Representation of Tones in Noise in the Responses of Auditory Nerve Fibers in Cats

I. Comparison with Detection Thresholds[1]

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Abstract

Rate and temporal responses evoked by 1-kHz or 8-kHz tones in continuous broadband noise are described for large populations of auditory nerve fibers in anesthetized cats. The signal-to-noise ratios (S/Ns) of the tone and noise stimuli were above behavioral detection thresholds. Stimulus combinations were presented (1) over a range of moderate to high noise intensities at a constant S/N and (2) using high intensity noise and varying S/N. Responses of low (<1 spike/sec) and medium (1 to 19 spikes/sec) spontaneous rate (SR) fibers were compared with those of high SR (>19 spikes/sec) fibers. Low and medium SR fibers with best frequencies in the region of the test tone frequency exhibited tone-evoked rate changes at all sound levels tested. High SR fibers, in contrast, exhibited much weaker tone-evoked rate changes at the lowest noise level tested. In the presence of high intensity noise, high SR fibers did not exhibit tone-evoked rate changes due to saturation by the noise. Fibers with best frequencies in the region of 1 kHz also exhibited strong phase-locking to the 1 kHz tone which increased as the tone level increased but which did not differ for the various SR groups. Results suggest that information in the rate responses of low and medium SR fibers can account for the encoding of information about tones in noise by the nervous system.

Auditory nerve fibers respond to changes in the intensity of tones by changing their average discharge rates. For most auditory nerve fibers, however, rate changes occur over a restricted range of sound intensities. This raises the problem of how rate activity of auditory nerve fibers can account for representation of spectral information at moderate and high sound intensities, where, presumably, most fibers' responses are saturated. Recent studies have described two fundamental properties of auditory nerve fibers that may extend the operating range of average rate activity over a wide range of intensities. First, fibers that have spontaneous discharge rates in the region of 0 to 15 spikes/sec exhibit wider dynamic ranges and generally higher and more widely dispersed absolute thresholds than do the majority of fibers (Kiang et al., 1970; Kim and Molnar, 1979;

Evans and Palmer, 1980). Studies of the physiological properties of these fibers suggest that this group may comprise two populations, low spontaneous rate (SR) and medium SR fibers, and that the widest dynamic ranges and most widely dispersed thresholds are typical of the low SR group (Liberman, 1978; Schalk and Sachs, 1980; Liberman and Oliver, 1984). Although it is not clear whether low and medium SR fibers represent functionally separate groups, recent anatomical evidence indicates that, with regard to the size and location of peripheral terminals (Liberman, 1980), axonal diameter (Liberman and Oliver, 1984), and the size and number of simple synapses terminating in the cochlear nucleus (Rouiller et al., 1983), low and medium SR fibers apparently form a group distinct from the high SR group. Also, it has been shown that the dynamic ranges of auditory nerve fibers are labile under certain circumstances. The dynamic ranges that fibers exhibit in response to best frequency (BF) tones in quiet are shifted to higher tone intensities in the presence of broadband noise (Rhode et al., 1978; Geisler and Sinex, 1980; Palmer and Evans, 1982; Costalupes et al., 1984). Such shifting of dynamic ranges to higher tone intensities extends the overall operating range of the rate responses of auditory nerve fibers.

The dynamic range limitation of auditory nerve fibers has prompted some investigators to speculate that phase-locking, discharge patterns that reflect the fine temporal structure of the stimulus, provides a basis for the representation of spectral information. Phase-locking to tones in the presence of noise (Abbas, 1981; Costalupes and Hellstrom, 1984) and to certain components of steady-state vowels (Young and Sachs, 1979) is preserved at high intensities. Phase-locking only occurs, however, for frequencies up to about 5 kHz (Johnson, 1980). Hence, theories of neural coding that invoke temporal coding of low frequency spectral information must allow for average rate coding of high frequency information.

The saliency of rate and temporal information in the discharge patterns of auditory nerve fibers can be evaluated by describing response properties of fibers to stimuli that are within the range of the animals' hearing. In the case of the representation of tones in the presence of noise, behavioral studies using cats have reported detection thresholds of tones in noise at spectrum levels from −17 to 43 dB sound pressure level (SPL) (Pickles, 1975, 1979; Costalupes, 1983).

This study describes the responses of auditory nerve fibers in the cat to tones in noise at signal-to-noise ratios (S/Ns) that are slightly above mean behavioral masked threshold for detection. Responses to a selected frequency are obtained from a large number of fibers covering a range of BFs (i.e., a population of fibers) in each cat in order to describe responses of fibers as a function of "place" along the cochlear partition (Liberman, 1982). The objectives of the present

study were to compare rate and temporal responses of populations of low and medium SR fibers with those of high SR fibers to moderate or high intensity tone and noise stimuli under two conditions: (1) S/N is kept constant and overall level is varied, or (2) noise spectrum level is kept constant and S/N is varied. Test tone frequencies used were 1 kHz, where rate and temporal information were available, and 8 kHz, where only rate information was present.

