A MODEL OF THE PERIPHERAL AUDITORY SYSTEM RESPONDING TO LOW-FREQUENCY TONES

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ABSTRACT A model of the peripheral auditory system responding to low-frequency tone stimulation is given. The model is of the type previously introduced by Weiss (1966). It includes three interconnected parts: a linear model of the ear's mechanical system, a model of the cochlear transducer, and a stochastic model of an auditory nerve fiber. The output of the model accurately mimics many characteristics of the output of some auditory nerve neurons responding to sinusoidal stimuli but is unable to successfully match all reported aspects of data obtained from other of these neurons. Characteristics of the model neurons are discussed.

INTRODUCTION

A model of the peripheral auditory system responding to various stimuli has been proposed by Weiss (1966). Output from this model was obtained under conditions of no stimulation (spontaneous activity) as well as in response to sinusoidal and pulse stimuli. The statistical character of the model's spontaneous activity and click-driven activity agreed fairly well with similar data obtained from cat auditory nerve fibers by Kiang (1965). The sinusoidally driven output of the model was not, however, closely compared with similar neural data. More data on the responses of mammalian auditory nerve fibers to sinusoidal stimuli have just become available (Rose et al., 1967), and the ability of the Weiss type of model to mimic such data can now be tested. This report concerns just such a comparison between neural and model data.

METHODS

The Weiss (1966) type of model of the peripheral auditory system was utilized exclusively in this study. This model is composed of three interconnected parts: a mechanical system model, a transducer model, and a model neuron. The model of the mechanical system has as its input the applied acoustic wave form and gives as its output the vertical displacement of a point on the basilar membrane. The model transducer in turn transforms this vertical membrane displacement into a voltage. This voltage forms the input to the model neuron, whose output is a train of pulses. Briefly speaking, this type of model assumes that the motion of a single point of the basilar membrane is translated into one component of an auditory nerve fiber's membrane potential.

The mechanical system is represented in this study by a linear model. Therefore, its output for sinusoidal input is a sinusoid of the same frequency as the input, but generally differing from it both in phase and amplitude. At any one frequency, no further requirements are placed on the mechanical system model; it is a more general one than that used by Weiss (1966).

The transducer is represented in the present study initially by a linear system. No further restrictions are placed on it at the present time. Hence, in the first part of this paper, the input voltage to the model neuron is sinusoidal for a sinusoidal acoustic pressure wave. A nonlinear form of the transducer will be introduced below.

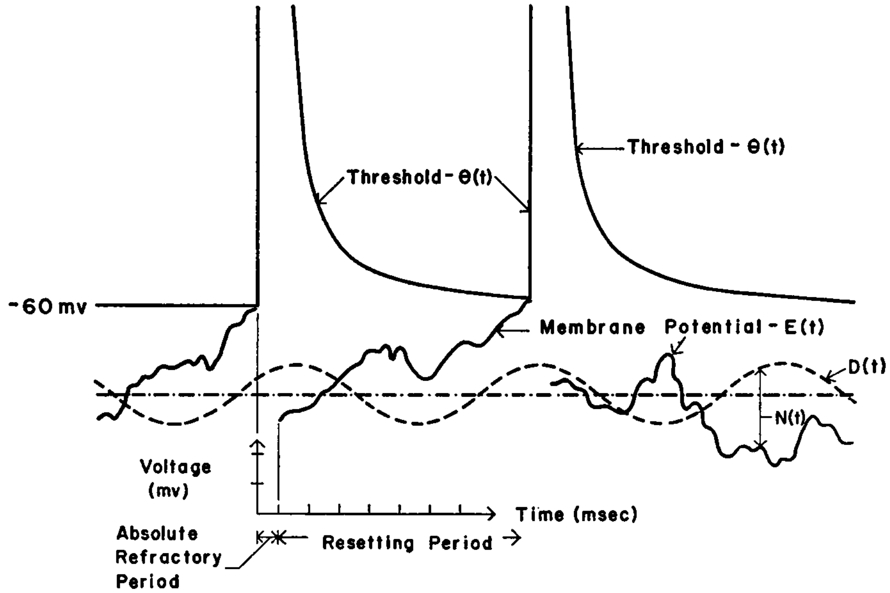

FIGURE 1 Diagram illustrating the characteristics of the neuron model used in this paper. The threshold function $\theta(t)$ is given by equation 1 with $\tau = 5$ msec.

A recently developed neural model (Geisler and Goldberg, 1966), closely related to that used by Weiss (1966), was utilized as the final stage. This model is presented schematically in Fig. 1. Two wave forms are represented in the figure: the threshold and membrane potentials. The membrane potential is composed of two independent components, a deterministic voltage $D(t)$ and an additive random voltage $N(t)$ having a gaussian amplitude distribution of zero mean and an exponential autocorrelation function (low-pass noise). Whenever the membrane potential exceeds the threshold voltage, the model discharges. After the occurrence of an impulse, the threshold is infinite for 700 μsec and then gradually returns to its resting value according to the equation

$$\begin{aligned}\theta(t) &= -60 + \exp\left[-(t - R)/\tau\right]/\{1 - \exp\left[-(t - R)/\tau\right]\}\,mv,\\ t &\geq R = 0.7\text{ msec},\end{aligned} \tag{1}$$

