

Physiological Modeling of Cochlear Nucleus Responses Perception of complex sounds

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Abstract. The cochlear nucleus integrates the sensory information carried by auditory nerve fibers. Several types of neurons contribute to the processing of the peripheral output. In the cochlear nuclei (CN), chopper units respond to the summated low-frequency components of their inputs. This feature is due to intrinsic membrane characteristics (i.e. the time constants of the membrane potential) and also the result of a strong refractoriness. We propose a physiologically plausible model for the electrical properties of the membrane of chopper units. This model is derived from Hodgkin-Huxley equations. The refractoriness is controlled by the voltage-dependent time constant of K⁺ movement through membrane during hyperpolarization. This model correctly predicts the response of chopper units to single tone stimuli for varying stimulus amplitude and frequency, i.e., the high regularity of the spike discharge behavior. Moreover, the model exhibits phase-locking, with its synchronization index decreasing rapidly to zero > 200 Hz. We are concerned particularly with post-cochlear mechanisms for enhancing the phase-locked activity of auditory neurons in response to sinusoidally amplitude-modulated (AM) white noise. The model also exhibits phase-locking for modulation frequencies around 200 Hz. The results of these simulations are discussed in terms of their relevance to acoustic pitch perception as a temporal phenomenon.

1. Introduction

The classical study on the "cocktail-party effect" refers to the surprising ability of human listeners to separate a target sound from a noisy background. In this paper, we are primarily interested in the extraction of pitch in the separation process. Pitch is a subjective quality of sounds in which variations constitute melody. For normal hearing subjects, the pitch of a sound is a complex function of its fundamental frequency, waveform and level. Within the auditory system, two basic mechanisms control the encoding of pitch information: 1) the first mechanism of pitch extraction is based solely on spectral cues, i.e., the mapping of the frequency onto position along the basilar membrane. This process is giving rise to the "place pitch"; 2) the second mechanism is based only on temporal cues, i.e., the mapping of frequency onto temporal patterns of neural firing. This process is giving rise to the "periodicity pitch". There are arguments for each of these as independent mechanisms of pitch

perception. We are concerned principally with the "periodicity pitch" theory, consistent with a number of psychophysical, neurophysiological and anatomical observations. Psychophysical data reported that listeners were able to identify simple melodies "played" by varying the modulation frequency of sinusoidally amplitude modulated (AM) wideband noise (Burns and Viemeister, 1981). However, the long-term spectrum of modulated white noise is uniform. This implies that pitch elicited by AM noise is mediated by temporal cues.

These psychophysical observations possess correlates that are investigable electrophysiologically. In response to low-frequency tones (<5kHz), discharges of single auditory-nerve fibers tend to cluster at a preferential phase angle of the waveform cycle. This phenomenon is termed phase-locking and gives rise to a purely temporal aspect of pitch perception. Moreover, this observation corresponds to the upper frequency limit (5 kHz) of the residue pitch phenomenon. Time intervals between successive discharges of an auditory nerve fiber in response to AM tones are seen related to the temporal fine structure of the "effective waveform". These data demonstrate that, at the level of the peripheral auditory system, information regarding pitch of AM tones is encoded within the phase-locked aspects of neuronal discharge patterns. The temporal firing patterns of auditory-nerve fibers are altered or preserved in the cochlear nuclei (CN). Chopper units in the CN shape the peripheral firing patterns. They can phase lock at low frequencies (<1 kHz) but this ability decreases significantly above 1 kHz (Rhode and Smith, 1986). Moreover, at high intensity levels, chopper units show a strong phase-locked response to AM tones. The mean gain of chopper units (i.e., the strength of the response to AM) suggests that they extract and enhance the phase-locked AM responses that they receive as inputs from auditory-nerve fibers (Frisina et al., 1990). Regarding to their participation in temporal pitch extraction, chopper cells represent an interesting challenge in modeling. To date, there are models of the stochastic activity of chopper cells (Berthommier, 1991, 1992) based on a limited set of parameters (the connectivity between inputs channels and the cell, the durations of excitation and refractory period) but only few are physiological models (Arle and Kim, 1991).

