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ELECTRICAL STIMULATION MODEL OF THE AUDITORY NERVE: STOCHASTIC RESPONSE CHARACTERISTICS

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INTRODUCTION

We are developing a neurophysiological model for electrical stimulation of the auditory nerve. Such a model will improve our ability to design electrode arrays and speech processing systems for cochlear implant recipients. In this brief report we will only consider the stochastic component of such a neural model. An understanding of the stochastic aspects of electrical excitation may be essential for accurate interpretation of patient performance with cochlear implants.

In this report we will consider an important relationship between the anatomy and the physiology of auditory nerve fibers. In particular, Verveen's stochastic model [5] allows us to predict the shape of a fiber's probability-of-firing function based on simple anatomical measurements.

THE STOCHASTIC NEURAL MODEL

Verveen [4,5] has postulated that neural membrane noise is generated by individual ions or packets of ions as they pass through channels in the semi-permeable membrane. The flow of ions can be described as the sum of two components: one representing the steady-state or average rate of flow (i.e. the DC component of the ionic currents), and the second representing the stochastic variations around the steady-state average. In large nodes of Ranvier, with presumably large numbers of independent conduction channels, the stochastic component of current flow will be relatively small when compared to the average current flow. [This is analogous to what occurs in standard signal averaging. As we increase the number of trials (analogous to increasing the number of conduction channels) the noise becomes less significant when compared to the average.] For very small nodes, the stochastic current becomes a very significant component of the total membrane current. This is particularly relevant because auditory nerve dendrites can be quite small.

Verveen has measured how the probability of discharge varies with stimulus intensity for a wide range of fiber diameters. For a large range of stimulus conditions, estimated discharge probability versus stimulus amplitude functions were well fit by integrated Gaussian functions. This finding is consistent with a model where Gaussian noise is added prior to an ideal threshold detector. The idealized threshold detector "generates" an action potential whenever the voltage at its input reaches or exceeds the threshold voltage. The RMS noise voltage V_{noise} and the threshold voltage V_{thr} completely determine how the probability of firing will vary with stimulus amplitude. Normalizing V_{noise} with respect to V_{thr} provides a realtive noise level measure R defined as:

$$R = V_{noise} / V_{thr}$$

Nodes with low normalized noise levels (small R) produce steep input-output functions.

Equivalently, the steepness of the integrated Gaussian function is simply determined by the ratio of the standard deviation of the threshold stimulus level to the mean threshold stimulus level.

$$R = \text{Std Deviation} / \text{Mean}$$

If the relative noise level R is small the node's input-output function will be relatively steep. Verveen [4] found that the steepness of the "best-fit" integrated Gaussian function was a strong function of the fiber's nodal surface area, expressed as a function of nodal diameter. For smaller diameter fibers, relatively large changes in stimulus amplitude were necessary to cause a given change in discharge probability. The value of R determines the steepness of the integrated Gaussian function. Verveen found the following relationship between fiber diameter D in microns and the relative noise level R:

$$R = 0.03\ D^{-0.8}$$

This equation was derived from measurements of invertebrate myelinated fibers having node diameters ranging from microns to hundreds of microns using single short-duration pulses.
We expand Verveen's equation to express nodal surface area in terms of nodal length and diameter and recompute the scaling constant for Verveen's original equation assuming 2.0 micron nodal

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lengths for the fibers originally studied by Verveen [3].

$$R = 0.052\ (L\ D)^{-0.8}$$

where L and D are in microns.

ANATOMY

Liberman and Oliver [2] measured the diameter and length of the nodes of Ranvier of Type I afferent neurons in the cat cochlea. These neurons are typically bipolar in shape with thin peripheral dendrites and thicker centrally-projecting axons. Anatomical data for these cat neurons are summarized in Table I.

PHYSIOLOGY "PREDICTED" FROM ANATOMY

These anatomical data were applied to our modified Verveen model to predict probability-of-firing characteristics for electrically stimulated primary afferents in the cat cochlea. Such predictions can be directly compared with the electrophysiological measurements of Javel et al [1]. Model predictions are presented in Table II. For the purpose of this paper, model predictions include estimates of the R ratios for the integrated Gaussian curves and estimates of the "dynamic ranges" of the nodes. "Dynamic range" is defined as the increase in stimulus amplitude required to cause the probability of discharge to increase from 0.1 to 0.9. Dynamic ranges are expressed in dB.

Recently, Javel et al. [1] recorded VIII nerve single unit responses to electrical stimulation in the cat cochlea. As expected, they found that discharge probability increased when they increased the amplitude of short biphasic pulse stimuli. The rate at which discharge probability increased with stimulus amplitude varied considerably across fibers. In some fibers, as little as a 1 dB increase in stimulus amplitude was required to cause the probability of discharge to increase from 0.1 to 0.9. Other fibers required as much as a 6 dB increase in stimulus amplitude to cause this same increase in discharge probability. "Dynamic ranges" of fibers were evenly distributed over this 1-6 dB range. In other words, there were about the same number of "1 dB fibers" as "3 dB fibers", as "6 dB fibers", etc.

DISCUSSION

Predicted dynamic ranges were nearly identical to those directly measured by Javel et al. [1] in the auditory nerve of cat. The agreement between model prediction and measurement is particularly remarkable considering that equations (1) and (2) were obtained from measurements using fibers that are quite different from those in the cat cochlea. Specifically, equations (1) and (2) were derived from measurements of invertebrate myelinated fibers ranging from microns to hundreds of microns.

In this brief report we have illustrated only one example of the predictive power of this stochastic excitation model. This model has proven useful in simulating psychometric functions, intensity discrimination and dynamic range functions.

TABLE I. CAT AUDITORY NEURON ANATOMICAL SUMMARY

	Central Axons (in microns)	Peripheral Dendrites (in microns)
Node Length	1.0	1.0
Node Diameter	0.7 - 2.25	0.1 - 0.7

TABLE II. PREDICTED PROBABILITY-OF-FIRING CHARACTERISTICS FOR CAT NEURONS

	Central Axons	Peripheral Dendrites
R	.027 - .07	.07 - .33
Steepness of I-O curve	steep	shallow
Dynamic Range (dB)	0.6 - 1.56	1.56 - 7.84

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