auditory nerve fiber, received in reply to pairs of pulses without noise (A) and mixed with a band-pass noise (B). Levels of pulses and noise are shown as parameters above histogram. The delay between the beginning of noise and the pair of pulses is equal 60 ms. The interval between pulses of pairs is equal 3 ms. The relative amplitudes of reactions to the second pulse, being received when pairs of pulses are mixed with noise, are given as parameters to the right of histograms. On the abscissa axis: time in s, on the ordinate axis: the number of spikes, being obtained on each step of calculation on 100 multiple presentation of stimulus.

Fragments of post-stimulus histograms of the reactions evoked by the pair of pulses and by the mixture of pair of pulses and noise are displayed on Figure 3. The gradual growth of the pulse's level reduces relative amplitude of reaction to second pulse N2/N1, when the pairs are presented in isolation (Figure 3, column A). The gradual growth of noise's level reduces both synchronization of reaction of set of auditory nerve fibers, arisen on the first pulse, and masking of the second pulse by the first one, when the pairs are presented in combination with broad-pass noise (Figure 3, column B). The amplitudes Nr2/N1, generated by the repeated mechanism at any intervals between pulses, have remained approximately identical at any noise levels. But the amplitudes Ns2/N1, generated by the stochastic mechanism, have gradually increased with growth of noise level (Figure 3, parameters to the right of histograms).

There is the optimal signal/noise ratio, which the most effectively unmasks the second pulse of the pairs, for each level of pulses (Figure 4). External noise reduces the synchronization of the response of fiber's set with the first pulse (due to the fiber's adaptation) and, therefore, increases reaction on the second pulse, having been formed by the stochastic mechanism. Thus, external noise allows one to restore sensitivity of coding of pairs of pulses by the set of excited auditory nerve fibers.

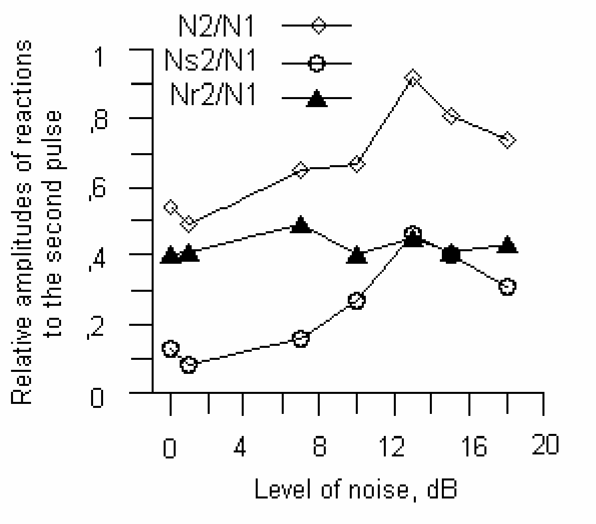

Figure 4: Dependence of relative amplitudes of reactions to the second pulse on the level of external noise. On the abscissa axis: the noise level in dB, on the ordinate axis: amplitudes of reactions.

3.2 Responses of the model on the sine-amplitude-modulated signal

A positive role of external noise in the peripheral coding of sounds indicates also the other example. Stimuli were a mixture of the SAMS and external band-pass noise. Reactions of the auditory nerve fibers with different spontaneous activity were investigated [Rimskaya-Korsakova 2004]. These are displayed on Figure 5 in columns A, B and C. Parameters of these fibers are given in rows A, B and C of the Table 2, accordingly. It is necessary to remember, that spontaneous activity of the real and model fibers is closely connected with properties of adaptation, with steepness of the I/O characteristic and with properties of the extraction of the sound modulations [Rimskaya-Korsakova 2003, 2004].