Materials and Methods

Healthy, adult cats, free of external ear obstruction and middle ear infection, were anesthetized initially with ketamine hydrochloride (120 mg, i.m.) and were given 1.2 mg of atropine sulfate to retard mucous secretions. Cats were tracheostomized and placed in an IAC 1204A sound-attenuating chamber. A small hole was drilled in the bulla, and a 20-cm piece of small-bore plastic tubing was inserted and cemented in place to allow pressure equalization in the middle ear cavity while leaving the bulla intact. The left external auditory meatus was transected and the eardrum was inspected with a microscope to verify that it was undamaged and that there was no evidence of wax on the eardrum. The head was placed in a stereotaxic frame and a hollow ear bar was inserted into the external meatus. The auditory nerve was exposed by cutting a hole in the posterior fossa of the skull just behind the tentorium and retracting the cerebellum medially with cotton balls or with a metal retractor. The nerve was bathed in a solution of 100 USP units of heparin/ml of saline to keep it moist and to retard coagulation of blood on the nerve. Anesthesia was maintained during the experiment by administering pentobarbital as needed through an intravenous cannula. Rectal temperature was kept at approximately 37°C by a thermostatically controlled heating pad placed under the cat. The cat was given about 3 ml of intravenous saline every 3 hr to prevent dehydration. Experiments typically lasted 24 to 48 hr.

Tones and pseudorandom broadband noise were synthesized digitally and presented via a digital-to-analogue converter. Acoustic stimuli were delivered through a closed acoustic system using an electrostatic driver mounted on the hollow ear bar. The system was designed to produce an approximately flat sound field. Sound levels near the eardrum were calibrated with a high impedance probe tube at the beginning of each experiment and are shown for selected experiments in Figure 1. The spectrum level of the electrical noise signal at the input of the earphone amplifier was calibrated with a General Radio 1900A wave analyzer. Noise spectrum levels are specified as dB re 20 μPa/$\sqrt{\text{Hz}}$, and tone intensities are specified as dB re 20 μPa (i.e., dB SPL). Noise spectrum level varies in accordance with the acoustic calibrations shown in Figure 1. Noise spectrum levels given in this paper were determined at the frequency of the test tone for which data were obtained.

Recordings were obtained from individual auditory nerve fibers using 3 M NaCl-filled glass micropipettes with 10 to 40 megohms resistance. Noise bursts were used as a search stimulus to isolate fibers. BF for each fiber was determined by manually sweeping frequency and intensity of tone bursts to determine the most sensitive frequency. Spontaneous discharge rate of

each fiber was determined by collecting approximately 200 spike discharges in the absence of acoustic stimulation. In the case of low SR fibers, spikes were collected for approximately 60 sec.

The responses of large numbers of auditory nerve fibers were recorded to a limited stimulus set consisting of 1-kHz or 8-kHz tone bursts in the presence of continuous background noise. Test stimuli were usually 200-msec tone bursts with 10-msec rise/fall times. The background noise was turned on at least 15 sec prior to beginning testing and was left on continuously so that a steady state of noise-evoked activity was obtained (Costalupes et al., 1984). Tone bursts were presented once per second and were repeated until approximately 1000 spikes were collected during the test tone bursts. The 200-msec tone burst was followed by an 800-msec period during which the noise background alone was on.

In most experiments, test tones were delivered in the presence of noise at three spectrum levels at a constant S/N. The three noise spectrum levels and corresponding tone intensities were spaced at 20-dB intervals. In experiments 1/17/84 and 3/09/84, tones were delivered in the presence of one high intensity noise spectrum level selected for each experiment. Three tone intensities were used so that the stimulus set comprised three S/Ns.

The following experimental protocol was used in all experiments. After a fiber was isolated and its BF, threshold, and SR were determined, responses were obtained to a BF tone 50 dB above the fiber's threshold. Responses were then obtained to 1- or 8-kHz tone bursts in continuous noise. Recovery periods (60 sec) were inserted to help prevent fatigue of fiber responsiveness as a result of exposure to high intensity noise.

Signal-to-noise ratio (S/N) is defined in this paper as

$$S/N = L_{to} - L_{No} \tag{1}$$

where L_{to} is the level of the test tone and L_{No} is the noise spectrum level. S/Ns were selected that were above mean behavioral threshold for detecting tones in noise by cats (Costalupes, 1983). In behavioral studies, the S/N at the threshold for detecting a tone in broadband noise calculated according to equation 1 is known as the critical ratio. Critical ratios for 1-kHz tones for cats are approximately independent of noise intensity over a range of noise spectrum levels from 13 to 43 dB, and an average of 22 dB. Critical ratios for 8-kHz tones are approximately constant over the range of noise spectrum levels from −7 to 23 dB and an average of 27 dB.

