RESPONDING TO ELECTRICAL STIMULATION OF THE COCHLEA: IDENTIFICATION OF CUES FOR CURRENT AND TIME-INTERVAL CODING

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A model of the response of auditory nerve fibers to electrical stimulation of the cochlea is presented. Auditory nerve fiber responses are described in terms of cochlear regions activated by the stimulus: region A, in which the discharge rate equals a value of the pulse rate plus spontaneous activity, and region B, in which the discharge rate is less than pulse rate plus spontaneous activity but greater than spontaneous activity. The cues for intensity and time-interval coding provided by regions A and B are discussed.

INTRODUCTION

This is a descriptive model of responses of the auditory nerve to pulsed electrical stimulation of the cochlea using stimulus parameters set within the range of a cochlear implant (biphasic charge-balanced current pulses, 100 to 200 microseconds per phase, amplitude 0.2 to 2 mA, pulse rates 50 to 400 pulses per second). The model looks at responses to electrical stimulation as populations of auditory nerve fibers (ANFs) in two cochlear regions, A and B. Region A encompasses the cochlear region around the stimulating electrodes, in which discharge rate is "saturated" at a value equal to the pulse rate plus spontaneous activity. Region B is a population of ANFs in which the discharge rate is less than the pulse rate but greater than the spontaneous discharge rate. Region B surrounds region A and is therefore more distant from the stimulating electrode. The model is described mathematically, and cues for the coding of intensity (current) and time intervals (pulse rate) are identified.

MATHEMATICAL DESCRIPTION OF AUDITORY NERVE MODEL

Figure 1 illustrates the input-output function of an ANF to electrical stimulation of the cochlea at pulse rates of 100, 200, 300, and 400 pulses per second. Javel et al. noted from these data that the curves lie virtually on top of each other, which implies 1) that there are no differences in growth rate for different pulse rates, 2) eliciting a discharge rate is dependent on stimulus current and not pulse rate, and 3) the growth of discharge rate is logarithmic against current. Thus, (1) \( R = k(I - IT) + S \)

where

- \( R \) = discharge rate (spikes per second)
- \( k \) = the growth rate of discharge (50 to 127 spikes per second per decibel, mean = 70, \( \alpha = 20 \), reanalysis of auditory nerve data from this laboratory
- \( S \) = log stimulus current (dB re 1 \( \mu A \))
from a current source, and hence auditory nerve threshold, can be described as follows:

\[
ithold = \text{the local current (microamperes) at the auditory nerve fiber required to generate a threshold response}
\]

\[
I_t = \text{stimulus current (microamperes) required to generate a threshold response from the auditory nerve fiber (dB re 1 \mu A)}
\]

Note that \( R > 0 \) and \( S = (PR + S) \), where PR is pulse rate.

Single unit and evoked potential studies have revealed that current decays exponentially along the scala tympani (2) if

\[
ithold = Ite - d/I \quad \Rightarrow \quad I = ithold/e - d/I
\]

where

\[
ithold = \text{spontaneous activity (0 in deaf animals)}
\]

(Fig. 1, Input-output functions from auditory nerve fiber in response to electrical stimulation at 100, 200, 300, and 400 pulses per second (pps). Pulse width was 200 milliseconds per phase. Ordinate is discharge rate, and abscissa, stimulus current. These data were collected by Javel et al. in this laboratory.)

\[
S = \text{spontaneous activity (0 in deaf animals)}
\]

(Fig. 2, Neural density distributions (NDDs) were generated by implementation of auditory nerve model. Abscissa plots distance from point current source, and auditory nerve fiber discharge rate is plotted on ordinate. Solid lines demonstrate NDDs created at pulse rates of 50, 100, 200, and 400 pulses per second with stimulus current constant (k = 70 spikes per second per decibel, l = 3 dB/mm). Dashed lines demonstrate NDDs for 200-pulse per second stimulus at current I = 1.9, 3.5, and 6 dB above threshold (k = 70, 1 = 3 dB/mm). Region A represents level at which discharge rate equals pulse rate plus spontaneous activity, ie, flat-topped portion of any of trapezoidally shaped NDDs. Region B for trapezoids is sloped shoulder of distribution at which discharge rate is less than pulse rate plus spontaneous activity. Further example of region B is (dashed) NDDs of 1-dB suprathreshold, 200-pulse per second stimulus.)
model predicts that the total cochlear region activated will become broader as current increases: 1) at low stimulus currents region B is expanding and region A does not exist; 2) at higher currents the extent of region A will broaden and region B will move to a cochlear region further away from the electrode (Fig 2). Note from Fig 2 that the neural excitation distribution generated by this model resembles the trapezoidal distribution proposed empirically by Tong et al.7 At very high stimulus levels, current spreads into the modiolus,1 and the model breaks down.

If pulse rate is increased but the stimulus current kept constant the model predicts 1) the total extent of the cochlear region activated will not change, 2) region A will narrow in extent and region B will broaden as the pulse rate increases, and 3) in region B the discharge rate of an individual auditory nerve fibers is independent of pulse rate1 (Fig 2).

CURRENT (INTENSITY) CODING

Stimulus current (intensity) could be coded in the discharge rate of individual nerve fibers (rate coding), as discharge rate rises steeply against current until it reaches the same value as the pulse rate plus spontaneous activity. Additional cues for the coding of current (intensity) may be provided by the cochlear extent of regions A and B.

It has been proposed that rate coding operates > 130 dB for acoustic intensities.8,9 Rate coding is thought to involve a multiple-ANF analysis, by integration of rate information from ANFs with thresholds and dynamic ranges encompassing the range of acoustic intensities. Intensity cues for high acoustic intensities are believed to derive from the low-spontaneous rate ANFs,8,9 as this subgroup has dynamic ranges operative at high acoustic intensities at which other ANFs have reached rate saturation. In cochlear implants, rate coding operates over a small range of stimulus currents (10 to 15 dB). This operative range is smaller than for acoustic stimulation, since ANF responses to electrical stimulation when compared with acoustic stimulation reveal 1) the dynamic range of individual ANFs is smaller (6 to 10 dB), 2) the rate of growth of discharge against current is steeper (50 to 127 spikes per second per decibel), 3) the range of thresholds observed from ANFs is smaller (approximately 12 dB), 4) the maximum discharge rate of ANFs achievable is the pulse rate plus spontaneous activity, and 5) there is no evidence that low-spontaneous rate ANFs have higher thresholds or wider dynamic ranges than other ANFs to electrical stimulation.1,10,11

Cues for coding of current (intensity) may be provided by the extent of regions A and B. To recapitulate, at low currents region B is expanding and region A does not exist, and at higher currents region A is expanding and the size of region B is constant. Cues for current (intensity) discrimination are provided by the changes in ANF rate,8,9 which occur at the periphery of the cochlear region excited, where, as current is increased, ANFs in region B join region A, and more distant ANFs are activated to join region B. Note that within region A no cues for current (intensity) discrimination are available, since discharge rate is "saturated" at the value of the pulse rate plus spontaneous activity.

Loudness is the psychophysical correlate of stimulus current for the implantees,12 and it is possible to create loudness models from the auditory nerve model presented. For example, a simple model is to assume that loudness is directly proportional to the total discharge rate of all ANFs activated by the electrical stimulation, and that there is a constant density of surviving ANFs along the cochlea (Fig 3). This model predicts nonlinear loudness growth against log-current at low stimulus currents, and a linear relationship between log-current and loudness at higher currents, consistent with psychophysical loudness growth functions that reveal differing rates of growth at low and high currents.13
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