Table 2: Parameters of the model of the auditory nerve fiber; stimuli are sine-amplitude-modulated signal

Type of fiber's model	SA, pps	R_{max}	Slope	τ_f,ms	H_{of} / H_o	τ_s,ms	H_{os} / H_o
A	30	0,12	0,5	3	0,7	30	0,2
B	0	“	0,025	“	“	“	“
C	0	0,34	0,025	4	1,5	45	0,4

Let's show influence of a steepness of the I/O characteristic, being given of the parameter Slope in Eq. (3), on the range of levels of noise and SAMS, within which the SAMS is well synchronized with the fiber response (Figure 5, columns A and B). For this purpose one will consider the dependencies of the synchronization coefficient K on levels of noise, received for fiber's models in case of the stimulus in the form of the subthreshold SAMS, and when the latter are combined with weak noise.

Reactions of fiber’s models with different SA are well synchronized with SAMS, having been mixed with weak broad-pass noise, when levels of SAMS are above threshold and levels of noise are less 10 dB (Figure 5, A, B, the top row). Synchronization of reaction of the fiber’s model with SAMS falls when the level of noise is increased. The fiber's model with low SA and the flat I/O characteristic does not synchronize reaction, when the level of SAMS is less of threshold (less of 0 dB) (Figure 5, A, the top row). However the fiber's model with high SA and the steep I/O characteristic still continues to synchronize reaction, when the level of SAMS has gone down up to -4 dB (Figure 5, B, the top row).

The local maximum of synchronization of the fiber’s reaction with SAMS arises in reply to mixture of the SAMS of certain subthreshold levels and weak noise also of certain levels (Figure 5, A, B, the top row). The size of this local maximum depends on the steepness of the I/O characteristic. These characteristics are displayed on the middle row of Figure 5. The significant local maximum of synchronization is found out in fiber's model with the steepness I/O characteristic and high SA, but such maximum is absent in the fiber's model with the flat I/O characteristic and low SA.