where R is the absolute refractory period and τ is the resetting time constant. It should be noted that the individual magnitudes of the cell potential and the threshold potential are not important, but the difference between them is crucial: this difference determines how much voltage must be added to the cell potential in order to produce a discharge. Hence, the threshold potential is not necessarily meant to represent the actual firing threshold of a neuron, but is simply a term with which to handle all of the factors (e.g. relative refractoriness, afterpotentials, and the buildup of synaptic excitation) that are involved in the resetting of a neuron to its steady-state condition. It is clear that these resetting processes will not, in general, be exactly represented by the single wave form, but, as a first approximation, it is convenient to so characterize them. The function $D(t)$ is composed of a DC level, held fixed during the modeling of any one neuron, and of the transducer's output, the "drive," which represents the cell's excitation resulting from sinusoidal acoustic stimulation.

The wave forms of the neuron part of the model were simulated on the Control Data Corporation 3600 digital computer of the University of Wisconsin Computing Center in the manner already described (Geisler and Goldberg, 1966). One improvement in technique was introduced: gaussian random numbers were generated by the inverse method (Muller, 1958) instead of the relatively slow and inaccurate method of summing uniform deviates (Muller, 1959). The particular phase angle of the model neuron's input voltage was assigned arbitrarily. This choice corresponds to specifying that the model transducer's input came from motion of an arbitrarily picked point on the basilar membrane. The amplitude scale of the model neuron's input voltage was also picked arbitrarily; this choice corresponds to assigning an arbitrary amplitude gain to the transducer model.

RESULTS

Different auditory neurons studied by Rose et al. (1967) were mimicked by the model neuron. Fig. 2 shows output generated by the model neuron in imitation of neuron 65-48-1 (Rose et al., 1967). The DC level of the neuron model's membrane potential was set so that the rate of spontaneous activity was 24 discharges per second, approximately the same spontaneous rate observed in the indicated neural unit, and sinusoidal drives of various frequencies were applied to the model. For each frequency, the amplitude of the drive was adjusted so that the firing rate of the model neuron was approximately that of the neural unit when stimulated at or near that frequency at an intensity level of 80 db SPL. This arbitrary adjustment of amplitudes is equivalent to specifying the relative amplitude of displacement of the pertinent point on the cochlear partition as a function of frequency.

For each frequency, the interspike interval histogram is composed of many separate clusters: the model neuron has preferred values of firing interval. These preferred values are due to the fact that the model neuron has a strong preference for firing only on one half of the cycle (see below). Hence, as illustrated in Fig. 1, interspike intervals tend to be integer multiples of the stimulus period. Therefore, the mode of each cluster, except for the first in each histogram, lies near an integer multiple of the stimulus period. For frequencies between 800 and 1200 Hz, the modal value of the first cluster lies near the value of the stimulus period, while for frequencies above 1200 Hz, the first cluster's modal value is greater than the period. The latter effect is due to the fact that the refractory and resetting properties of the model

