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Description	

EFFECT OF THE BASILAR MEMBRANE NONLINEARITIES ON RATE-PLACE REPRESENTATION OF VOWEL IN THE COCHLEAR NUCLEUS: A MODELING APPROACH

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Effects of the basilar membrane (BM) nonlinearities on fine representation of vowel formants of chopper units in the anteroventral cochlear nucleus (AVCN) are investigated using an auditory model. A functional model of ventral cochlear nucleus (VCN) units is proposed and is evaluated by comparing responses of the model with the physiological data. Rate-place representation of the models to the vowel /ε/ is recorded for a wide range of characteristic frequencies (CFs) at both low and high sound levels. Evaluation shows that the model is able to simulate shape of post-stimulus time histogram to short-tone bursts, discharge regularity and phase locking properties of actual chopper units. Simulation using vowel /ε/ as stimulus shows that inhibitory inputs from the AN model have effectively suppressed firing rate of the model of VCN units having CF between the first and the second formant of the vowel /ε/ at high sound revel only. This results from change of frequency selectivity of the nonlinear BM model related sound level. This rate-place representation is similar to that of actual chopper units in the AVCN. The simulated results suggest that BM-nonlinearities-related sound level play an important role for fine representation of vowel formants of the chopper units in the AVCN. This modeling approach can effectively be applied for a clear representation of speech in the auditory pathway.

1 Introduction

Effects of the basilar membrane (BM) nonlinearities on fine representation of vowel formants of chopper units in the anteroventral cochlear nucleus (AVCN) are investigated using an auditory model.

Physiological experiments have made clear the rate-place representation of chopper units to the steady-state vowel in the AVCN.

Both regular chopper (Ch S) and irregular chopper (Ch T) units maintain better rate-place representations of the vowel spectra than does the population of auditory nerve fibers (ANFs) at high sound level. The rate-place representations closely resemble those of low and medium spontaneous rate (SR) ANFs at high stimulus level (Blackburn and Sachs, 1990).

However, the complete mechanisms are still unknown and the computational model, that is able to reproduce rate-place representation of actual chopper units to the vowel, has not been proposed.

The paper discusses the robust rate-place representation of vowel spectrum of chopper units using its computational model. Especially, relation between the representation and basilar membrane (BM)-nonlinearities related sound level is investigated.

2 Model description

The proposed model consists of models of auditory peripheral system and ventral cochlear nucleus (VCN) units.

2.1 Auditory peripheral model

The auditory peripheral model is based on the work of Maki, et. al. (1997, 1998) and its output are auditory-nerve like spikes. The model is able to simulate basic AN firing patterns and responses to vowel in both temporal and rate coding (Maki, et. al., 1998).

2.2 Functional model of VCN units

A functional model of VCN units is proposed to be able to reproduce firing patterns of chopper units in VCN.

Input to the model of VCN unit is output of the AN model $t_{ij}(\in \mathbf{R})$, where $i(\in \mathbf{Z}^+)$ is the number of AN models and $j(\in \mathbf{Z}^+)$ is the firing number of output of a single AN model.

The output of the model of the VCN unit at time t consists of an all-or-none nerve-like firing S given by Eqs. (1), (2) and (3).

$$s(t) = \begin{cases} 1 & V(t-t_c) \geqq U(\alpha,\beta) \quad \text{and} \quad S(t') = 0 \text{ for } t' \in [t-t_r,t] \\ 0 & \text{otherwise} \end{cases} , \tag{1}$$

$$t_r \sim N\left(\mu_r,{\sigma_r}^2\right), \tag{2}$$

$$t_c \sim N\left(\mu_c,{\sigma_c}^2\right). \tag{3}$$

Firing of the model is generated when the membrane potential V of the model crosses a threshold U if under the condition that the model has not fired for the refractory period t_r. The thresholds U have a uniform random distribution in the range from α to β. t_c is a normal distribution with mean μ_c and variance ${\sigma_c}^2$. It modeles firing latency and phase-locking properties of VCN units. The membrane potential V with time is modeled by Eq. (4).

$$V(t) = \sum_{i=1}^{N} \sum_{\{j|t_{ij}<t\}} a_i t \ e^{-(t-t_{ij})/\tau_i}. \tag{4}$$

If input of the AN model is excitative, a_i is a positive real number. Otheriwise, it is negative. τ is the time constant of a single post-synaptic potential.

