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Modelling the Sensitivity of Cells in the Anteroventral Cochlear Nucleus to Spatiotemporal Discharge Patterns

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Modelling the sensitivity of cells in the anteroventral cochlear nucleus to spatiotemporal discharge patterns

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SUMMARY

This study investigates a potential mechanism for the processing of acoustic information that is encoded in the spatiotemporal discharge patterns of auditory nerve (AN) fibres. Recent physiological evidence has demonstrated that some low-frequency cells in the anteroventral cochlear nucleus (AVCN) are sensitive to manipulations of the phase spectrum of complex sounds (Carney 1990*b*). These manipulations result in systematic changes in the spatiotemporal discharge patterns across groups of low-frequency AN fibres having different characteristic frequencies (CFs). One interpretation of these results is that these neurons in the AVCN receive convergent inputs from AN fibres with different CFs, and that the cells perform a coincidence detection or cross-correlation upon their inputs. This report presents a model that was developed to test this interpretation.

1. INTRODUCTION

It has been known for several decades that the temporal discharge patterns of low-frequency auditory nerve (AN) fibres convey information about the spectrum of an acoustic stimulus (see, for example, Kiang *et al.* (1965); Rose *et al.* (1967)). For responses to pure tones, the interpretation of temporal response patterns is straightforward: the dominant periodicity of a histogram of the response represents the frequency of the tonal stimulus. However, for complex sounds, the interpretation of temporal information is not so simple: periodicities within the responses of single fibres do not uniquely encode a peak frequency in a stimulus spectrum (Carney & Yin 1988). This complication arises because the temporal responses of AN fibres to complex sounds are influenced by a combination of the spectral properties of the stimulus and the filtering properties of the basilar membrane. However, because these filtering properties change systematically as a function of characteristic frequency (CF), by combining information encoded across a population of fibres of different CFs the central nervous system could accurately interpret information encoded in the temporal discharges. Thus, when considering the temporal encoding of complex sounds, we must consider not single fibre discharge patterns but rather spatiotemporal discharge patterns; that is, temporal patterns of activity across populations of fibres varying in CF.

The first opportunity for the processing of spatiotemporal discharge patterns arises in the anteroventral cochlear nuclear (AVCN), where AN fibres converge upon single cells (see Osen 1970). Convergence of individual fibres onto postsynaptic neurons provides a potential neural substrate for coincidence detection; that is, a postsynaptic cell will in general be most likely to discharge when its inputs discharge simultaneously. The only exception occurs when activity of a single presynaptic input is capable of eliciting a postsynaptic discharge.

The processing of incoming information performed by a cell depends upon both the nature of its inputs and the cell's biophysical properties. For a cell in the AVCN: (i) the size and location of each input terminal will influence whether it can drive the cell alone or only when summed with other coincident inputs; (ii) the distribution of CFs and the number of inputs will play a role in determining the sensitivity of the cell to different input patterns; and (iii) the electrical properties of the cell's membrane, which influence its ability to summate inputs spatially and temporally, will determine the sensitivity of the cell to changes in the relative discharge times of its inputs.

Cells in the AVCN are known to display diversity in many of these aspects. At one extreme are the large spherical bushy cells, in the most rostral pole of the AVCN, that receive a single AN input in the form of a large somatic terminal (for examples, see Osen (1970); Lorente de No (1981)). In this case, each and every input discharge is thought to evoke a postsynaptic discharge (Pfeiffer 1966). At the other extreme are the stellate cells that receive many small AN terminals on the dendrites and the cell body (see Osen 1970). This study focused on the globular bushy cells, which receive convergent input from a few to several AN inputs including the relatively large modified end-

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bulbs of Held (Osen 1970; Liberman 1991). Many of these cells have low spontaneous discharge rates and some have been shown to have subthreshold excitatory postsynaptic potentials *in vivo* (Smith & Rhode 1987). This result implies that, at least in some cases, individual input fibres are not capable of driving the cell to discharge, and so coincident inputs may be necessary to drive the cell. Furthermore, globular bushy cells have nonlinear membrane properties that reduce their ability to summate their inputs temporally (Wu & Oertel 1984), and thus their performance as coincidence detectors should be enhanced.

We do not know the relative CFs of the inputs that converge upon single cells in the AVCN, yet this feature will determine the functional significance of coincidence detection. In a previous study, it was shown that some cells with globular bushy response types were sensitive to manipulations of spatiotemporal patterns across frequency (Carney 1990*b*). An interpretation of that result is (i) that these cells receive input from fibres of different CFs, and (ii) that they perform a crosscorrelation upon their inputs. To understand better the implications of a cross-correlational mechanism for processing of complex sounds, we developed a model for globular bushy discharge patterns. We can use this model in future studies to explore the effects of the number of inputs, the distribution of the CFs of the inputs, and the coincidence requirements of the postsynaptic cell, as well as to identify ways to estimate these parameters in future physiological experiments.