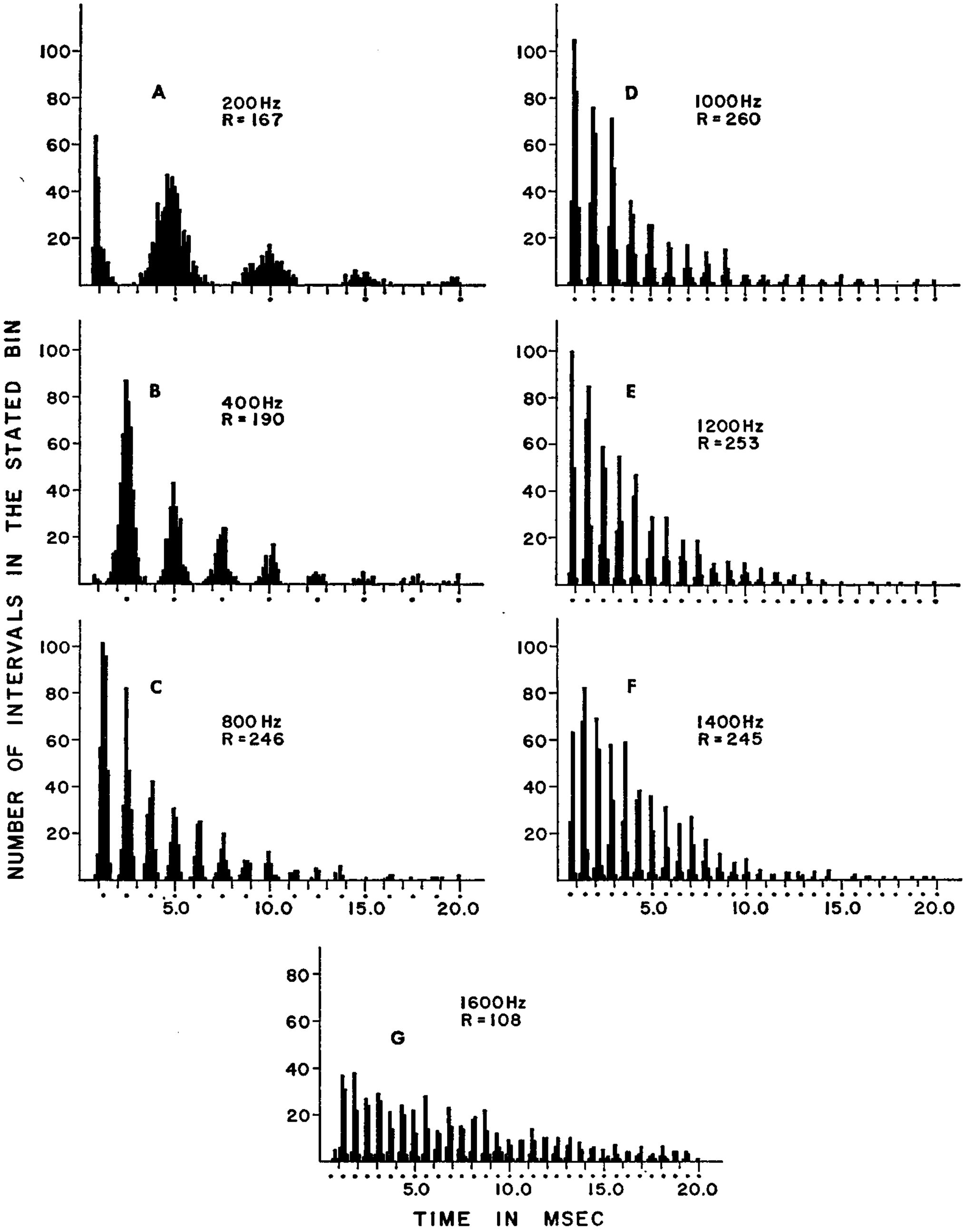

FIGURE 2 Histograms of interspike intervals generated by the model neuron when sinusoidal drive of different frequencies was used. *Abscissa:* time in milliseconds; each bin = 125 μsec. Dots below abscissa indicate integer multiples of the period of the stimulus frequency employed. *Ordinate:* number of interspike intervals in the bin. Each graph contains 1000 consecutive intervals. Stimulus frequency and average discharge rate, R (in discharges per second), are indicated on each graph. For each of graphs B–G the amplitude of the sinusoidal drive used was that which generated a discharge rate comparable to the discharge rate of neuron 65-48-1 at that frequency for 80 db SPL (Rose et al., 1967, Fig. 1); in graph A, the amplitude of the sinusoidal drive was the same as in graph B. Model parameters: τ = 80 μsec, Δt (sampling interval) = 31.25 μsec, DC cell potential = −62.85 mvolt, σ_n = 1.0 mvolt, f_1 = 500 Hz. Spontaneous discharge rate was 24 discharges per sec.

make it very unlikely that the model will fire within 800 μsec of a previous firing. Hence a cluster with a mode less than 714 μsec (the period of a 1400 Hz sinusoid) is practically impossible. For frequencies of 200 and 400 Hz, all of the intervals in the first cluster have a value of less than one half a stimulus period and hence are due to multiple firings during a single half-cycle of the stimulus. In all respects, the data in Fig. 2 agree very closely with similar data obtained from neural unit 65-48-1 (Rose et al., 1967, Fig. 1).

Table I presents the estimates of the conditional probabilities of discharge[1] obtained from the data shown in Fig. 2. Each number in the table is the fractional number of times that an interval has a value falling within the stated cluster, provided it was known that the interval would not fall in a preceding cluster. (For low frequencies, the first cluster, corresponding to second firings during a single half-cycle, was discarded.) Each number, therefore, is an estimate of the probability that the model neuron will be triggered by a stimulus cycle, provided that the last firing occurred n cycles before. Comparable numbers obtained from the output of unit 65-48-1 (Rose et al., 1967, Table I) are shown in the table in parentheses. Notice that the estimated conditional probabilities for the neural and model data are very similar. For any one frequency of stimulation this estimate is approximately constant for all cycles except the first. This constant value is closely estimated by the average number of spikes per cycle, determined over the entire stimulus period, and decreases consistently as the period shortens. Note, however, that in the neural data there is a tendency for the estimated conditional probabilities of the second cycle to be slightly lower than those of the following cycles. Although a linear transducer model was used in the creation of the data presented in Fig. 2 and Table I, very similar results were produced by the model using the nonlinear form of the transducer introduced below.

The important parameters of the neuron model used in the generation of the data summarized in Fig. 2 and Table I are the standard deviation (σ_n) of the gaussian process, the threshold resetting time constant (τ), and the half-power frequency (f_1) of the low-pass noise. The standard deviation of the noise was arbitrarily set at 1 mv. This choice is not considered restrictive because previous work (Geisler and Goldberg, 1966) has intimated that the ratio of τ/σ_n is important rather than the numerical values of each variable. The specific value of τ used to generate the data so far presented is 80 μsec. Hence, the resetting period, which started 700 μsec after each firing, was essentially completed after another 240 μsec (3 time constants) had elapsed: the model was, for practical purposes, completely reset 1 msec after a firing. Larger values of τ prolong the resetting period, decreasing the number of short intervals that occur and causing a shrinking in the size of the initial clusters of an interspike interval histogram. The value of τ needed to mimic the various squirrel-

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[1] This conditional probability is sometimes referred to as the hazard function (Perkel, Gerstein, and Moore, 1967).