3 Evaluation

The model is evaluated with respect to the ability to reproduce firing patterns of chopper units by comparing responses of the model with the physiological data.

3.1 PST histogram and discharge regularity

In Blackburn and Sachs (1990), the chopper units are subdivided into Ch S and Ch T units on the basis of the change in firing rate and regularity as a function of time.

Figure 1 shows computation results of modeled Ch S and Ch T units with comparable physiological data.

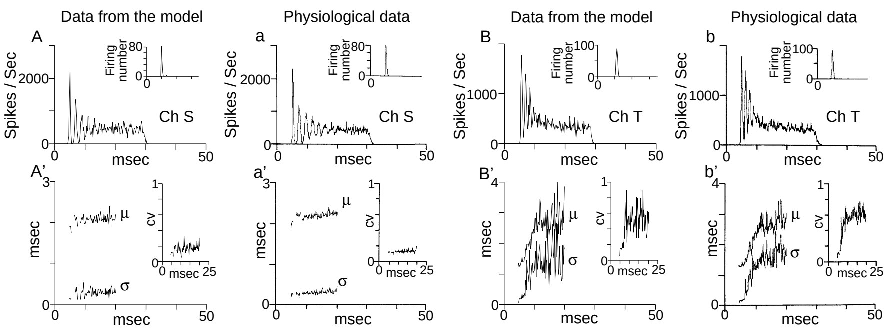

Figure 1: PSTHs (top) and regularity analysiis (bottom) for Ch S and Ch T units. (A),(B): Data from the model. (a),(b): Physiological data (Blackburn and Sachs, 1990). Stimulus was 25ms STB with 1.6ms rise and fall time. PSTHs were generated from 200 presentations of the STB in the model and 300 or 500 presentations in physiological data. First-spike latency histograms are shown on the same time scale above the PSTHs. (A'),(a'),(B),(b): Regularity analysis for the data shown above. μ is the mean inter-spike interval (ISI), σ is the SD of the ISI, and CV is the ratio μ/σ.

In Fig.1, PST histograms (PSTHs) for modeled Ch S and Ch T units quantitatively agree with that of physiological data in regular spaced peak for first 10ms after stimulus input.

Distributions of firing numbers with time in first spike latency histograms of the models also quantitatively agree with that of physiological data.

Modeled Ch S unit in Fig.1(A') reproduces a mean ISI change of actual Ch S type unit (Fig.1(a)) that is nearly constant throughout the entire response to the STB. The mean and SD of actual Ch T units increase with time as shown in Fig.1(b'). Modeled Ch T unit simulates these properties as shown in Fig.1(B').

3.2 Phase-locking property

The synchronization index of modeled Ch S and Ch T units in response to a BF tone are plotted as a function of BF in Fig.2.

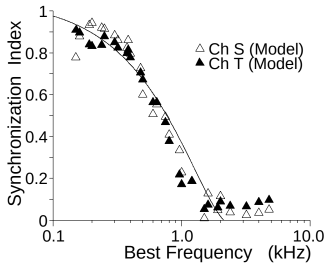

Figure 2: Synchronization index v.s. BF of modeled Ch S and Ch T units. Calculation are based on the entire response (10-400ms) to 400ms long-tone burst. Line shows least squares fitting of actual Ch S and Ch T units (Blackburn and Sachs, 1990).

Line in fig.2 shows least squares fitting of actual Ch S and Ch T units (Blackburn and Sachs, 1990). The ability of Ch S and Ch T chopper units to phase-lock to BF tones decreases rapidly with BF in the range from 0.3 to 1.5–2.0 kHz.