The purpose of this study is to develop a neurophysiologically plausible model to account for the response properties of chopper cells and their ability to extract and enhance pitch information.

2. Properties of the chopper cells

In the CN, several distinct types of cells are found. At least, two different kinds of responses can be recorded in the anteroventral part of the CN (AVCN): chopper responses (stellate cells) and primary-like responses (bushy cells).

Chopper units have electrical properties characterized by linear current-voltage relationships. Primary-like properties are characterized by nonlinear current-voltage relationships (Oertel, 1985).

The measured synaptic delay of the excitatory inputs is 0.7 ms and the duration of the excitatory postsynaptic potential (EPSP) is about 5.2 ms for a chopper unit and 2.3 ms for a primary-like unit. The mean latency of first spike responses to tones is at least 1 ms longer than the shortest auditory-nerve fiber mean latencies (Young et al., 1988), indicating temporal integration. Chopper units sum their inputs both spatially and temporally while primary-like units cannot sum peripheral inputs temporally because the refractory period is longer than the duration of the excitation (Oertel,

1985). We don't yet know how many auditory-nerve fibers converge on a single chopper cell but recent modeling suggests that chopper units could receive about 50 fibers.

There is also evidence for feed-forward inhibition in the AVCN. Intracellular recordings show that chopper cells receive late inhibition disynaptically through interneurons within the VCN.

Chopper units fire in a sustained regular manner, resulting in a multimodal post-stimulus-time-histogram (PSTH) during the first 15 ms of stimulation and a narrow unimodal interspike interval histogram (ISIH) centered between 2 and 6 ms. The coefficient of variation (CV) is equal to the ratio of standard deviation to mean interspike interval and is rarely greater than 0.5 and remains approximately constant during the response to pure tones. The regularity of interspike intervals could be due to the refractory period. Thus, the decrease in the peak height of the PSTH can be explained by both the variability of the refractory period and an increase of this error.

We propose two possible explanations for the high synchronization index at low frequencies:

- 1) a mechanism of dendritic low-pass filtering or bandpass filtering (activation-inhibition);
- 2) a non-linearity in the filtering mode produced by a long refractory period (approximately 5 ms).

In summary, these two basic mechanisms depend on a limited set of physiologically plausible parameters:

- an average convergence on the chopper unit (about 50 auditory-nerve fibers),
- the long EPSP duration (about 6 ms),
- the specific time course of the cellular membrane potential during the long cellular refractory period (about 5 ms).

The two first parameters have already been introduced in earlier models. In the present paper, we focused on simulating the specific time course of the cellular membrane potential during stimulation. We attempt to show links between chopper unit biological characteristics and their role in the processing of complex stimuli. We examine the chopper unit model output using PSTH's, ISIH's, the time course of the CV of the interspike interval and the synchronization index. The model was tested with stimuli commonly used in physiological studies (i.e., pure tones) in order to compare the chopper unit model output with real recordings. The model was also tested with stimuli commonly used in psychoacoustical studies (i.e., AM white noises) in order to find correlations with perceptual phenomena.

3. Basis of the model

This paper outlines a simple model of the auditory nerve and a physiological model which generates the discharges of chopper units in the AVCN. To achieve chopper units particular properties as spike discharge behavior, we used the Hodgkin-Huxley (HH) model. This model describes the change of membrane potential along a piece of axon membrane as a function of three ionic currents, sodium, potassium, and a leak current. We postulate that chopper units properties are linked to the specific time course of the membrane potential during the long refractory period. Consequently, we fitted the time constant of the variable that describes the behavior of potassium channels in the membrane.