TABLE I

ESTIMATED CONDITIONAL PROBABILITIES OF DISCHARGE

Each number is the estimated probability that a unit which discharged at time zero will discharge again in response to the *n*th cycle following the time zero discharge, provided that the intervening ($n - 1$) cycles have been free of discharges. Last column on right: quotient of number of spikes discharged divided by number of cycles delivered. *Model data* were obtained from Fig. 2. Probability not computed if the remaining population was smaller than 100 intervals. Intervals attributed to second discharges during a single stimulus half-cycle (Figs. 2 *A* and 2 *B*) were ignored in all calculations. *Neural data* (shown in parentheses) were obtained from Table I of Rose et al. (1967).

Frequency (Hz)	Rate (spikes per second)	Cycle										Spikes / Cycle
		1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
200	167	0.68	0.71	—	—	—	—	—	—	—	—	0.69
400 (412)	190 (189)	0.48 (0.42)	0.45 (0.47)	0.48 (0.48)	0.50 (0.56)	— (0.58)	— —	— —	— —	— —	— —	0.47 (0.46)
800 (900)	246 (249)	0.32 (0.23)	0.32 (0.27)	0.28 (0.27)	0.30 (0.31)	0.29 (0.31)	0.33 (0.33)	— (0.37)	— (0.32)	— (0.28)	— —	0.31 (0.28)
1000	260 (259)	0.26 (0.22)	0.27 (0.26)	0.30 (0.27)	0.26 (0.26)	0.27 (0.27)	0.22 (0.28)	0.22 (0.29)	0.26 (0.31)	— (0.29)	— (0.32)	0.26 (0.26)
1200	253 (256)	0.16 (0.15)	0.23 (0.19)	0.21 (0.20)	0.21 (0.25)	0.23 (0.25)	0.21 (0.22)	0.21 (0.22)	0.22 (0.32)	0.26 (0.28)	0.20 (0.26)	0.21 (0.21)
1400	246 (242)	0.09 (0.11)	0.18 (0.16)	0.19 (0.17)	0.18 (0.18)	0.20 (0.19)	0.20 (0.21)	0.19 (0.18)	0.20 (0.21)	0.18 (0.21)	0.28 (0.19)	0.18 (0.17)
1600	1C8 (108)	0.01 (0.03)	0.08 (0.05)	0.07 (0.05)	0.07 (0.07)	0.08 (0.06)	0.05 (0.07)	0.07 (0.08)	0.06 (0.06)	0.07 (0.07)	0.05 (0.05)	0.07 (0.07)

monkey auditory nerve fibers reported by Rose et al. (1967) would range from 80 μsec up towards 0.3 msec. The half-power frequency (f_1) of the noise used to generate these data was 500 Hz. A half-power frequency as high as 1000 Hz could have been used to generate data similar to those of Fig. 2, but half-power frequencies as low as 31.25 Hz were found to cause a gross swelling of the initial cluster of an interspike interval histogram.

For sinusoidal stimuli, the dynamic range of the auditory neurons studied by Rose et al. (1967) generally extended over an intensity range of 40 to 50 db. Over this dynamic range, the effectiveness of the stimuli, judged either by discharge rate or by average number of spikes occurring per cycle, was approximately a logarithmic function of stimulus strength. Above and below the dynamic range the firing rate was essentially constant. Any satisfactory model of these neurons must exhibit similar behavior. Using the linear transducer, dynamic ranges of approximately 30 db were commonly obtained by the model, regardless of parameter values. It was very difficult, however, to extend the dynamic range much beyond this 30 db. Of even more importance was the finding that the model's discharge rate increased exponentially with the logarithm of the sine wave's amplitude rather than linearly (cf. Weiss, 1966, Fig. 20). Clearly the model in the form presented so far is unsatisfactory.

A discharge rate which increases linearly with the logarithm of the amplitude is approximately obtained when the transducer model is changed. If the sinusoidal input to the transducer is specified by $S(t)$ and its output by $R(t)$, the particular form chosen for the transducer model is

$$R(t) = \begin{cases} 0, & |S(t)| < m \\ A[S(t)/|S(t)|]\log_{10}[|S(t)|/m], & m < |S(t)| < M \\ A[S(t)/|S(t)|]\log_{10}(M/m), & |S(t)| > M \end{cases} \quad (2)$$

where A, m, and M are arbitrary constants. Notice that the transducer is logarithmic in its dynamic range. This particular form of the transducer was carefully chosen as representative of the small class of fixed-parameter, single-valued transducers that cause the model neuron to discharge at a rate which is approximately a logarithmic function of the amplitude of sinusoidal stimulation. The output of the transducer is set to zero for inputs less than m simply to avoid log functions with arguments less than unity. In order to mimic the discharge-rate plateau reached by auditory neurons for high intensities of stimulation the absolute value of the transducer's output is limited to a maximum value, $A \cdot \log_{10}(M/m)$.