Steady-state average discharge rates for auditory nerve fibers were computed from the last 180 msec of the 200-msec test tone interval. Rate changes evoked by the test tone in the presence of continuous broadband noise were determined by subtracting the average rate during the noise alone from the average rate during the tone and noise interval. Noise-evoked rate was determined from the last 200 msec of the 1000-msec testing period.

Phase-locking was determined from period histograms computed with 32 bins/cycle. A discrete (fast) Fourier transform of period histograms was computed. The amplitude of the *n*th harmonic of the discrete Fourier transform gives a measure of phase-locking of fibers' responses to the *n*th harmonic of the stimulus in spikes per second, referred to as synchronized rate. Synchronized rate was not normalized in any way since normalizing tends to reduce variability between SR types.

All cats exhibited absolute thresholds for tones that were within the ranges reported for "routine-normal" cats by Liberman (1978).

Results

Results are presented based on recordings from 1254 fibers in 12 cats. Auditory nerve fibers are classified on the basis of spontaneous discharge rates according to the scheme used previously (Costalupes et al., 1984). High SR fibers (>19 spikes/sec) accounted for 68.2% of the fibers in the sample, medium SR fibers (1 to 19 spikes/sec) accounted for 21.5% of the fibers, and low SR fibers (<1 spike/sec) accounted for 9.5% of the fibers in the sample. These results are similar to previous distributions of SR groups reported by Kiang et al. (1970), Evans and Palmer (1980), and Liberman (1978). Kim and Molnar (1979), however, reported a much reduced proportion of low and medium SR fibers (24%) in their sample. The reasons for the discrepancy are not known.[3]

Figure 1. Acoustic calibrations for selected experiments. Plots show maximum tone intensity in dB SPL as a function of frequency. Calibrations are shown for experiments from which rate change profiles are presented in this paper. Calibrations repeated at the end of the experiments had changed by less than 5 dB.

[3] Kiang et al. (1970), Kim and Molnar (1979), and Evans and Palmer (1980) defined fibers with SR < 15 spikes/sec low SR fibers. Liberman (1978) defined low and medium SR fibers as exhibiting < 0.5 spikes/sec and < 18 spikes/sec, respectively. There are very few fibers in the region of 15 to 19 spikes/sec (less than 1% of the fiber sample in this study). Comparisons of low and medium SR distributions with high SR distributions are thus reasonable despite differences in criteria for SR types.
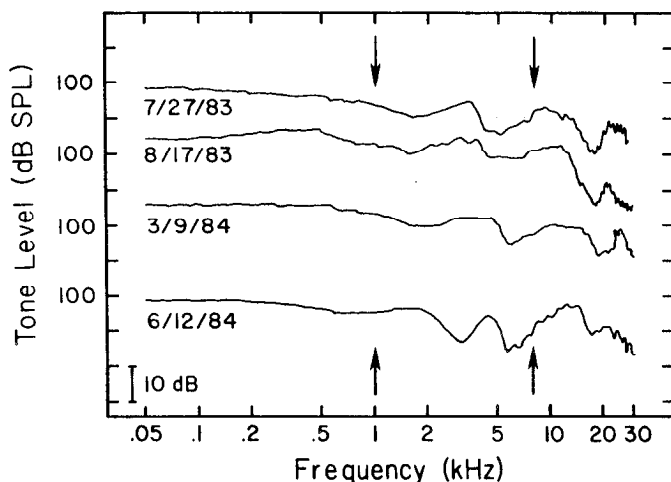
The rate responses of the populations of auditory nerve fibers evoked by 1- and 8-kHz tones in noise were similar in most respects. Average discharge rates elicited by 8-kHz tone bursts in the presence of continuous broadband noise are shown for a population of auditory nerve fibers in Figure 2A. The intensity of the tone and the noise spectrum level produced an S/N of 36 dB, or 9 dB above mean behavioral detection threshold for 8-kHz tones in noise for cats. In all experiments, the distributions of total discharge rates based on SR group were similar to that of Fig. 2A: low SR fibers exhibited generally the lowest total discharge rates, medium SR fibers exhibited intermediate rates, and high SR fibers exhibited the highest overall rates.