Model description

We describe three stages in the chopper physiological model. The first stage is a model of hair cell transduction: the signal is sampled at 10 kHz, half-wave rectified and coded with the Schroeder & Hall's model (1974). The output of the hair cell model is then processed by an array of 50 probabilistic models of neural firing. Spikes are generated, followed by a 1 ms absolute refractory period. The discharge rate is limited to 200 spikes/s. The duration of a spike is 0.1 ms. The resulting 50 spikes trains are processed by the chopper physiological model. The spatially summated inputs generate EPSPs of 6 ms duration. The temporally summated EPSPs are finally processed by a model of excitable membrane. The HH equations describe the electrical properties of the membrane of the chopper axon. The model involves the voltage V and n , m and h , three variables ranging from 0 to 1 which can be thought of as the probabilities of potassium (K^+) and sodium (Na^+) channels subunits to be active or inactive. K^+ movement through the membrane depends on the state of the gate of the K^+ channel. The latter can exist in two states, α and β . If the gate of the K^+ channel is in the state α , the fraction of the membrane specialization is n and:

$$\begin{aligned} dn/dt &= \alpha_n (1 - n) - \beta_n n \\ n_\infty &= \alpha_n / (\alpha_n + \beta_n) \\ \tau_n &= 1 / (\alpha_n + \beta_n) \end{aligned}$$

where α_n and β_n are voltage dependent rate constants, n_∞ is the steady-state value of n and τ_n the time constant of the process. $g_k = n^4 \bar{g}_k$ gives the delayed rise in the potassium current i_k , where \bar{g}_k is the maximum potassium conductance. The expression of the potassium current is the product of g_k and the potential difference between the membrane voltage V and the ionic equilibrium voltage V_k :

$$i_k = \bar{g}_k n^4 (V - V_k)$$

The probabilities m and h , the sodium current i_{Na} and a leak current i_L are defined similarly. Current I_i carried by ions crossing the conductive pathway through the membrane is given by the sum of i_K , i_{Na} and i_L . The total current through the membrane I is finally the sum of the capacitive current $C_m dV/dt$ and ionic currents I_i , where C_m is the membrane capacitance which is assumed constant:

$$C_m dV/dt = I - I_i$$

The voltage-dependent time constant of K^+ movement through membrane during hyperpolarization τ_n is modified in order to obtain a 5 ms refractory period. All simulations are performed on a Sun station IPC. Programs are written in C.

4. Results

The model was tested with tone bursts of a 50 ms duration, repeated 250 times and sampled at 10 kHz.

Figure 1 shows the PSTH of the chopper model for a stimulus intensity of 4 arbitrary units (u.a.) of current and a stimulus frequency of 4kHz. The discharge rate is seen to be very regular, reflected in the strong chopping pattern. The chopping period of the PSTH is proportional to the duration of hyperpolarization of the model. The chopper model loses completely the synchronization on the stimulation after 20 ms and the peak height of the PSTH decreases gradually because of a random shifting of the responses.

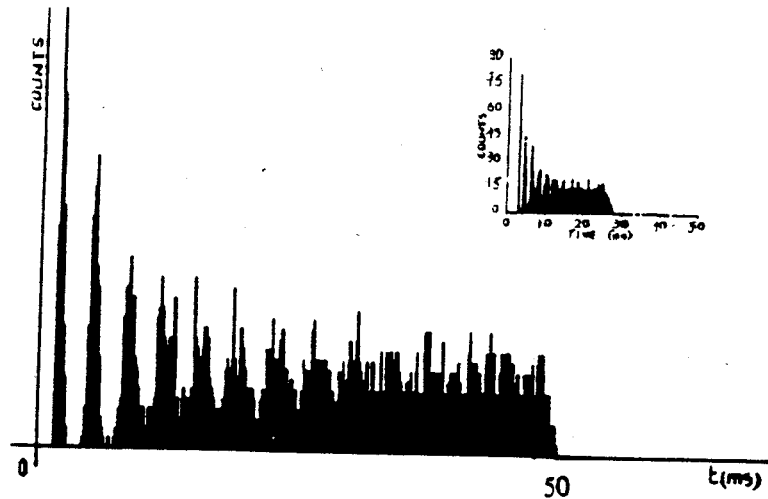


Fig. 1. The Post-Stimulus Time Histogram (PSTH) of the simulations is compared with real records (in the corner) performed by Rhode and Smith (1986), with the same number of stimulations (250) and the same frequency sampling (10 kHz). The stimulus, during 50 ms, is a pure tone at 4000 Hz, sampled and converted into spikes trains by the Schroeder & Hall's model of the transduction (1974). The distribution is closely compatible with the real data.

