NEURAL MECHANISMS IN PERCEPTION OF SOUNDS WITH DIFFERENT TIME PARAMETERS

E.A.Radionova

I.M.Sechenov Institute of Evolutionary Physiology and Biochemistry and

I.P.Pavlov Institute of Physiology, St.Petersburg, Russia

ABSTRACT

Two functional systems of neurons with opposite time characteristics are distinguished in the auditory system: a system of neurons responding to sound transients and a system of neurons which reflect in their activity stationary parameters of sound signals. It is supposed that complex sounds (including speech sounds) are processed in relation to their time parameters simultaneously in two ways which are characteristic of the above two neuronal systems.

INTRODUCTION

While studying responses of the auditory system neurons to sound signals with different parameters two functional systems of neurons were distinguished which differed sharply in a number of their characteristics - both in responses to stationary signals and in responses to signals with pronounced transients [1, 2]. The difference between the two systems concerns such properties of neurons as their response pattern, temporal summation, response dependence on the sound initial phase and rise time of its amplitude, sensitivity to phase spectrum of stationary sounds, threshold and latency characteristics. The present work is devoted to description of these two neuronal systems and possible role of each of these systems in the process of the auditory analysis of acoustical signals with different time characteristics. (A system of neurons with intermediate properties is not considered here in view of a limited space of this paper).

The present description concerns mainly the lower levels of the auditory system, namely cochlear nuclei at the medullar level of the brain and inferior colliculus at the midbrain level. Just at these levels of the auditory system the properties of the above neuronal systems are most pronounced.

It is supposed that complex sounds (speech sounds included) can be processed in relation to their time parameters simultaneously in different ways which are characteristic of the above two neuronal systems. The role of the higher levels of the auditory system (medial geniculate body and the auditory cortex) in this process is considered in DISCUSSION.

MATERIAL AND METHODS

Recording technique

Responses of neurons from the cochlear nucleus and inferior colliculus to sound signals were investigated in electrophysiological experiments on anaesthetized cats with the help of isolated tungsten microelectrodes (the electrode tip of about 0.001 mm, 1-5 megohm resistance as measured at 1 kHz). Impulse activity of single neurons as well as summed neuronal activity was recorded. The latter was registered as on-, off- evoked potentials (EPs) and as sustained activity - either synchronized with the sound signal (the so called frequency following response) or non-synchronized activity (summed asynchronous response).

Stimuli

Experiments were performed in a screened sound-attenuated chamber. Sound signals were presented through the electrostatic earphone with ±4 dB frequency dependent characteristic in the range 0.07-30 kHz, under the closed field conditions (all measurements with the Bruel and Kjaer 135 type microphone). Sound signals were tone or noise bursts, as well as complex signals of 2-6 harmonic components. Only linear range of sound intensities was used. The following time characteristics of sound signals varied: 1/ sound duration (within 1-200 ms); 2/ rise time of the signal envelope (in the range 0-40 ms); 3/ initial phase (from 0 to 360 degrees, initial and the end phases being of the same value); 4/ the wave form of complex signals - at the cost of changing either frequency or phase of its harmonic components. The rate of stimulus presentation amounted to 0.3-1/s.

Data processing

Neuronal responses were accumulated over 5-20 stimulus presentations: impulse activity was recorded with the "dot" method or as poststimulus histograms, single realizations of summed activity were superimposed. The following response characteristics were estimated: response pattern and the response value - as the number of impulses (for single neurons) or as the summed response amplitude; response duration, latency, and threshold values, as well as the wave form of summed evoked potentials and of summed synchronized activity. All these characteristics were evaluated depending on the sound signal time characteristics enumerated above.

RESULTS

General characteristic of two extreme neuronal systems

Initially, two types of neuronal systems with opposite properties were distinguished basing on the value of the neuron latency augmentation following intensity decrease of the best frequency tone down to its threshold value (long- and short-latency response types). Further it was found that this property was connected with other special features of neuron response to sound stimulation, especially with those connected with signal transitory and stationary parameters. All these features in common determine the neuron response type. It should be noted that the long-latency response type determined at the best frequency tone stimulation can change for the short-latency response type at other frequencies.