Figure 2B is a rate change profile that shows responses evoked by the test tone (computed by subtracting average rate during the noise-alone period from total discharge rate for each fiber) for the same data shown in Figure 2A. Rate change profiles were used in other studies to describe rate responses of populations of auditory nerve fibers (Sachs et al., 1983). The data points in Figure 2B were
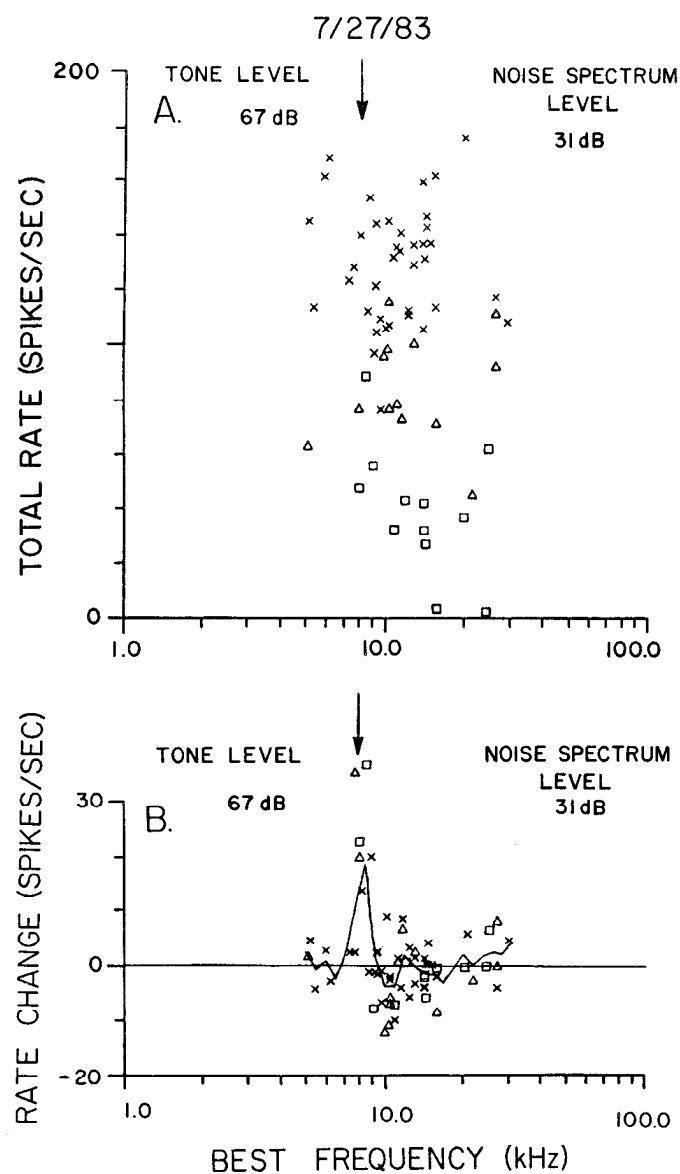

Figure 2. A, Total average discharge rates in response to 8-kHz tone bursts in the presence of continuous noise as a function of BF. Tone and noise intensities are indicated in dB SPL. The *arrow* indicates the frequency of the 8-kHz test tone. □, low SR fibers; △, medium SR fibers; x, high SR fibers. B, Rate change profile for the same data shown in A. The *solid line* is a triangularly weighted moving average of the data points.

fit by a triangularly weighted, quarter-octave-wide moving average spaced at eighth-octave intervals. The moving average is indicated by the *solid line*. The peak in the moving average at approximately the 8-kHz place shows that fibers with BFs near 8 kHz on the whole responded to the test tone in noise by increasing their rate of discharge, whereas fibers with BFs remote from 8 kHz on the whole showed no rate change over the response to the noise alone.

Tone and noise presented at constant S/N

Average rate. In this section, results are described in terms of average rate for experiments in which three moderate to high intensity tone and noise spectrum levels were used and S/N was kept constant. Results are discussed first for the 1-kHz stimulus and then for the 8-kHz stimulus. Figure 3 shows typical rate change profiles for an experiment in which the S/N was 7 dB above mean behavioral detection threshold for 1-kHz tones in noise. Three tone and noise intensities were spaced at 20-dB intervals and are indicated by the three rows. Rate change profiles for high SR fibers are shown in the *left column*. A small peak in the moving average near 1 kHz in Figure 3A indicates a weak tone-evoked response among high SR fibers at the lowest overall intensity used in this experiment. A larger peak in the moving average is noted, however, among the low and medium SR fibers in response to the same stimulus combination (Fig. 3D). In all experiments, low and medium SR fibers with BFs near 1 kHz exhibited larger tone-evoked rate increases than did their high SR counterparts in response to a given stimulus intensity over the range of intensities tested. High SR fibers showed no evidence of tone-evoked activity in the presence of high intensity noise (Fig. 3C), whereas low and medium SR fibers responded differentially to the test tone at all noise levels tested (Fig. 3, D to F).

Figure 3 also shows that low and medium SR fibers with BFs in the region of 1.3 to 2.0 kHz exhibited reduction of their noise-evoked discharge rates by the tone stimulus. When S/N was held constant and overall level varied, the largest rate reductions were noted at the highest intensities.

Responses to 8-kHz test tones in noise were essentially the same as those to 1-kHz tones. Figure 4 shows that low and medium SR fibers with BFs near 8 kHz exhibited larger tone-evoked responses than did high SR fibers in response to the same stimulus combination (Fig. 4, A and D, B and E, C and F). At high intensities, high SR fibers showed little or no tone-evoked activity (Fig. 4C), whereas low and medium SR fibers still responded to the test tone.