Phase-locking ability of modeled Ch S and Ch T units corresponds to physiological data as shown in Fig.2.

4 Vowel representation

4.1 Responses of auditory peripheral model

Rate-place representation of the auditory peripheral model to the vowel /ε/ with comparable physiological data is shown in Fig.3. The vowel stimulus used in Fig.3 is a steady-state /ε/ with formant frequencies at 0.512. 1.792 and 2.432 kHz and is periodic with a fundamental frequency of 112Hz, that is the same as physiological experiment (Blackburn and Sachs, 1990).

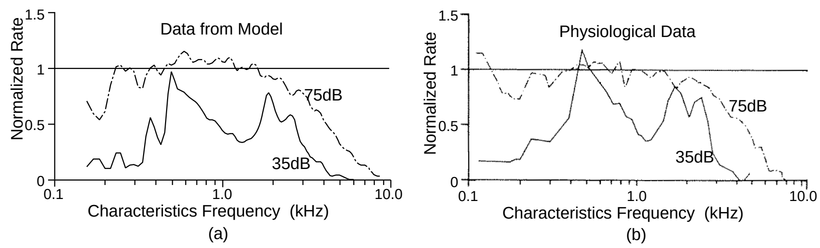

Figure 3: Rate-place representation of modeled and actual ANFs. (a): Data from the the model (High SR). (b): Physiological data (High SR) (Blackburn and Sachs, 1990). Stimulus is vowel /ε/ at 35 and 75 dB SPL. The line is weighting moving average whose base was 0.25 octave wide. The normalized rate defined as "rate minus SR" divided by "saturation rate minus SR".

In Fig.3 (b), rate-place representation of actual ANFs shows a peak in the region of the first formant (F1) and another in the region of the second and third formant (F2 and F3) at low sound level (35dB). At high level (75dB), these peaks disappear.

As shown in Fig.3 (a), the model is able to simulate these physiological properties.

4.2 Responses of a single modeled chopper unit

Responses of a single modeled chopper unit are computed at both low and high sound levels using vowel /ε/ as stimulus. The vowel is the same used as in Fig.3.

Modeled chopper unit having CF F1, F2 and F1–F2 (valley between F1 and F2 in spectrum of vowel /ε/: V1=1400Hz) is presented with 66 excitatory inputs and 53 inhibitory inputs from the AN model.

As shown in Fig.4, CF of all excitatory inputs is the same as CF of the modeled chopper unit. Only CF of inhibitory input is changed around CF of the modeled chopper unit. CF of all inhibitory inputs is the same.

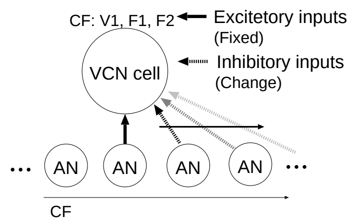

Figure 4: The method of calculation in this section. CF of all excitatory inputs is the same as CF of the modeled chopper unit. Only CF of inhibitory inputs is changed in the range from 0.2kHz to 10kHz. and CF of all inhibitory inputs is the same.

Computing results are shown in Fig.5.

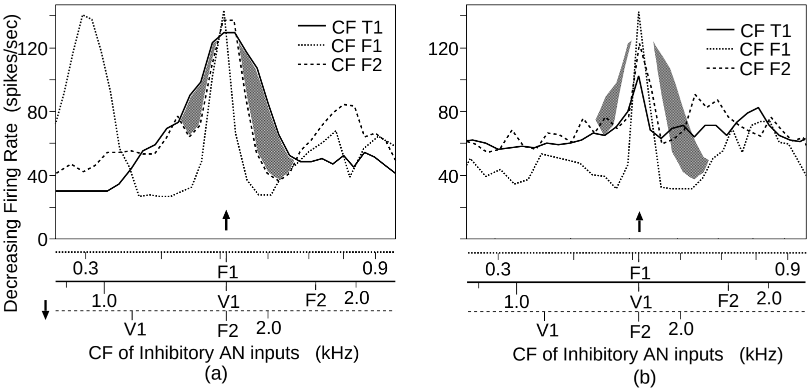

Figure 5: Responses of modeled chopper units with CF F1, F2 and V1 to the vowel /ε/. Arrays show CF of models with CF F1 F2 and V1. (a): High sound level (75dB). (B): Low sound level (35dB). The method of calculation is shown in Fig.4.