At the cochlear nucleus level (which is the first central level of the auditory system receiving all projections from the ipsilateral auditory nerve) about 90% of neurons respond with a tonic discharge pattern following stimulation with a tone burst of the characteristic (best) frequency (i.e. the frequency of the lowest response threshold for a given neuron). With the sound signal duration of about 100 ms and intensity high enough (approximately 40 dB or higher above the neurons' response threshold) the neuron discharge pattern usually consists of about 10-20 impulses covering the whole time of stimulus duration. The latency of such a response pattern amounts to about 2 ms. Decrease in stimulus intensity down to its threshold value results in a great latency augmentation - up to several dozens of milliseconds. Just this phenomenon is characteristic for neuronal responses of the so called long-latency type. Of interest is also the fact of great latency fluctuation (within dozens of milliseconds) at the response threshold.

At the higher, inferior colliculus level, percent of neurons of this type is significantly lower and amounts to about 35% of all neurons investigated. Naturally, quantitative values of their functional characteristics differ essentially from those established for the cochlear nucleus neurons: number of impulses in discharge is lower (usually about 5-10 impulses), the shortest latency value is higher (most often about 5-7 ms), and the latency at the reaction threshold is generally lower (within 20 ms in half of cases) than at the cochlear nucleus level.

Unlike the long-latency neurons, neurons of the other, short-latency type usually respond to the best frequency tones with phasic on-responses of 1-2 impulses or of a short burst of impulses. Their latencies (which are usually short at high intensities of stimulation) remain nearly unchanged at threshold intensities. Neurons of this type are rather rare at the cochlear nucleus level but amount to about 50% at the level of the inferior colliculus.

Neuronal responses to sound signals of different durations

As it was mentioned above, neurons of the long-latency type usually respond to sound signals of long enough duration (of the order of dozens of milliseconds) with a tonic discharge pattern, duration of the latter corresponding to stimulus duration. In result, the sound signal wave form can be reflected in the summed sustained activity of this type neurons. With diminution of the signal duration down to 1-2 ms, the neuronal response becomes shorter and reduced to 1-2 impulses. In case the sound signal intensity remains constant the latency of the neuron response does not depend on stimulus duration and remains constant at any duration of the sound signal. However response threshold and the range of its fluctuation depend greatly on stimulus duration. At the level of the cochlear nucleus, diminution of signal duration from 100 to 1 ms results in response threshold augmentation for dozens of decibels; the range of its fluctuation augments for several decibels. Neurons of the inferior colliculus level also show augmentation of the response threshold following decrease of stimulus duration, though to somewhat lesser extent than cochlear nucleus neurons; meanwhile the range of threshold fluctuation augments to a greater extent than at the cochlear nucleus level.

As to the short-latency type neurons, characteristics of their responses practically do not depend on the sound signal duration. These neurons, usually responding to sounds with a phasic on- or on-off discharges of 1-2 impulses (or of a short burst of impulses) show (at any stimulus duration) short latencies of minimal fluctuations and nearly constant thresholds of relatively high values (higher for about 20 dB as compared with the long-latency type neurons, at an average).

Thus, only long-latency type neurons can reflect in their activity stimulus duration, its wave form, and their changes.

Neuronal responses to sound signals with different rise time of their envelope

Augmentation of the rise time of the signal envelope evokes certain changes in the initial part of discharge of the long-latency type neurons, which results in desynchronization of their activity. Neuronal response value, its duration are decreased, and the latency value increases - due to intensity decrease over the sloping part of the signal envelope. Meanwhile the response threshold does not show any changes.