The amplitude of the average rate increases evoked by 1- or 8-kHz tones in noise among low and medium SR fibers declined as overall intensity was raised when S/N was held constant. This is illustrated in Figure 5, which summarizes the relationship between overall intensity of the stimulus combination and amplitude of the tone-evoked rate increase (i.e., peak amplitude in the moving average) among low and medium SR fibers for data from several experiments. An exception, indicated by the *solid squares*, is attributable to the low overall intensity of the tone and noise stimulus at the lowest level tested.

Analyses of onset responses to test tones were obtained by averaging spike counts from 5 to 15 msec following stimulus onset. Figure 6 illustrates that, for all SR types, onset responses were greatly reduced or absent as compared with steady-state responses of fibers with BFs near the test tone frequency. Similar results were reported by Sachs et al. (1983) for vowels in noise.

Temporal responses. Figure 7 shows phase-locking to the 1-kHz test tone in noise as a function of overall intensity at a constant S/N. Data are from the same experiment shown in Figure 3. Strong phase-locking was noted in all 1-kHz experiments among low and medium as well as high SR fibers, with BFs near 1 kHz at all S/Ns tested. S/Ns that were slightly below detection threshold in pilot studies revealed no tone-evoked rate response but produced phase-locking among fibers in the 1-kHz region. For all S/Ns tested, no consistent difference in the amount of phase-locking for fibers with BFs near 1 kHz was noted between low and medium SR and high

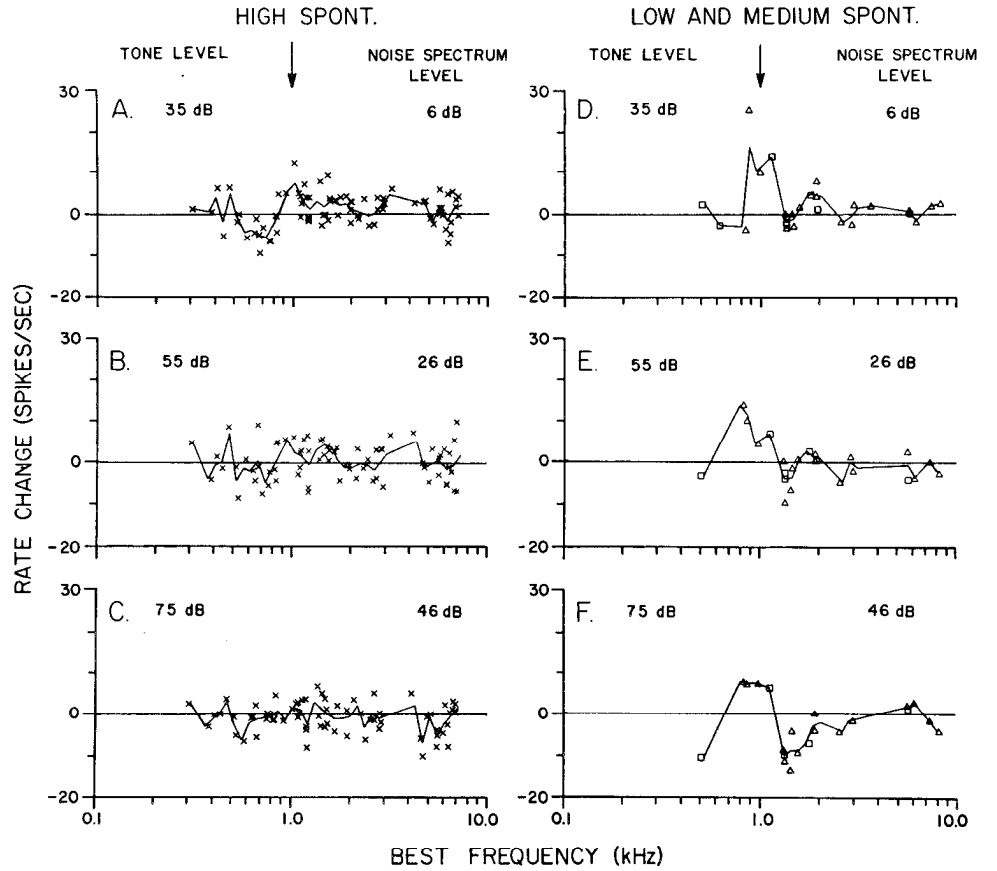HIGH SPONT.   LOW AND MEDIUM SPONT.

Figure 3. Rate change profiles for auditory nerve fibers in response to 1-kHz test tone in noise. *Left-hand column,* High SR fibers. *Right-hand column,* Low and medium SR fibers. The noise spectrum levels and corresponding tone intensities are indicated in each *panel.* S/N in each case was 29 dB. *Symbols* are described in the legend to Figure 2.