2. METHODS

Inputs to the AVCN cell model were produced by a recently developed model for the responses of low-frequency AN fibres (Carney 1990*a*, 1992). The AN model takes arbitrary complex stimulus waveforms, and consists of four main stages: (i) a time-varying band-pass filter, representing the mechanical tuning of the basilar membrane with a compressive nonlinearity; (ii) a memoryless saturating nonlinearity followed by low-pass filtering, representing inner hair cell transduction and membrane properties; (iii) synaptic adaptation; and (iv) spike generation with refractoriness.

The AVCN cell was modelled by a simple shot-noise threshold model similar to those of Colburn *et al.* (1990) and Young *et al.* (1991) (figure 1). In this model, each input discharge produces an instantaneous increase in the postsynaptic voltage which then decays exponentially with a fixed time constant. Inputs from different fibres that overlap in time are summed, and when the postsynaptic voltage reaches a fixed threshold value, an output spike is recorded. The postsynaptic voltage is then reset to zero, and a period of refractoriness is imposed during which no output spikes can be generated. The two most important parameters for this coincidence mechanism are (i) the amplitude of the individual inputs relative to the threshold, and (ii) the time constant determining the duration of each input.

Because the model AN inputs could have different CFs and thus different response latencies, it was necessary to adopt a rule for the relative neural delays that would determine the arrival times of input discharges converging on a postsynaptic cell. Based on the strong responses of cells with globular bushy response types to transient stimuli such as clicks, it was decided to 'align' the times of the inputs in response to the click by eliminating the differences between the traveling wave delays for inputs having different CFs.

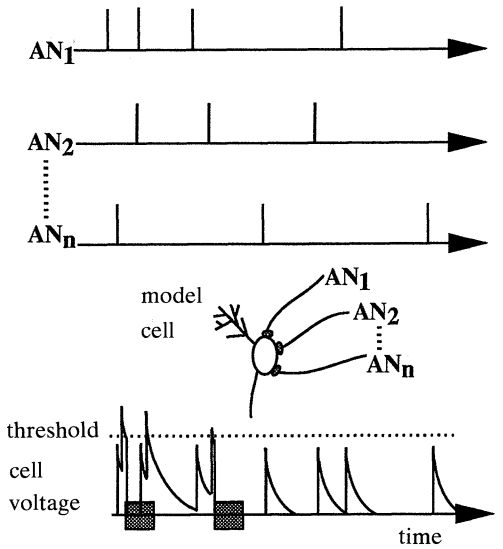

Figure 1. Schematic diagram of the AVCN cell model. At the top are responses of model AN fibres. A spike on any of the input fibres causes an exponentially decaying change in the postsynaptic cell voltage (lowest trace). When the voltage crosses the threshold value, an output spike is recorded for the model cell. After the occurrence of an output spike, the cell voltage is reset, and there follows a period of refractoriness (grey box) during which further spikes are ignored. The travelling wave delays for the different CFs are normalized before performing the coincidence detection.

3. RESULTS

Figure 2 shows the responses of a model cell to three Huffman sequences. These stimuli have a flat magnitude spectrum, but contain a phase transition of 2π that can be positioned at any frequency (F_t) and varied in slope (see Carney (1990*b*) for full description of the stimulus). The phase transition in the Huffman sequence provides a way to manipulate the relative discharge times of AN fibres with CFs near F_t; because individual fibres phase lock to components in the stimulus near their CF, the phase transition in the stimulus is represented in the phase-locked responses of the fibres. The model cell received inputs from 17 AN fibres with CFs distributed between 850 and 1150 Hz. Each input had an amplitude that was 0.8 times the threshold of the model cell, and the time constant for decay of each input was 0.05 ms. The model responses show a similar pattern of sensitivity to changes in the stimulus phase spectrum as that observed in physiological recordings from many cells, with the lowest threshold and the highest probability of response to the stimulus with the most gradual slope

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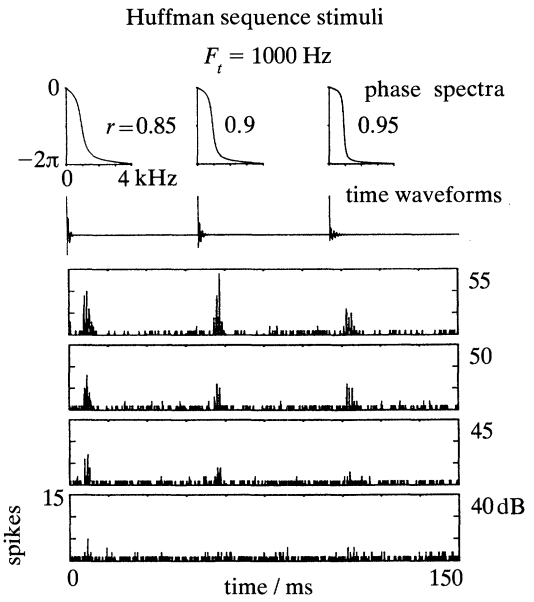

