Coding of envelope modulation in the auditory nerve and anteroventral cochlear nucleus

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SUMMARY

We have investigated responses of the auditory nerve fibres (ANFs) and anteroventral cochlear nucleus (AVCN) units to narrowband 'single-formant' stimuli (SFSs). We found that low and medium spontaneous rate (SR) ANFs maintain greater amplitude modulation (AM) in their responses at high sound levels than do high SR units when sound level is considered in dB SPL. However, this partitioning of high and low SR units disappears if sound level is considered in dB relative to unit threshold. Stimuli with carrier frequencies away from unit best frequency (BF) were found to generate higher AM in responses at high sound levels than that observed even in most low and medium SR units for stimuli with carrier frequencies near BF.

AVCN units were shown to have increased modulation depth in their responses when compared with high SR ANFs with similar BFs and to have increased or comparable modulation depth when compared with low SR ANFs. At sound levels where AM almost completely disappears in high SR ANFs, most AVCN units we studied still show significant AM in their responses. Using a dendritic model, we investigated possible mechanisms of enhanced AM in AVCN units, including the convergence of inputs from different SR groups of ANFs and a postsynaptic threshold mechanism in the soma.

1. INTRODUCTION

Natural sounds like speech can be thought of as combinations of narrowband stimuli (Flanagan 1972). The waveform of a narrowband signal is characterized by two major features: a carrier frequency and an envelope. The temporal patterns of auditory nerve fibre (ANF) spike trains can be phase-locked both to carrier frequency, and to the envelope of narrowband stimuli like amplitude-modulated sounds (Moller 1976; Rose et al. 1967). The phase locking to stimulus envelope is an important phenomenon, because it reveals properties of the cochlear filter that can not be studied with pure tone stimuli, but also has implications for possible mechanisms underlying the extraction of the pitch of complex stimuli from ANF firing patterns (De Boer 1976; Schouten 1940).

A detailed description of ANF responses to narrowband stimuli is also relevant to the analysis of signal transformations in the cochlear nucleus. For example, low spontaneous rate (SR) ANFs have higher thresholds and wider dynamic ranges for rate responses to tones than do high SR ANFs (Liberman 1978; Sachs et al. 1989). It has been suggested that spectral features of complex stimuli are represented in the average discharge rate of low SR ANFs at high sound levels, where the rates of low threshold, high SR ANFs are saturated (Delgutte 1982; Winslow et al. 1987). At low sound levels below the thresholds of low SR ANFs, spectral features are represented in the discharge rate of the high SR ANFs (Sachs & Young 1979). Blackburn & Sachs (1990) present evidence that chopper units in the anteroventral cochlear nucleus (AVCN) may 'listen selectively' to high SR ANF inputs at low sound levels and to low SR ANF inputs at high sound levels. However, details of the processing are not known. Evidence suggests that both low and high SR ANFs contact stellate cells (Liberman 1992; Ryugo et al. 1992), the source of chopper responses (Rhode et al. 1983), but we know little about how stellate cells integrate inputs from different ANF SR groups. One way to investigate such problems is to establish a physiological 'marker' that can distinguish low and high SR fibres at all sound levels and then study this marker in chopper units. We will show that the envelope fluctuations of temporal discharge patterns of responses to narrowband sounds can be used as such a marker.

2. METHODS

Single-unit recordings were made from nembutal anaesthetized cats. Surgical procedures were the same as those reported previously (Blackburn & Sachs 1989; Sokolowski et al. 1989) and approved by the Johns Hopkins Animal Care and Use Committee. Figure 1a illustrates generation of the narrowband

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‘single-formant’ stimuli (sfs) used in this study. An example of an sfs with carrier frequency equal to 2.0 kHz is shown in figure 1b. The stimuli were digitally synthesized to approximate the response of an RLC circuit to a periodic impulse train. For each unit studied, the carrier frequency of the stimulus was usually set as close as possible (always within 1% ) to the unit’s best frequency (bf); in some cases responses to off-bf carriers were studied. The bandwidth of the stimulus was set equal to the average bandwidth of vowel formants at the carrier stimulus frequency. The formant bandwidth versus frequency function was taken from Dunn (1961) for frequencies less than 3.0 kHz, and set to a constant at higher frequencies (figure 1c). The fundamental frequency of the stimulus was the subharmonic of the carrier frequency closest to 125 Hz. For each unit, the appropriate sfs was presented at a number of sound levels. Period histograms were constructed from the responses and the envelopes extracted from the histograms. Details about computation of period histograms and their envelopes can be found in Wang (1991). The amplitude modulation (AM) in the sfs and neural responses is measured by modulation depth, which is defined in figure 1b.

We separated ANFs into low sfr (sfr < 18.0 spikes per second) and high sfr (sfr > 18.0 spikes per second) groups. The low sfr group in this presentation includes both low and medium sfr ANFs as defined in many other studies because our data do not show significant difference between low and medium sfr ANFs in coding sfs. AVCN units were classified into six types using a classification scheme similar to that used by Blackburn & Sachs (1989).

