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Coding of Envelope Modulation in the Auditory Nerve and Anteroventral Cochlear Nucleus [and Discussion]

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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 1*a* illustrates generation of the narrowband

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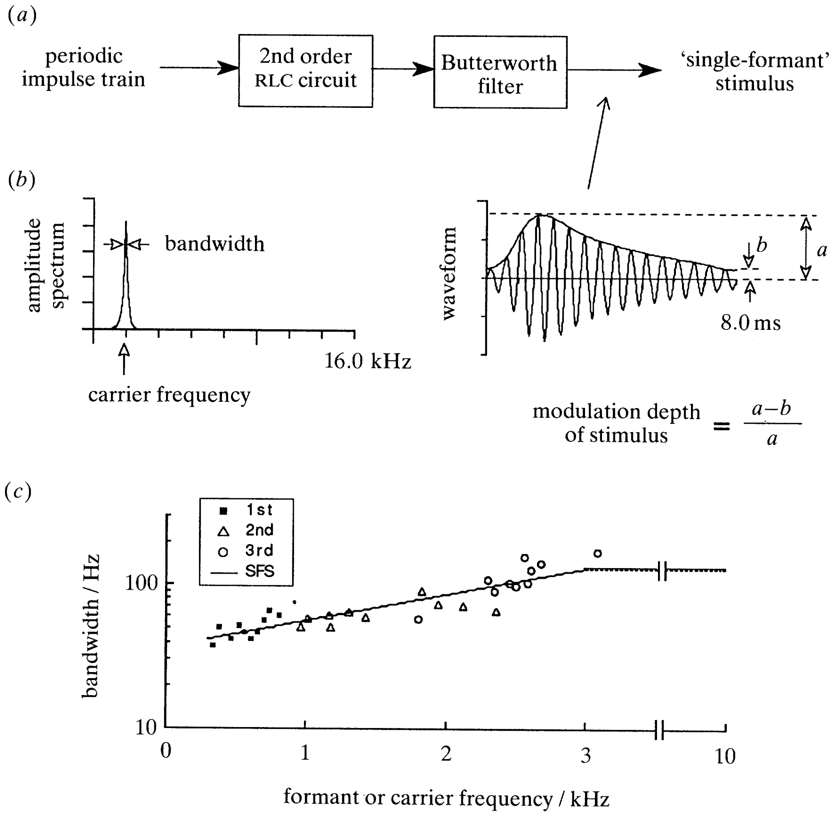

Figure 1. (*a*) Illustration of the process to generate 'single-formant' stimuli (SFSs). (*b*) An example of an SFS whose carrier frequency is 2.0 kHz. Both the stimulus waveform and its amplitude spectrum are plotted. Superimposed on the waveform is the computed envelope. (*c*) Plot of 3 dB bandwidth of formants of vowel sounds measured by Dunn (1961) (filled squares, first formant; open triangles, second formant; open circles, 3rd formant) and those of the SFSs (solid line) versus formant or carrier frequency.

'single-formant' stimuli (SFSs) used in this study. An example of an SFS with carrier frequency equal to 2.0 kHz is shown in figure 1*b*. 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 stimulus carrier 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 1*c*). 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 SFSs and neural responses is measured by modulation depth, which is defined in figure 1*b*.

We separated ANFs into low SR ($\text{SR} < 18.0$ spikes per second) and high SR ($\text{SR} \geqslant 18.0$ spikes per second) groups. The low SR group in this presentation includes both low and medium SR ANFs as defined in many other studies because our data do not show significant difference between low and medium SR ANFs in coding SFSs. 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 SFSs 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 2*a*, *c*) show greater modulation than do those at 70 dB SPL (figure 2*b*, *d*). Low SR ANFs maintain higher envelope modulation at higher sound levels (dB SPL) than do high SR ANFs as can be seen by comparing period histograms of the high SR ANF to those of the low SR ANF in figure 2. This difference is a direct consequence of the higher thresholds of low SR ANFs (Wang 1991) and suggests that information about envelope modulation is carried by low SR ANFs at high sound levels.