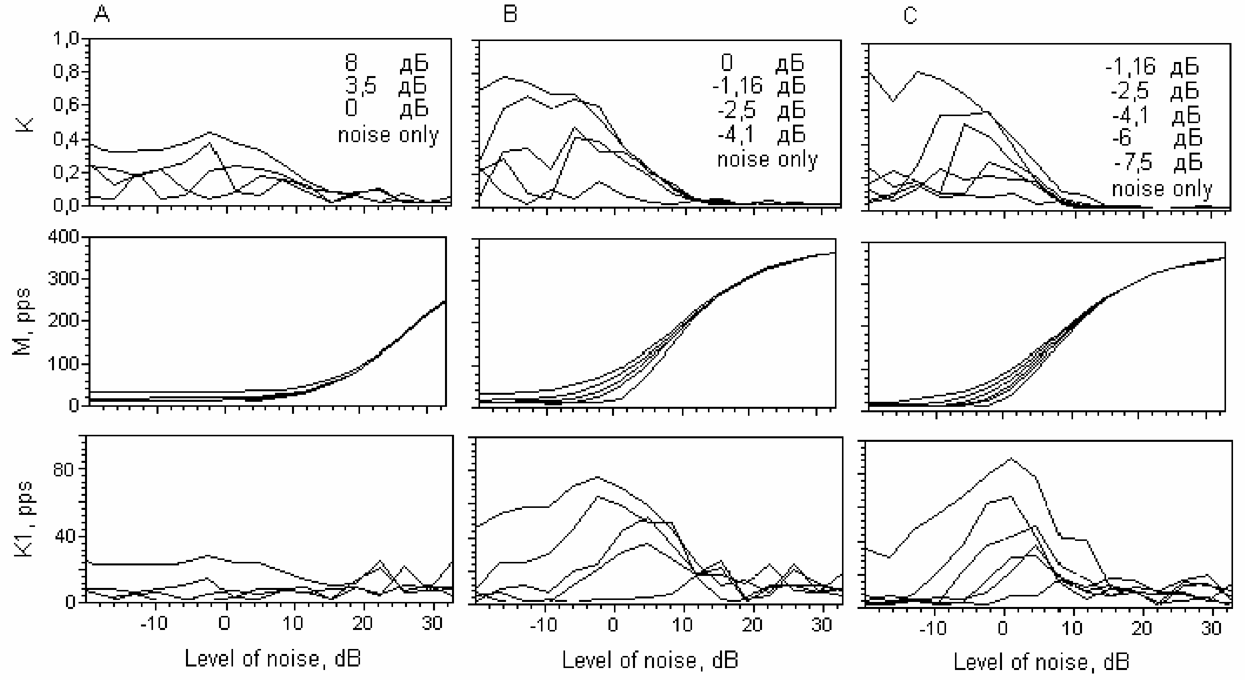

Figure 5: Reactions of three models of auditory nerve fibres, received in reply to additive mixture of SAMS and noise. Parameters of models are specified in table 2. Synchronization coefficients K are shown on the top row; on the middle row – I/O characteristics, in pps; on the bottom row – the fundamental component of the Fourier transformation of the phase histogram K1, in pps. Levels of SAMS in dB, specified as parameters, correspond to curves following from top to down. The nearest curves to the abscissa axis correspond to the reactions, received in reply to noise only. The noise levels are shown in dB on the abscissa axis.

Dependences the fundamental component of the Fourier transformation of the phase histogram (factor K1) on the noise level in reply to the additive mixture of SAMS and weak noise are displayed on the bottom row of Figure 5, A, B. (K1 = 2M*K.) These dependencies allow estimating modulations of the instantaneous firing rate of the fiber's model. They also allow measuring some power characteristics of the envelope reproduction of SAMS on the modulation frequency. These power characteristics even more emphasize local maximums, which have been found out in dependences of the synchronization coefficients K on noise level. At the same time it is possible to estimate the signal/noise ratio, using the ratio of the factor K1, received in reply to the mixture of the SAMS and noise, to the factor K1, received in reply to noise alone. It is easy to understand that the maximum of signal/noise ratio will be found out in the same optimum range of noise levels, as maximum of the factor K1. This maximum corresponds to area of the occurrence of a stochastic resonance [Ward 2002, Rimskaya-Korsakova, 2003, 2004]. The stochastic resonance is not present in reactions of fiber's model with the flat I/O characteristic (Figure 5, A, the bottom row), but the stochastic resonance reveals itself in the fiber's model with the steepness I/O characteristic (Figure 5, B, the bottom row). Thus, weak noise reduces the threshold of detection of SAMS up to - 4,1 dB due to the phenomenon of the stochastic resonance.

Properties of threshold function H(t) have also influence on the range of the levels of SAMS and noise in which the stochastic resonance are appeared. The increase of parameters of threshold function H(t) results in increase of adaptation properties of the fiber's model. Reactions of models of auditory nerve fibers with identical steepness of the I/O characteristic, but with different parameters of function H(t) are displayed on columns B and C of Figure 5. The threshold of detection of SAMS decreases up to - 7,5 dB in the fiber's model, in which parameters of the threshold function H(t) is the greatest and, hence, the adaptation's property is more expressed (Figure 5, C).

3.0 CONCLUSIONS

It is possible to assert that the sensitivity of coding fine temporal and amplitude features of the pulse's pair may be restored, when the pair with the average level mixes with broad-pass noise of average level and when this pair is encoded by a number of excited auditory nerve fibers, each of which has stochastic character of reactions.

The stochastic resonance, which is found out in the auditory nerve fiber with the steep I/O characteristic, allows detecting the SAMS of the subthreshold level with the weak modulation depth if the SAMS is mixed with weak broad-pass noise. Fibers with steeper I/O characteristics and with more expressed adaptation properties detect the SAMS with the least subthreshold level.

Studying of real coding principles of the auditory information might be helpful in choosing of signal preprocessing strategy in bionic recognition systems [Dubrovsky 1994].

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