TONE LEVEL   NOISE SPECTRUM LEVEL   TONE LEVEL   NOISE SPECTRUM LEVEL

A. 35 dB   6 dB   D. 35 dB   6 dB

B. 55 dB   26 dB   E. 55 dB   26 dB

C. 75 dB   46 dB   F. 75 dB   46 dB

RATE CHANGE (SPIKES/SEC)

BEST FREQUENCY (kHz)

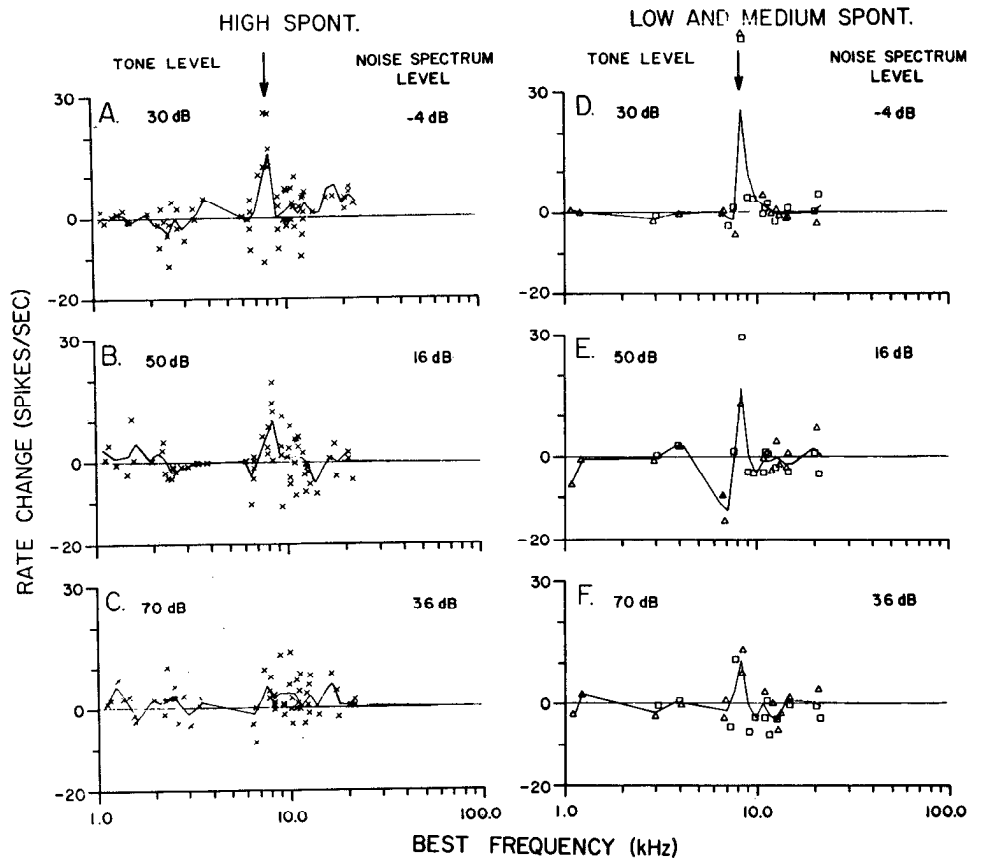HIGH SPONT.   LOW AND MEDIUM SPONT.

Figure 4. Rate change profiles for a population of auditory nerve fibers in response to 8-kHz test tone in noise. S/N was 34 dB. *Symbols* are described in the legend to Figure 2.
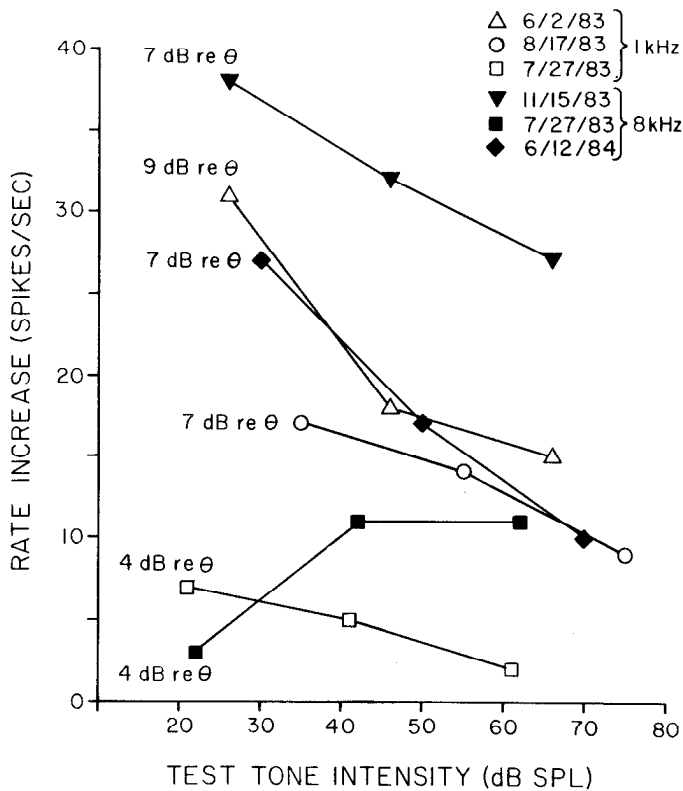
TONE LEVEL   NOISE SPECTRUM LEVEL   TONE LEVEL   NOISE SPECTRUM LEVEL