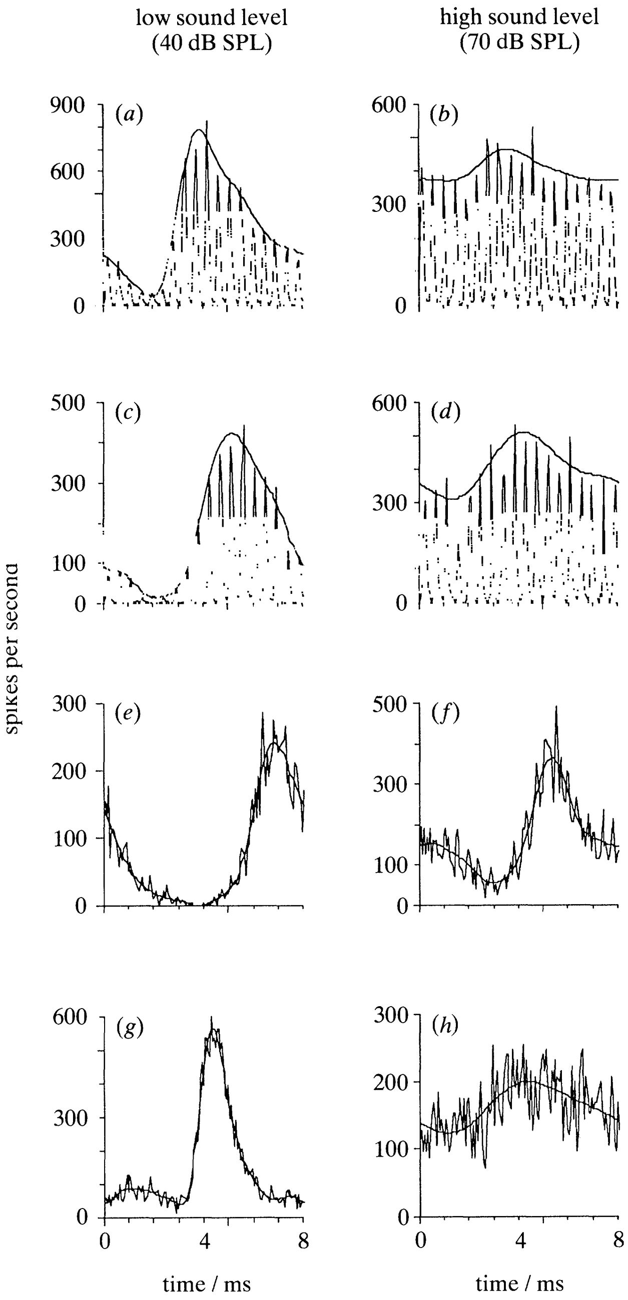

Figure 2. Period histograms with superimposed envelopes from (*a*, *b*) a high SR ANF (unit 1.05, 8/10/1990, BF 2.215 kHz, SR 51.0 spikes per second), (*c*, *d*) a low SR ANF (unit 2.01, 17/9/1990, BF 2.215 kHz, SR 2.2 spikes per second), (*e*, *f*) an AVCN chopper unit (unit 7.03, 7/8/1990, BF 2.215 kHz), and (*g*, *h*) simulated chopper responses. All auditory units have the same BF (2.215 kHz). Period histograms plotted in the left column are at a low sound level (40 dB SPL), whereas those in the right column are at a high sound level (70 dB SPL). For simulated chopper period histograms in (*g*) and (*h*), 10 ANF inputs at the soma were used. The inputs for the simulated period histograms shown in (*g*) were from the high SR ANF at the low sound level (shown in (*a*)); inputs in (*h*) were from the low SR ANF at the high sound level (shown in (*d*)).

Stimuli with carrier frequencies centered away from unit BF were found to generate large AM in responses at high sound levels, larger than that observed even in most of low SR ANFs for stimuli with carrier frequencies near BF (data not shown). This result reflects both the higher thresholds for off-BF stimuli as well as a much more gradual decrease in modulation with increasing sound level above threshold. Therefore, off-BF inputs to cells in AVCN provide another potential source of envelope modulation 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*e*, *f* show period histograms with envelopes, from a chopper unit whose BF is equal to that of the ANFs in figure 2*a–d*. Note that the amount of modulation at 70 dB SPL in the chopper unit (figure 2*f*) 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 SFS 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 2*g*, *h*. The histogram in figure 2*g* shows the model response with inputs generated from the high SR ANF at low sound level (40 dB SPL; figure 2*a*). The histogram in figure 2*h* was generated with inputs from the low SR ANF at the high sound level (70 dB SPL; figure 2*d*). 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 2*b*) 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 2*h*) 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 without 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 2*h* 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).

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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.