ing) and EO (some appearing unresponsive) population. Lateral inhibition, however, does not appear to be as important for ipsilateral electrical stimulation, as C(acoust)I(elect) data in the Table do not show an enhanced EI and reduced EE population. It may be, as argued earlier, that some units that respond as EI under C(acoust)I(acoust) stimulus conditions may under the C(acoust)I(elect) stimulus conditions become EE-responding. That is, both the lateral inhibition and pre-stimulus threshold shift mechanisms may be involved. As a consequence of monaural deafening and/or electrical stimulation, there could also be some reorganization of the central auditory system.

CONCLUSIONS

For C(elect)I(acoust) stimulation, the EE- and EO-driven populations appear reduced by lateral inhibition and/or pre-stimulus threshold shift mechanisms, and increased by modiolar stimulation. This has resulted in the emergence of a large OE population primarily derived from units that would respond EE under C(acoust)I(acoust) stimulus conditions. For C(acoust)I(elect) stimulation there appears to be a slight reduction in EE and an increase in EI population that appears balanced by some higher-frequency units that would respond as EI under C(acoust)I(acoust) conditions, becoming EE-responding under C(acoust)I(elect) stimulus conditions.

This study shows that a large number of units, when electrically driven, show no excitatory response. Finally, this study has important consequences for masking of electrical stimuli, particularly for the sequential progression of electrodes in the basal to apical direction.

REFERENCES


MODEL OF DISCHARGE RATE FROM AUDITORY NERVE FIBERS RESPONDING TO ELECTRICAL STIMULATION OF THE COCHLEA: IDENTIFICATION OF CUES FOR CURRENT AND TIME-INTERVAL CODING

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This is a descriptive model of responses of the auditory nerve to pulsatile electrical stimulation of the cochlea using stimulus parameters set within the operative 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 activity. The cues for intensity and time-interval coding provided by regions A and B are identified.

INTRODUCTION

This is a descriptive model of responses of the auditory nerve to pulsatile electrical stimulation of the cochlea using stimulus parameters set within the operative 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 activity. The cues for intensity and time-interval coding provided by regions A and B 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,

\[ R = k(I - IT) + S \]

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 laboratory¹
- \( I \) = log stimulus current (dB re 1 μA)

¹ Reference 1.
from a current source, and hence auditory nerve threshold, can be described as follows:

$$\text{Ithold} = \text{It} - \text{d}$$

where

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

$$\text{It} = \text{stimulus current (microamperes) required to generate a threshold response}$$

Note that R is $\geq 0$ and $s(PR + S)$, where PR is pulse rate.

Single unit and evoked potential studies\(^2\)\-\(^6\) have revealed that current decays exponentially along the scala tympani from a current source, and hence auditory nerve threshold, can be described as follows:

$$\text{Ithold} = \text{It} - \text{d}$$

$$(1) \quad \text{Ithold} = 0$$

$$(2) \quad \text{Ithold} = \text{It} - \text{d}$$

where

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

$$\text{It} = \text{stimulus current (microamperes) required to generate a threshold response}$$

Regions A and B are dynamic, and vary in cochlear location and extent with current and pulse rate.

Consequently, the effective driving current of an ANF (I - IT) decreases with d, affecting discharge rate as determined by equation 1.

The limitations of the current distribution implementation of the model (equations 2 and 3) have been discussed in detail elsewhere.\(^6\) The major simplification is that the stimulating electrode in the model has been idealized as a point source. In bipolar stimulation, the distance between the source and sink electrodes complicates the current distribution, particularly within region B. For clarity, the following discussion applies to ANFs with equal threshold, Ithold, but the principles discussed could also be applied to ANF populations with a range of ANF thresholds.

Fig 3. In this model it was assumed that loudness is directly proportional to total discharge rate of all auditory nerve fibers activated by electrical stimulation, and that there is constant density of surviving auditory nerve fibers along cochlea. Hence, total discharge rate, which was measure of relative loudness, was equal to area under neural density distribution calculated from auditory nerve model (k = 70 spikes per second per decibel, l = 3 dB/mm, pulse rate = 400 pulses per second). This loudness model predicts different rates of growth for lower and higher currents.

EFFECTS OF CURRENT AND PULSE RATE ON REGIONS A AND B

Regions A and B are dynamic, and vary in cochlear location and extent with current and pulse rate. If the stimulus current is increased and the stimulus pulse rate kept constant, the
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 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 implantee,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 loudness 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

PULSE RATE (TIME-INTERVAL) CODING

The perception of pulse rate (time intervals) could operate through interspike intervals of auditory nerve fibers, as these are integral multiples of the stimulus interpulse interval.1 This model proposes the following relations between time-interval cues and the auditory nerve populations in regions A and B. In region A the interspike interval equals the interpulse interval and strong cues are provided for time-interval detection. The cochlear extent of region A decreases as pulse rate increases. In region B the cues for time-interval detection are less strong than in region A, as the interspike intervals are integral multiples of the interpulse interval. The cochlear extent of region B increases as pulse rate increases.

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