3. RESPONSES OF AUDITORY NERVE FIBRES

For stimuli centered at unit bf, responses of low-bf ANFs to sfs are phase-locked to carrier frequency and to stimulus envelope; responses of high-bf units are phase-locked only to stimulus envelope. Period histograms from two low-bf ANFs are shown in figure 2 (a-d), with computed envelopes superimposed. The amount of modulation in the envelope of the period histogram is a function of sound level, increasing as sound level exceeds bf threshold and decreasing dramatically at high sound levels (Wang 1991). Period histograms at 40 dB SPL (figure 2a, c) show greater modulation than do those at 70 dB SPL (figure 2b, d). Low sfr ANFs maintain higher envelope modulation at higher sound levels (dB SPL) than do high sfr ANFs as can be seen by comparing period histograms of the high sfr ANF to those of the low sfr ANF in figure 2. This difference is a direct consequence of the higher thresholds of low sfr ANFs (Wang 1991) and suggests that information about envelope modulation is carried by low sfr ANFs at high sound levels.
4. RESPONSES OF AVCN UNITS

We studied AVCN units using the same stimulus used in the study of ANFS described above. Figure 2, f show period histograms with envelopes, from a chopper unit whose BF is equal to that of the ANFS in figure 2a–d. Note that the amount of modulation at 70 dB SPL in the chopper unit (figure 2f) is much higher than that in either of the ANFS at the high sound level. The period histograms from this chopper unit show no phase locking to the carrier, as is typical of chopper units at this BF (2.215 kHz; Blackburn & Sachs 1989). Period histograms from primarylike units (recorded from AVCN bushy cells) show phase locking to the carrier comparable to that of ANFS. On the other hand primarylike units also show greater phase locking to the envelope than do ANFS at high sound levels (Wang 1991). In fact, all types of AVCN units show higher or comparable modulation depth at moderate to high sound levels than do ANFS (Wang 1991). At sound levels where AM almost completely disappears in high SR ANFS, most of AVCN units studied still show significant AM in their responses.

5. MECHANISMS OF MODULATION ENHANCEMENT

The enhanced modulation depth observed in AVCN units can result from several mechanisms. Based on our analysis of ANF and AVCN responses to SFSS, we suggest that these mechanisms include: (i) convergence of both low and high SR ANFS onto an AVCN cell; (ii) convergence of inputs from ANFS with BFS different from that of the AVCN cell; and (iii) the threshold effect due to temporal summation of subthreshold excitatory postsynaptic potentials (EPSPs) and inhibitory inputs at soma. These mechanisms were examined in a dendritic model of chopper units originally developed by Banks & Sachs (1991). Spike times of ANF responses to SFSS were used as inputs to the model whose output was then compared with real chopper responses to SFSS. Two period histograms generated by the model are shown in figure 2g, h. The histogram in figure 2g shows the model responses with inputs generated from the high SR ANF at low sound level (40 dB SPL; figure 2a). The histogram in figure 2h was generated with inputs from the low SR ANF at the high sound level (70 dB SPL; figure 2d). In both cases, ten inputs converge on the soma. We found that the peak to trough amplitude of the envelope of model period histograms is proportional to the amount of envelope modulation in the input. Thus if the high SR ANF at 70 dB SPL (figure 2f) is used as the input to the model, model output shows very little envelope modulation (Wang 1991).

Responses of the model with only low SR inputs
(figure 2a) show little enhancement of modulation relative to that in the inputs. When inputs consist of both low and high sr ANFs at high sound levels, the modulation depth of the model output is lower than that obtained with high sr ANFs. To compensate for the decrease in modulation depth due to high sr ANFs, which have almost no modulation in discharge patterns at high sound levels, and to achieve higher modulation depth in model output than that of low sr ANFs, a postsynaptic threshold mechanism is needed. This mechanism must work in such a way that a chopper cell gives output spikes only when input spike rate exceeds a threshold value. We implemented such a threshold mechanism in the model by modifying the steady-state activation and inactivation curves of the model spike generator on the basis of physiological observations (Oertel 1983; Smith & Rhode 1989). The model period histogram shown in figure 2a was obtained using the original model as described in Banks & Sachs (1991). A simulation using the modified model with the same ANF inputs does produce increased modulation depth (Wang 1991). Simulated inhibitory input to the soma, which effectively raises discharge threshold, also increases envelope modulation in the period histogram (data not shown).

REFERENCES


Discussion

E. F. Evans (Department of Communication and Neuroscience, University of Keele, U.K.). In respect of the hypothetical threshold device, could inhibition be an adequate mechanism for this?

X. Wang. Our simulations with a compartment model showed that somatic inhibition can be an adequate mechanism for the proposed threshold device.