Fig. 3 shows data obtained from the modified model presented along with data taken from auditory neuron 66-86-17 (Rose et al., 1967, Fig. 10). The data are presented in the form of "folded" histograms (Rose et al., 1967) in which each time bin contains a bar whose height is the percentage of discharges which were synchronized to that particular part of the stimulus cycle. The numbers shown in Fig. 3 refer to the model's data and in all respects are very close approximations to the comparable numbers obtained from the neural data. S, the synchronization coef-

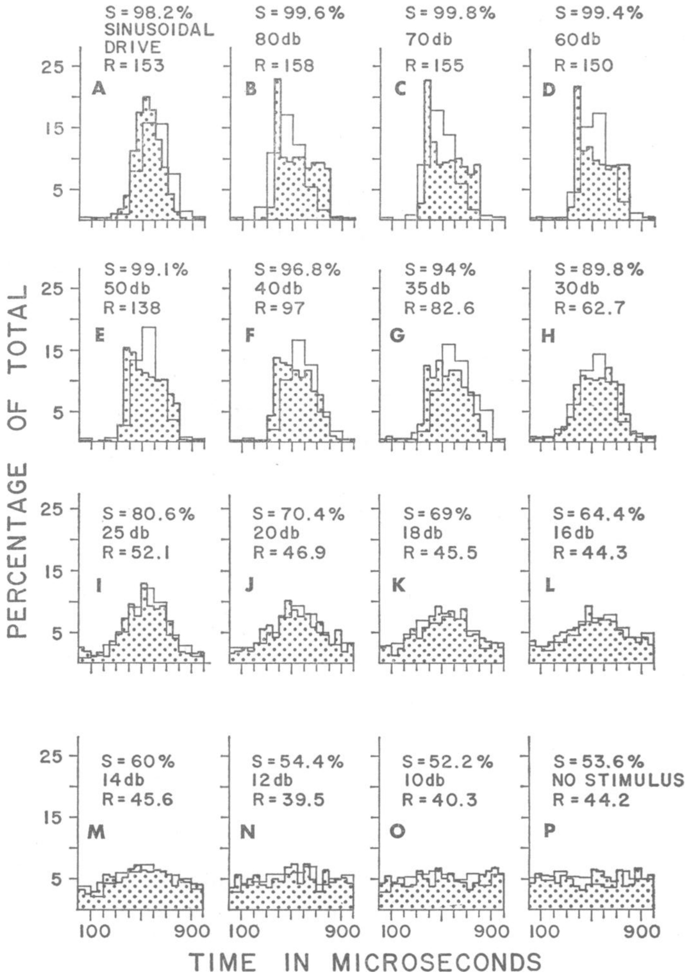

FIGURE 3 "Folded" histograms (dotted) for the model neuron superimposed on comparable folded histograms (clear) for auditory nerve fiber 66-86-17. Each discharge is timed in relation to a specified point in the wave shape of the particular stimulus cycle during which the discharge occurred. *Abscissa:* time in microseconds; each bin = 50 μsec. *Ordinate:* percentage of discharges in each bin. Origin of each folded histogram is arbitrarily related to stimulus wave form, but it is the same in each graph. *Model data:* the data shown in graphs B–P were generated by a 1000 Hz sine wave applied to the logarithmic transducer of equation 2, with $A = 0.44$ mv, $m = 0.042$ mv, and $M = 4.45$ mv. Stimulus amplitude (re 0.0158 mv) is shown on each graph. The data in graph A were generated with 1000 Hz sinusoidal drive (i.e. logarithmic transducer removed) of an arbitrarily set amplitude. Synchronization coefficient S and average discharge rate R (in discharges per second) are shown on each graph. Graphs A–H each contain 1000 consecutive intervals; graphs I-P each contain 500 consecutive intervals. Model parameters: $\tau = 80$ μsec, $\Delta t = 50$ μsec, DC cell potential = -62.6 mv, $\sigma_n = 1.0$ mv, $f_1 = 500$ Hz. *Neural Data:* copied (rescaled) directly from Rose et al. (1967, Fig. 10). Stimulus frequency was 1000 Hz. Intensity (re 0.0002 dyne/cm^2) is the same as the model's for all graphs except A; intensity for graph A is 90 db.

ficient, is the percentage of spikes occurring during the most effective half of the stimulating cycle, the so-called "major half cycle" (cf. Rose et al., 1967). For each intensity below 30 db (Fig. 3 *H*), there is close agreement between the folded histograms derived from the model and from the neuron. For higher intensities, the mode and shape of the folded histograms derived from the model's data change considerably and can no longer be considered good imitations of the neural data. This change in the model data is due to the flattening and clipping that the transducer model imposes on large-amplitude signals. For the highest intensities, extreme clipping occurs and the drive on the model cell becomes a square wave. In contrast to the model's data, the shape of the folded histograms obtained from the neuron does not change appreciably at the higher intensities. Fig. 3 *A* shows data obtained from the model using the linear form of the transducer model as well as data obtained from the neuron during high-intensity stimulation. Notice the fairly good agreement between the two histograms. Similarly, a folded histogram that closely matches any *one* of the neural histograms shown in Fig. 3 could be generated by the model using a linear transducer model with suitable amplitude gain.