A. 30 dB   -4 dB   D. 30 dB   -4 dB

B. 50 dB   16 dB   E. 50 dB   16 dB

C. 70 dB   36 dB   F. 70 dB   36 dB

RATE CHANGE (SPIKES/SEC)

BEST FREQUENCY (kHz)

Figure 5. Amplitude of the tone-evoked rate response (*ordinate*) as a function of the intensity of the test tone (*abscissa*). Response amplitude was measured as the highest point in the moving average (in spikes per second) in the region of the test tone frequency on the rate change profile. Each set of *symbols* represents one experiment using three tone and noise intensities at a constant S/N.
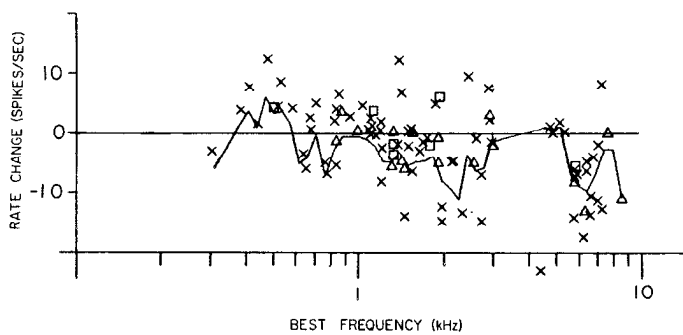

Figure 6. Rate change profile based on onset responses of fibers. Data are from the same fibers shown in Figure 3, *B* and *E*. *Symbols* are described in the legend to Figure 2.

SR groups. For a given stimulus S/N, however, two properties were noted. First, there was a slight decline in synchronized rate as overall intensity was raised. Second, phase-locking spread to fibers with successively higher BFs as overall intensity was raised. Little or no phase-locking was noted at BFs below 500 Hz.

Tone and noise presented at variable S/N

Average rate. The second objective of this study was to describe responses of populations of fibers to tones in noise at several suprathreshold S/Ns. Figure 8 shows rate change profiles for a population of fibers in response to a 1-kHz tone in the presence of high intensity noise at three S/Ns. Noise spectrum level in each case was 43 dB SPL and tone levels were 78, 74, and 70 dB, which represented 13, 9, and 5 dB, respectively, above mean behavioral detection threshold. High SR fibers did not show peaks in the profiles at any of the three S/Ns tested, whereas low and medium SR fibers

showed tone-evoked rate changes at all three S/Ns. The amplitude of the tone-evoked rate increase among low and medium SR fibers increased when S/N increased.

Low and medium SR fibers with BFs slightly above the test tone frequency exhibited rate reduction that increased monotonically in amplitude and spread to fibers with successively higher BFs as S/N was raised. Low and medium SR fibers with BFs slightly below the frequency of the test tone also exhibited some rate reduction, although this did not change consistently with S/N. The rate reduction is attributable to rate suppression described for two-tone stimuli (Sachs and Kiang, 1968). For the tone in noise condition, the test tone is analogous to a suppressor tone and noise energy in the region of the fiber's BF is analogous to an excitor tone. The rate reductions among low and medium SR fibers generally exhibited the following properties: (*1*) greater suppression was noted at moderate to high sound levels among low and medium SR fibers than among high SR fibers; (*2*) greater suppression was noted at moderate to high sound levels at BFs above the test tone (below BF suppressors) than at BFs below the test tone (above BF suppressors); (*3*) the
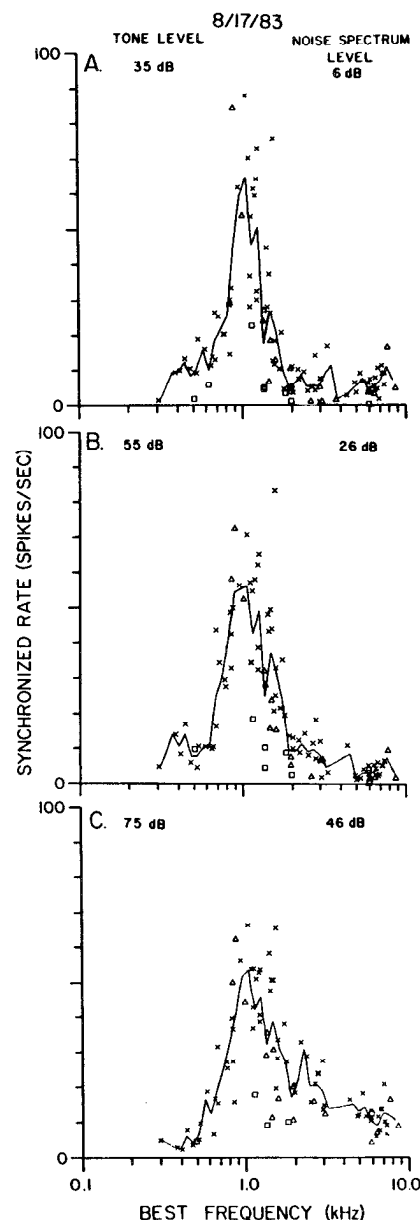