Figure 2 shows the ISIH of the chopper model computed in the same conditions. The lower interspike interval indicates the limitation introduced by the absolute refractory period. The interval distribution has a narrow unimodal shape centered on 4 ms, showing a highly regular discharge. This pattern (symmetric, unimodal and narrow) distinguishes this as a sustained chopper (Cs) unit.

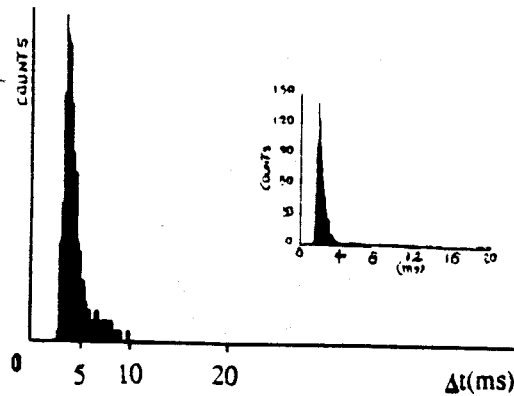


Fig. 2. The interspike interval histogram (ISIH) of the simulations is compared with real records (right in the corner) performed by Rhode and Smith (1986).

The regularity analysis is illustrated in figure 3 by plotting the mean μ_T and standard deviation σ_T of interspike intervals as a function of time. The time axis is divided

into 0.2 ms bins. A measure of irregularity is the coefficient of variation CV, defined as the ratio σ_T / μ_T . Plots of CV are shown in figure 4. Once again, these results indicate a regular discharge: μ_T , σ_T remain fairly constant and the CV is never greater than 0.5. These results are quite similar to experimental data (Young et al., 1988). Moreover, the mean CV = 0.3 allows us to classify the model as a Cs unit model. The ability of the chopper model to follow the temporal features of the acoustic signal is traditionally measured using the synchronization coefficient. This coefficient has been computed at increasing stimulus frequencies and intensities and plotted in figure 5. Each value indicates the preferential discharge of the model during a limited portion of the cycle of the sinusoidal stimulus. The model exhibits strong phase-locking for very low frequencies, with a maximum synchronization coefficient at 200 Hz. The coefficient drops rapidly to zero for upper frequencies. The model correctly predicts the chopper phase-locked response as a function of frequency, although our results show a downward shift in frequency compared to experimental data (Rhode et al., 1986). The present model does not include the cochlear frequency filtering: this suggests that chopper units have a low-pass or bandpass filtering effect with respectively a cutoff frequency or a characteristic frequency of ~ 200 - 300 Hz. Both the time constant of the EPSPs and the specific time course of the membrane potential during hyperpolarization serve to limit the ability of chopper units to follow the fine structure of acoustic waveforms.



Fig. 3. The regularity plots of μ_T and σ_T : μ_T is the mean interspike interval and σ_T the standard deviation of interspike intervals of the simulations. Time axis is divided into 0.2 ms bins. The regularity plots are compared with real records (right in the corner) performed by Young et al. (1988). The simulated distributions are closely compatible with real data.

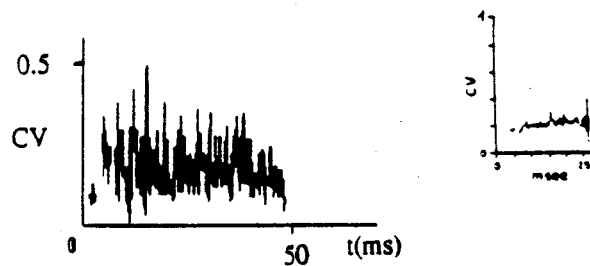


Fig. 4. Coefficient of variation (CV) is the ratio σ_T / μ_T : CV is plotted as a function of time and compared with real records (right in the corner) performed by Young et al. (1988). The CV is never greater than 0.5 and confirms this is an adequate model of chopper cell (Cs).