In Fig.5 (a), firing rate of the modeled chopper unit having CF V1 is decreased sharply if CF of excitatory input (V1) coincides with CF (V1) of inhibitory input at both high and low sound levels. Modeled chopper units with CF F1 and F2 exhibit similar phenomena as shown the model with CF V1.

The model with CF V1 is widely inhibited in rate compared to the models with CF F1 and F2 at high sound level. However, the model having CF V1 is narrowed and weak inhibited compared to the models with CF F1 and F2 at low sound level.

These inhibitions are caused by the change of frequency selectivity related sound level of the nonlinear BM model. Bandwidth of BM positioned between F1 and F2 of the vowel (V1, etc.) is strongly affected by sound level compared to BM positioned at F1 and F2. At low sound level, frequency components of BM positioned between F1 and F2 are below F1. At high sound level, that are almost equal to F1.

If inhibitory input from the AN model consists of shadow area in Fig.5, only the model CF with V1 is inhibited in rate at high sound level only. This suggests that the model reproduces fine representation of vowel formants of the actual chopper units.

4.3 Responses of population of modeled chopper units

Rate-place representation of population of modeled chopper units to the vowel /ε/ is recorded for a wide range of CFs at both low and high sound levels.

The vowel is the same as in Figs. 3 and 5. CF of all excitatory input (High

SR) is the same as CF of modeled chopper unit. CFs of inhibitory input (High SR) is located at both sides of CF of modeled chopper unit as shown in Fig.5 (shadow area). Computing results are shown in Fig.6(a).

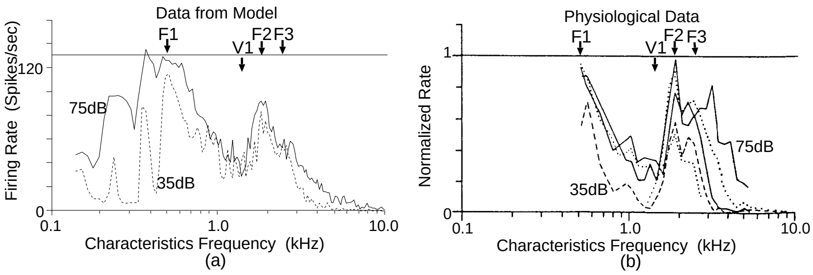

Figure 6: Rate-place representation of population of modeled and actual chopper units. (a): Data from the model. (b): Physiological data (Blackburn and Sachs, 1990).

At high sound level, the rate-place representation shows clear peaks in the region of formant frequencies, although that of both excitatory and inhibitory inputs from the AN model is smooth as shown in Fig.3 (75dB). This rate-place representation is similar to that of actual chopper units in the AVCN as shown in Fig.6(b).

The simulated results suggest that BM-nonlinearities-related sound level play an important role for fine representation of vowel formants fo the chopper units in the AVCN.

5 Conclusion

The functional model of VCN unit, that is able to simulate Ch S and Ch T type of chopper units in terms of PSTHs shape, discharge regularity, first-spike latency and phase-locking, is proposed. The computational model, that is able to reproduce rate-place representation of actual chopper units to the vowel /ε/, has been proposed.

The simulated results suggest that BM-nonlinearities-related sound level plays an important role for fine representation of vowel formants of the chopper units in the AVCN. This modeling approach can effectively be applied for a clear representation of speech in the auditory pathway.

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