A MODEL OF THE PERIPHERAL AUDITORY SYSTEM - A CASE STUDY IN NEURAL MODELING*

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Perhaps my brief talk should be retitled -- "A model of the peripheral auditory system - a case study in neural modeling". I would like first to describe this model to you, comment briefly upon its properties, limitations, and some of the questions raised by it, and second to attempt to relate this model to other models of peripheral nerve and related structures and thus I hope to fulfill my responsibilities as a discussant at this session.

The purpose of the work to be described is to explicitly formalize and test a mechanistic model of the peripheral auditory system which has been implicitly stated in the physiological literature for some time. Furthermore, this same objective has constrained the structure of the model from the outset. That is to say, the approach to this problem was essentially synthetic - take the parts of the system that are as specifiable, assume a structure for those parts of the system that are as yet unspecifiable and put everything together and see what comes out. Of course, such an approach makes sense only if the results can be compared to data that are comprehensive, quantitative and available. The recent electrophysiological results of Kiang, are the data to which I shall refer throughout this talk. Data were obtained from anaesthetized cats, with the use of 3 molar, KCl-filled glass micropipette electrodes. These electrodes were placed in the VIIIth-nerve anatomically peripheral to its entry into the cochlear nucleus.

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A current view of the physiology of the peripheral auditory system (presented in a schematic form) is illustrated in the first slide:

> Sound enters the outer ear, impinges on the eardrum, and is transmitted through the middle-ear structures to the fluids of the cochlear or inner ear. The resulting fluid motion leads to a motion of the cochlear partition, which in turn results in forces on and/or movements of the auditory receptor (or hair) cells. The hair cells are thought to be transducer elements whose function is to produce local excitation of nearby VIIIth-nerve fibers. The spike potentials resulting from this excitation are transmitted to the central nervous system via the VIIIth-nerve.

A model of the peripheral auditory which explicitly encompasses some of these notions is shown in the next slide. The model is intended to relate the firing patterns of auditory nerve fibers to sound impinging on the ear. The "Mechanical System" represents the functional relation between an acoustic pressure input to the ear and a displacement of the cochlear partition and is assumed to be representable as a linear system.

The transfer function of this part of the system for a particular point along the cochlear partition is assumed to be given by the work of von Bekesy. The "Transducer is intended to represent the functional relation between the displacement of the cochlear partition at a point along its length and the output of a hair cell located at that point. The final constituent of the model is a stereotyped or idealized "Model Neuron. In this "Model Neuron", the output of the transducer is filtered ahd then summed with Gaussian noise. The noise is included to account for both the spontaneous activity and probabilistic response behavior characteristic of VIIIth-nerve fibers. The resultant sum of the filtered and transduced acoustic signal and the noise (called the membrane potential) are then compared with a threshold in the box labelled "C". If the threshold is exceeded, then a spike is defined as occurring, and the threshold is reset to some larger value, by the box labelled "R". This process is indicated schematically in the next slide. R_R is the resting threshold, R_M is the maximum threshold. When the membrane potential rises to exceed the threshold potential a spike occurs, and the threshold is reset to its maximum value, R_M. The threshold then decays to its resting value, R_R.

Let me mention in passing that the Model Neuron is an extension of the model proposed by Verveen and his collaborators to account for the fluctuations in excitability of sciatic nerve fibers of frogs - a phenomenon investigated originally by Pecher and later by Verveen.

In summary, the assumptions of the model of the peripheral auditory system, here proposed, are:

(1) The mechanical part of the peripheral auditory system is assumed to be representable by a linear system.

(2) A point-to-point relation between the displacement of the cochlear partition and neural excitation is assumed. The transduction process is assumed to be memoryless.

(3) The process of neural excitation is represented by a simple model neuron which is probabilistic and contains threshold and refractory properties.

(4) The effects of activity in efferent pathways on the activity of afferent VIIIth-nerve fibers is ignored. No mechanism to account for active, neural inhibition is included in the model.

It was clear at the outset of this investigation that a model so constituted presented some rather imposing mathematical difficulties (we shall return to these matters a little later). As a consequence, the model has been simulated on the TX-2 digital computer at Lincoln Laboratory, M.I.T., and statistics of the spontaneous activity and response of the model to a variety of acoustic stimuli have been obtained and compared with the VIIIth-nerve data obtained by Kiang.

Rather than presenting a comparative study of the results produced by the model with the fiber data, let me summarize a few of the stimulus paradigms for which such comparisions have been made, discuss further the "goodness of fit" of the model and finally return to a more detached vantage point to inspect what I, at least, have learned from this endeavor.