Figure 2. Responses of a model AVCN cell to three Huffman sequences (same format as in Carney (1990*b*)). At the top are the phase spectra and time waveforms for each of the three transient stimuli. The phase spectra have a transition centered at F_t = 1000 Hz. This transition increases in slope as the parameter r increases; the magnitude spectra for all three stimuli are flat (see Carney (1990*b*) for further description of stimuli.) Histograms of the responses of the model cell to these waveforms presented at four different sound pressure levels are shown. The model cell's threshold is lowest for the stimulus with the most gradual phase transition (left), and it responds to this stimulus with a higher probability than for the other stimuli as sound pressure is increased over this range (100 repetitions of the stimulus; 0.1 ms bins).

in the phase spectrum (Carney 1990*b*). Thus the coincidence mechanism acting on a group of inputs with distributed CFs can produce the type of sensitivity observed in the AVCN. If the amplitude of individual inputs was increased to near or at the threshold of the model cell, the sensitivity disappeared, as expected. Also, the sensitivity disappeared for a model cell receiving inputs having the same CF.

There are several qualitative differences between the model response and those recorded in the AVCN. In particular, the responses of the model are not as strongly locked into an onset-like response, the model cell has relatively high spontaneous rate, and the probability of firing of the model is lower than that of most globular bushy response types that were studied. Some of these differences might be reduced by further increasing the numbers of inputs to the postsynaptic model cell, and at the same time increasing the requirements for coincidence. However, some of the differences, particularly the difference in timing at the onset, may be due to limitations of the AN model used to provide the inputs. For simplicity, the AN inputs all had high spontaneous rates (Liberman 1991) and similar thresholds, all inputs produced postsynaptic responses with the same amplitude, and the postsynaptic cell's threshold remained constant over time. Models being developed that include the nonlinear features of the globular bushy cell's membrane properties (Young *et al.* 1991) might improve some of these aspects of the responses. In addition, more accurate modelling might require the inclusion of other non-primary inputs, possibly including inhibitory inputs.

4. DISCUSSION

This study represents an initial test of the AVCN model's ability to reproduce the sensitivity to spatiotemporal patterns that was demonstrated physiologically. Coincidence detection in the AVCN might provide a mechanism for processing of the temporal information associated with responses to complex sounds. Different complex sounds evoke different spatiotemporal response patterns across the population of AN fibres, and thus a mechanism that is sensitive to differences in these patterns may be important in the processing of information that allows discrimination of complex sounds.

A coincidence mechanism acting upon convergent afferents with different CFs, as modelled here, may explain several response features of globular bushy cells that have been reported previously. A coincidence mechanism is consistent with the generally low spontaneous rate of this population (Smith *et al.* 1991). Also, coincidence detection could produce both the high synchronization coefficients that have been described for low-CF globular bushy cells and possibly small spherical bushy cells in response to low-frequency tones (Carney 1990*b*; Yin *et al.* 1988) and for high-CF globular bushy cells in response to low-frequency tones (Smith *et al.* 1991). Furthermore, this mechanism might explain the relatively high synchronization of these cells to the envelope of amplitude-modulated stimuli (Frisina 1990; Wang 1991). Coincidence detection, together with convergence of inputs of different CFs, might explain the relatively low sustained discharge rate following the strong onset response for many globular bushy cells to tone bursts at CF (Smith & Rhode 1987). Finally, the effect of convergence of different CFs on the sharpness of tuning need not be to broaden the tuning curve, which would be a result of convergence of different CFs without a coincidence requirement (see Carney (1990*b*) for discussion).

It is interesting to consider the possible functional significance of a coincidence mechanism in the AVCN. The pattern of sensitivity observed in the physiological recordings from several of these cells (Carney 1990*b*) suggests the hypothesis that this mechanism could enhance the signal-to-noise ratio of the temporal information that is transmitted from the cochlear nucleus to the binaural brainstem nuclei. Such an enhancement would be produced by the fact that the temporal responses to signal components (or spectral peaks) in complex sounds would be more highly correlated across fibres of different CFs than would be the responses to noise components of the stimulus. Thus the signal-related temporal information would pass more readily through the convergence and coincidence detection mechanism than would the noise-related temporal responses.

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