Fig. 4 shows data obtained from neuron 65-340-5 (Rose et al., 1967, Fig. 8) and from the model using the nonlinear form of the transducer. Although the neural and model data presented in any one graph were obtained for the same stimulus intensity and at similar discharge rates, the histogram shapes and synchronization coefficients match poorly at all but the lowest stimulus intensity level. At all intensities the neuron produced an appreciable number of firings which occurred outside of the major half cycle, and the mode of the histograms was not constant with intensity. Hence, the model is unable to mimic the neural data, even when using a linear transducer model with adjustable gain (Fig. 4 *A*). However, any *one* neural histogram in Fig. 4 could be closely approximated by output from the model using a linear transducer model, if arbitrary variations with intensity were permitted in its phase shift and also in the DC component of the cell potential.

DISCUSSION

Evaluation of the Model. The data presented in Figs. 2 and 3 show that the output of the model has many of the characteristics of the output of some auditory nerve fibers responding to sinusoidal stimulation. Like an auditory nerve fiber, the model gives discharges which are measurably phase-locked to the stimulus and which have, except for the first millisecond or so following a discharge, an essentially constant estimated conditional probability of discharge. Moreover, the discharge rate is approximately a logarithmic function of intensity over the dynamic range, and discharges do not occur more than once on the same stimulus cycle for frequencies above 400 Hz. However, it is evident that the model has shortcomings: it is unable to generate data at the higher intensities with realistic folded histograms.

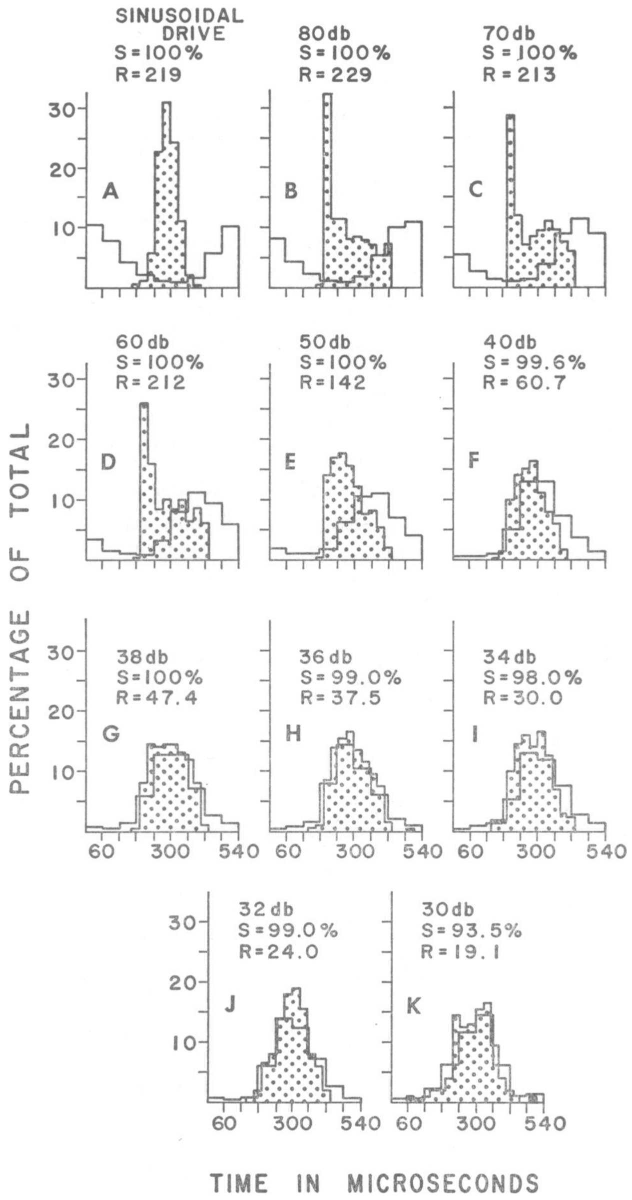

FIGURE 4 Folded histograms (dotted) for the model neuron superimposed on comparable folded histograms (clear) for auditory neuron 65–340-5. *Abscissa:* time in microseconds; each bin = 27 μsec. *Ordinate:* percentage of discharges in each bin. Origin of folded histograms arbitrarily related to stimulus wave form, but it is the same in each graph. *Model data:* the data shown in graphs B–K were generated by a 1852 Hz sinusoid applied to the logarithmic transducer of equation 2, with $A = 0.9$ mv, $m = 0.095$ mv, and $M = 6.5$ mv. Stimulus intensity (re 0.0158 mv) is shown on each graph. The data in graph A were generated with 1852 Hz sinusoidal drive of an arbitrarily set amplitude. Synchronization coefficient S and average rate R (in discharges per second) are shown on each graph. Graphs A–G each contain 500 consecutive intervals; graphs H–K each contain 200 consecutive intervals. Model parameters: $\tau = 80$ μsec, $\Delta t = 27$ μsec, DC cell potential $= -63.3$ mv, $\sigma_n = 1.0$ mv, $f_1 = 500$ Hz. Spontaneous discharge rate was very low. *Neural Data:* copied (rescaled) directly from Rose et al. (1967, Fig. 8). Stimulus frequency was 1852 Hz. Intensity (re 0.0002 dyne/cm^2) is the same as the model's for all graphs except A; intensity for graph A is 90 db.