Neurons of the short-latency type, on the contrary, are characterized by practically unchanged discharge pattern (on-, off-responses) and latency values. However their responses to sounds with sloping envelope are retained only within a very narrow range of the stimulus rise time values (below 10 ms at the cochlear nucleus level), since the response threshold rises greatly. Besides, under conditions of stimulation with signals with sloping envelope, neurons of the short-latency type show a significantly lower noise tolerance than the long-latency type neurons. It should be noted that the higher is the level of the auditory system the less sensitive are neuronal responses to augmentation of the signal front rise time (as it is shown in the works with evoked potentials, EPs, which reflect summed initial responses of neurons). This fact evidences that at higher levels of the auditory system, neurons' tolerance of the desynchronizing effect of increasing rise time of the signal envelope rises.

In general, neurons of the long-latency type prove essentially more tolerant of the sound signal front sloping than neurons of the short-latency type.

Neuronal responses to initial phase changes in tonal signals

Changes of the initial phase of tonal signals are essential for responses of the short-latency type neurons and practically produce no effect on the response characteristics of the long-latency type neurons. It is important that the phase effect observed on the short-latency neurons with on- or on-off responses depends on the sound frequency relation to the neuron characteristic frequency [3]. In case the sound signal frequency (F) is lower than the neuron characteristic frequency (CF), maximal response value (i.e. maximal number of impulses in the neuron's discharge or maximal amplitude of the EP) is observable at the signal initial phase of 90 and 270 degrees. At the initial phase of 0 and 180 degrees the response value is minimal. Therefore the function relating the number of impulses to the initial phase value (from 0 to 360 deg.) has an M-like shape. However in case F>CF, maximal response values correspond to the initial phase values of 0 and 180 degrees, whereas at the initial phase of 90 and 270 deg. the neuron response value is minimal. In result the function relating the response value to the initial phase has a W-like shape. The above phase effects are pronounced the more, the greater is

the difference between the CF and F. When F=CF the phase effect is minimal or absent.

Thus, only short-latency neurons show the possibility to differentiate the character of the transitory process at the moments of the signal on- and off-sets, determined by the signal initial phase value.

Neuronal responses to complex sounds of different wave form

The wave form of complex signals finds its reflection in poststimulus histograms of the long-latency neurons' activity and in the summed synchronized activity (the so called frequency following response, FFR) of neurons from the lower levels of the auditory system. At the cochlear nucleus level the wave form of acoustical oscillations is reproduced in the FFR with but slight distortions: nearly the whole oral speech is reproduced in the FFR (and can be listened to with the help of appropriate apparatus [4]). At the inferior colliculus level these distortions are more pronounced. Meanwhile a phase change for 15-30 deg. in one of the complex signal components produces a pronounced change in the wave form of the FFR recorded even at the inferior colliculus level.

Of interest is that phase change of the second (higher) harmonic of a two-tone signal results in different phase effects depending on the characteristic frequency of the long-latency type neurons [5]: functions relating response value to the phase change (from 0 to 360 deg.) show one maximum in low-frequency neurons (CF<5 kHz) but two maxima in high-frequency neurons (CF>11 kHz). Neurons with intermediate CFs demonstrate the functions of intermediate form [5-7].

It may be concluded that only long-latency type neurons can specifically respond to complex sounds and to changes of their wave form.

DISCUSSION

Thus, stationary and transient parameters of sound signals can be processed in parallel in two neuronal channels: a system of long-latency neurons (I) can perform analysis of the sound signal stationary parameters - on the basis of the neurons' ability for temporal summation, accumulating in time acoustical information, slight dependence of the response characteristics on the signal front slope, and neuronal ability to reflect the sound wave form in impulse and summed activity. A system of short-latency neurons (II) can perform analysis of signal transients - on the basis of their response pattern, short latency of practically no fluctuations at any parameters of sound stimulation, and pronounced dependence of response on the signal rise time. At higher levels of the auditory system the role of system I decreases and the role of system II augments. Besides, a system of neurons with intermediate properties manifests itself more and more, especially at the MGB and cortical levels. This may result from high convergence of impulsation from neurons of the lower systems I and II. Thus initial channelizing the responses (at the lower levels of the auditory system) according to stationary and transient properties of sound signals is changed for integration of these responses which seems necessary to form an integrated auditory image in the brain.

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