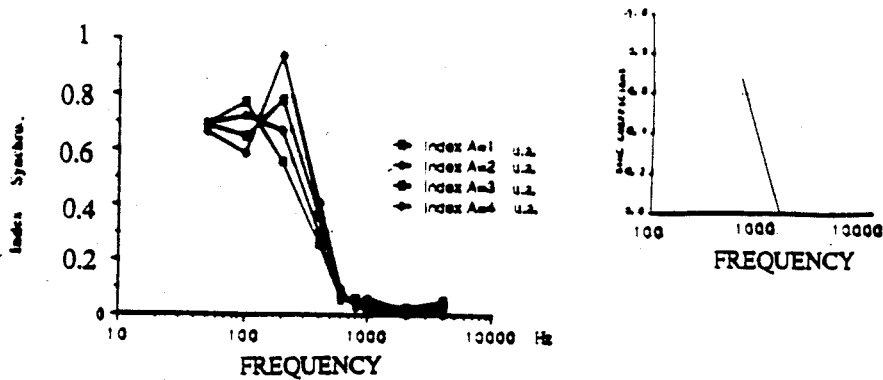


Fig. 5. The stimuli are pure tones sampled at 10 kHz. The synchronization coefficient is computed for increasing frequencies and intensities of stimulations. The frequencies are plotted from 50 to 1500 Hz and the intensities from 1 to 4 u.a. (arbitrary units). The simulations are compared with real records (in the corner) performed by Rhode & Smith (1986): the regression line fits with the synchronization coefficients for a real chopper cell unit. Frequency for simulations shifts downward.

The results of the second part of our study where AM white noises are applied into the chopper model are presented on figure 6. The stimuli were obtained by varying the modulation frequency of AM wideband noises from 50 to 800 Hz. The degree of phase-locking to the modulation frequency has been computed. The chopper model shows a strong phase-locked response to AM white noises for modulation frequencies between 100 and 300 Hz.

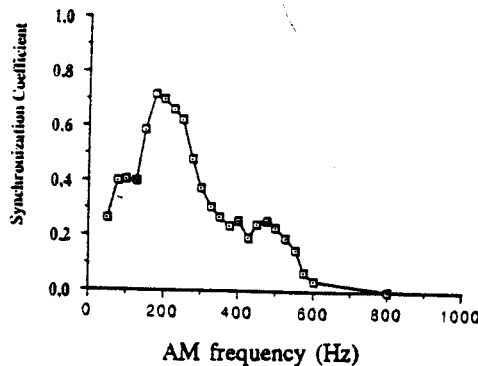


Fig. 6. The stimuli are AM white noises sampled at 10 kHz. The synchronization coefficient is computed for the various modulation frequencies (modulation depth: 100 %).

This result may be compared with some psychoacoustical observations reported by Burns and Viemeister (1981) who used the same stimuli to investigate pitch perception. The cutoff frequency of ~ 300 Hz seems consistent with the fact that performance in identifying the pitch of AM white noises deteriorates with modulation frequencies roughly below 500 Hz. The low-frequency perceptual sensitivity for the pitch of AM noise is consistent with the low-pass or bandpass character of the chopper unit transfer function. However, pitch extraction from temporal information

differs from AM extraction: the fine structure of the waveform close to adjacent envelope maxima is also determinant in the perception process.

5. Conclusion

The chopper responses found in the AVCN can be generated by single cells rather than networks. They are probably founded on a basic mechanism of integration depending on the degree of convergence of the peripheral inputs on each cell, the time constant of the EPSPs and the duration of the refractory period. However, the use of a non-linearity introduced by the HH equations improves the correlation between simulations and real recordings. The model exhibits a highly regular discharge pattern to a pure-tone stimulus ($CV < 0,5$). The use of this non-linearity finally provides an adequate model for low-frequencies processing in the auditory system (the model exhibits a poor phase-locked response to frequencies and modulation frequencies up to ~ 300 Hz). In the latter simulation, we showed that chopper neurons could roughly contribute to the extraction of the periodicity pitch of AM wideband noise. Nevertheless, pitch cannot only be mediated by the temporal information carried by such a chopper model. Other units, as onset cells in the posteroventral part of the cochlear nucleus, phase-lock better than chopper cells and could play a role in pitch encoding. These results allow us to postulate the existence of a selective channel capable of preserving temporal informations on the AM. This channel could be involved in the place/temporal multi-representation of complex sounds. We can expect this mechanism to provide cues for the separation process responsible for forming auditory objects.

6. References

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