The logarithmic form of the transducer model was needed in order to achieve the proper relation between discharge rate and stimulus intensity, but the transducer model distorted the sinusoidal wave form and caused the flattened folded histograms. If the nonlinear transducer model had been followed by a linear filter which passed only the fundamental frequency of the model transducer's output, the drive on the model neuron would have been sinusoidal at all intensities. Hence the folded histograms of the model data produced at any intensity of stimulation would have been properly shaped. The output of the model in this case would have closely mimicked that of neuron 66-86-17 in all reported characteristics (Fig. 3). However, the incorporation of such a filter into the model would not enable it to successfully duplicate the output of neuron 65-340-5 (Fig. 4): a phase shift dependent on intensity would also have had to be introduced, as well as changes in the cell's DC potential. It must, therefore, be concluded that the model incorporating the transducers and filters presented here produces realistic results for some, but not all, auditory nerve fibers responding to tones. Moreover, it seems doubtful that the use of any fixed-parameter transducers and filters would enable the model neuron to successfully mimic all reported aspects of all first-order auditory neurons responding to sinusoidal stimuli. Gray (1966), using a more general Weiss-type model than that presented here, came to a similar conclusion. The search for better models is under way.

The final form of the model presented in this paper is remarkably similar to that of Weiss (1966). Some similarity between our two models is to be expected because they are of the same type and utilize the same basic model of the neuron. However, it is striking that in each case an S-shaped nonlinear transducer function had to be included. Hence, Weiss's model (1966) responding to sinusoidal stimuli is practically the same as the model presented in this paper, and the ability of his model to respond realistically to sinusoidal stimuli can be fairly judged by the model data presented here. Furthermore, the model used in this paper is somewhat more general than that used by Weiss (1966): he assumed an explicit transfer function for the mechanical system model, but the only constraint on it in this paper, at any one frequency, is that it be linear. Hence, any shortcomings of a Weiss-type model (1966) that could be attributed to shortcomings in the explicit form of the mechanical system model (cf. Klatt and Peterson, 1966) are avoided in the model presented here.

In spite of the shortcomings of the model presented in this paper, the good agreement between its output and neural data such as that shown in Fig. 2 suggests that the concept of a short neural resetting time is sound. A short resetting time is also suggested by a comparison of the neuron model and of auditory nerve fibers firing spontaneously. When no stimuli are applied, the model's output has an estimated conditional probability of discharge that is practically constant after the first or second millisecond following a discharge and hence forms interval histograms that have a mode between 1 and 2 msec. By comparison, cat auditory nerve fibers discharging spontaneously were found to have an estimated conditional probability of discharge that also approached a constant value after a discharge, but recovery took longer, sometimes as long as 25 msec (Gray, 1966, Fig. 11). However, these estimated conditional probabilities were typically largely recovered within 2 msec of a discharge (Gray, 1966, Fig. 11), and consequently the mode of the interspike interval histograms usually occurred between 4 and 7 msec (Kiang, 1965). A limited amount of spontaneously generated data (unpublished) obtained from squirrel-monkey auditory nerve fibers 65-48-1 and 66-86-17 show similar characteristics. Hence, the major part of the resetting process for these mammalian auditory nerve fibers was generally completed within 2 msec of a discharge and can be characterized by a time constant no larger than 0.5 msec. A second, slower resetting process of relatively minor magnitude would have to be included in the neuron model for it to mimic accurately the typical spontaneously occurring activity. The need for inclusion of a small, second resetting process is also suggested by the squirrel-monkey neural data of Table I: the estimated conditional probabilities listed there do not quite attain their final values by the end of the model neuron's resetting period (i.e. 1 msec after a discharge), particularly at the low frequencies. A second resetting process was not in fact included in the model because this process would be relatively small and of much less importance than the faster one in determining the temporal course of the conditional probabilities of discharge of the model neuron. Weiss (1966) also found a rapid resetting process to be appropriate for modeling auditory nerve fibers: although he postulated a different resetting function, he used time constants of 0.3 and 1.0 msec.