First, the spontaneous activity generated by this model agrees substantially with the VIIIth-nerve data. Histograms of inter-event intervals of spontaneous activity from both sources show the features illustrated in the next slide. These data come from the VIIIth-nerve fiber of a cat. The histograms all show exponential tails - that is, the histograms can be described by exponential curves in the limit of large intervals. Refractory effects appear to limit the occurrence of short intervals. Furthermore, by adjusting the bandwidth of the noise in the model to exceed approximately 2 to 5 kc, successive inter-event intervals appear to be statistically independent. This property appears to hold for successive inter-spike intervals of VIIIth-nerve data.

Second, many features of the response of the model to simulated acoustic clicks are quite similar to the fiber data. The next slide shows the click response of the model. The dotted curves labelled $+F_3(t)$ and $-F_3(t)$ are the predictd displacements of the cochlear partition at a point along its length for rarefaction and condensation clicks applied to the ear. In this particular case, the locus of this response corresponds to a point along the cochlear partition that responds maximally to a frequency of 5 500 cps of sinusoidal stimulation. This frequency is referred to as the C.F. or characteristic frequency. The cochlear partition responses shown in the slide were computed by Flanagan and were derived from the data of von Bekesy. Below these dotted curves are the corresponding PST (or Post-stimulus-time histograms) computed from the response of the model. These PST-histograms are histograms of the times of occurrence of spike potentials following the onset of a stimulus. It can be seen that the peaks in the PST-histograms correspond to the peaks of the positive excursions of the predicted displacements of the cochlear partition. It is clear that the time interval between peaks in the PST-histograms generated by the model is the reciprocal of the characteristic frequency. The next slide shows data obtained by Kiang from several different VIIIth-nerve fibers together with the characteristic frequencies of each fiber.

The slide is intended to exhibit the relation of the click response to the characteristic frequency of an VIIIth-nerve fiber. Intensity of stimulation has been held constant for all these data.

There is clearly no time to discuss in any detail the comparision of the model and fiber data for various parameters of acoustic click stimuli. Let me simply summarize in the following way: For several reasons the assumption that a <u>linear</u>, memoryless transducer function could represent the action of the receptor cells has led to results which are incompatible with the VIIIth-nerve data of Kiang. The wave shapes of the PST-histograms of the fiber data could not be reproduced for all intensity and rate of stimuli even to the satisfication of a severly myopic person. A <u>non-linear</u>, saturating transducer function, however, improves the fit of the model. Although the incorporation of such an assumption materially improves the goodness of fit of the click data some discrepancies still remain. These discrepancies all indicate that the transducer function of the receptor cells can probably not be represented by a memoryless function. Further work using sinusoidal stimuli have also born out this thought.

challenged and modified in the light of this new evidence. Those compnents that remain valid representations of the empirical data can be left intact. Clearly, such a model can also guide the acquisition of further empirical data by revealing the inadequacies of the model in a precise manner.

It is unfortunate that the structure of the model of the peripheral auditory system proposed here and also the model proposed by Verveen to account for his data leads to serious mathematical difficulties. This is fundamentally a consequence of the assumed probabilistic structure. This structure is most certainly inappropriate for answering all questions about the peripheral auditory system, but I do not think it inappropriate for testing our understanding of the interrelations of the components of the peripheral system. The mathematical difficulties stem directly from the complexities of deriving distributions of successive crossings of a threshold by a noise process. In some cases, the analytic problems can be temporarily circumvented but this circumvention often leaves risidual problems that must eventually be faced.

Computer simulations offer a new dimension of flexibility in studying such problems. The cost of this flexibility may be many-fold. Most certainly economy of description is to some extent sacrificed as is the elegence that could come from an analytically tractable yet physiologically meaningful representation.

In summary of the results of the model work here discussed: the spontaneous activity, response to acoustic clicks, tones and tone bursts have been studied for a class of mechanistic models that consist of a linear mechanical system, a non-linear, memoryless transducer and a model neuron. Results generated by this model fit the VIIIth-nerve data quantitatively along some stimulus dimensions, semi-quantitatively along some dimensions and only in a very qualitative sense along other dimensions.

My intent in this presentation has been to focus more on the structure of the model than on the results produced by it. This structure is I believe consistent in the broadest sense with other models proposed recently for peripheral nerve and associated receptor structures. At the heart of this model is the representation of the excitation process which must occur in the vicinity of the hair cell-neuron junction. This is unfortunately also the locus of our greatest ignorance. However, in a mechanistic model such as here proposed, this component can be manipulated and studied somewhat independently of other components. Furthermore, the components of such a model are at least in principle independently verifiable. As more of the structure of the system is empirically revealed the model can constantly be reviewed and its components