Characteristics of a Group of Similarly Excited Model Neurons. The discussion above indicates that Weiss-type models of auditory nerve fibers responding to sinusoidal stimulation, to click stimuli, or to no stimuli at all, include resetting processes characterized by a time constant equal to or less than 1.0 msec. As a consequence, the likelihood of the model cell discharging is controlled almost solely by the stimuli applied to it, as long as at least 3 msec has occurred since the last discharge. Moreover, the model transducer's characteristics limit the drive on the model neuron to such a degree that, regardless of stimulus intensity, we can assume that a discharge will not occur on every peak of basilar membrane motion. If, now, we imagine looking at the summed output of a group of such model neurons, all receiving their drive from the same spot in the low-frequency region of a model cochlea, we could reconstruct with good fidelity the motion of that basilar membrane point in the excitatory direction by the following technique. The presence of more discharges than expected for spontaneous firings within a small time period (e.g. 100 μsec) would indicate that the basilar membrane had moved in the excitatory direction. And the actual number of discharges occurring in that time period would be a reflection of the magnitude of the displacement. Likewise, the number of discharges occurring in the next increment of time would indicate the magnitude of excitatory displacement for that period, and so on. At any one instant of time some model neurons might be resetting, but, because it would be practically impossible that all of the model neurons would have discharged within the past 3 msec, there would almost always be some model neurons in the reset state. In fact, for a very wide range of stimulus conditions, the relative number of model neurons resetting at any one moment would be small. Hence, almost all of the time, most of the model neurons would be in the reset state. The summed output of the model neurons would, therefore, generally be determined by the stimulus alone and so would be a faithful reflection, moment by moment, of the excitatory motion of the basilar membrane point. Whether or not such processing actually occurs in the mammalian nervous system is, of course, not known, but these considerations do suggest that sometimes the summated discharges of a group of similar cells is significant, rather than any one cell's output.

General Characteristics of the Model Neuron. The chief characteristic of the model auditory nerve neurons which enables such an easily calculated reflection of the transducer's displacement is the rapid resetting process. Longer resetting processes would mean that more model neurons might be resetting at any one instant. Hence, the past history of the model neurons would have more influence on the number discharging to any one basilar membrane excursion. For long enough values of τ, both the resetting and excitatory processes would have to be considered in interpreting the summed discharges, and a faithful reconstruction of the basilar membrane's motion would become much more difficult to achieve. Hence, rapid resetting processes seem advantageous for neurons which must respond to rapidly varying stimuli.

On the other hand, the model neurons having short resetting times respond to DC stimulation with a very irregular discharge. For instance, a model neuron with a resetting time constant of 1 msec responds to DC drive with a train of impulses characterized by a standard deviation of intervals that is almost as large as the mean interval. Generally speaking, the larger the time constant, the smaller is the standard deviation at a particular discharge rate (Geisler and Goldberg, 1966). Hence, if the mean discharge rate of the responses to DC drive were an important parameter to estimate, we would choose model neurons with long resetting time constants to carry the messages. The regularity of their discharge would make it very easy to obtain an accurate estimate of the average interval, and hence the average rate.

As an example of sensory neurons displaying these latter characteristics, let us consider the neurons arising from mechanoreceptive corpuscles studied by Werner and Mountcastle (1965). After an initial onset response, these neurons typically respond to a constant deformation with evenly spaced discharges. Hence, the average interspike interval can be closely estimated after observing only a relatively few discharges. This temporal regularity of discharge, coupled with a discharge rate which increases monotonically with stimulus intensity, makes these neurons well adapted for signaling the intensity of a constant deformation. On the basis of comparing plots of mean interval vs. standard deviation of intervals, these neurons can be fairly accurately represented by model neurons having resetting time constants ranging from approximately 15 to 100 msec (cf. Geisler and Goldberg, 1966). These time-constant values are quite compatible with the 60 msec resetting period observed in a neuron of this type following a discharge evoked by an applied electrical pulse (Tapper, 1964). By contrast, these mechanoreceptor fibers do not seem well adapted for carrying accurate information about rapidly changing stimulus wave forms. Not only is there the long lasting increase in threshold following a single firing, but the influence on the skin of stimulation has been observed to continue for as long as 2 sec after its termination (Werner and Mountcastle, 1965). These neurons could be expected to have the same type of difficulties encoding rapidly varying stimuli of small amplitude as do regularly discharging crustacean stretch receptors (Borsellino et al., 1965).

Possible Relevance of the Model to Other First-Order Neurons. A possible organization of first-order neurons is suggested by these considerations. Specifically, it is postulated that a first-order neuron will discharge as regularly as possible while retaining the ability to respond adequately to naturally occurring changes in the stimuli. Or to phrase it in terms of the neuron model, neurons which must encode rapidly varying stimuli will be characterized by short resetting times, and those neurons which monitor slowly varying stimuli will be characterized by long resetting times. Hence, for example, regularly discharging neurons would be expected to transmit information about slowly changing variables. Irregularly discharging neurons would be expected to monitor rapidly changing variables.

Of interest in this connection is the behavior of pacinian corpuscles. Corpuscles lying in deep tissue appear to be the mechanoreceptors involved in the transduction of high-frequency vibrations (Mountcastle et al., 1967). Moreover, mesenteric pacinian corpuscles are known to respond to low-intensity mechanical vibrations of up to 1000 Hz at body temperature and of up to 500 Hz at room temperature (Sato, 1961). Hence, we would expect that the corpuscles could be successfully modeled using short resetting time constants. In addition, the corpuscles observed at body temperature should be characterized by the shorter time constant. In accord with expectations, it has been directly demonstrated that mesenteric pacinian corpuscles do indeed have a very short recovery time. Undissected corpuscles reset themselves completely within 3 msec of a discharge (Gray and Malcolm, 1950); a time constant of about 0.7 msec would seem appropriate for them. Excised mesenteric pacinian corpuscles at room temperature need approximately 10 msec to reset (Loewenstein and Altamirano-Orrego, 1958), requiring a resetting time constant of approximately 3 msec for their model.

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