Figure 7. Synchronized rate profiles for 1-kHz test tone in noise at three tone and noise intensities (constant S/N). Data are from the same experiment shown in Figure 3. *Symbols* are described in the legend to Figure 2.
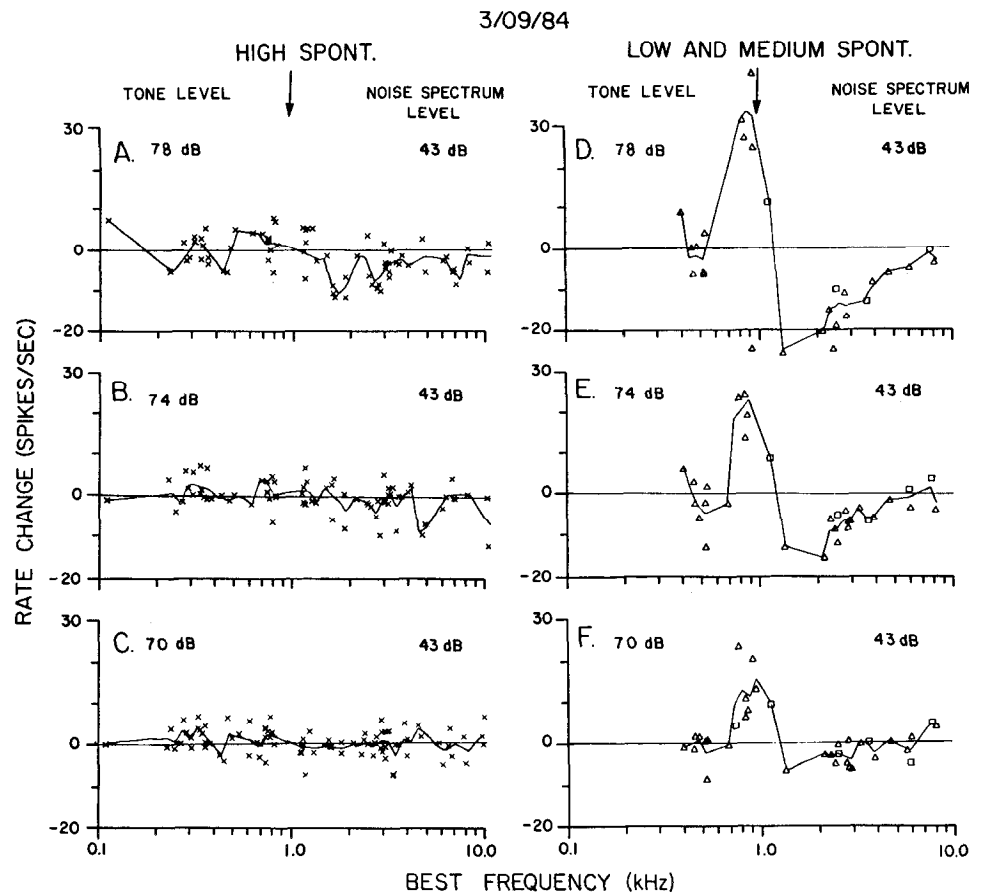
3/09/84

HIGH SPONT. LOW AND MEDIUM SPONT.

Figure 8. Rate change profiles for a population of auditory nerve fibers in response to 1-kHz test tone in noise at three S/Ns. Noise spectrum level in all cases was 43 dB SPL. Three tone intensities are arranged by row. S/Ns were 35 dB (*top row*), 31 dB (*middle row*), and 27 dB (*bottom row*), which are 13, 9, and 5 dB, respectively, above mean behavioral detection threshold. The moving average has been adjusted slightly. *Symbols* are described in the legend to Figure 2.

RATE CHANGE (SPIKES/SEC)

BEST FREQUENCY (kHz)

amount of rate suppression for fibers with BFs greater than 1 kHz was a function of the intensity of the test tone; and (*4*) suppression was greatest among fibers with BFs nearest the test tone, and there was an abrupt change to rate excitation. These properties are consistent with the characteristics of two-tone suppression reported for two-tone complexes (Sachs and Abbas, 1974; Abbas and Sachs, 1976; Javel et al., 1978), for band-limited noise (Schalk and Sachs, 1980), and tones in noise (Rhode et al., 1978; Geisler and Sinex, 1980; Costalupes et al., 1984).

Figure 9 summarizes the behavior of tone-evoked rate increases of low and medium SR fibers for tones in noise as a function of S/N. In order to permit comparison of data from different cats with mean behavioral thresholds, rate data were normalized by expressing rate change of each fiber as a proportion of its estimated dynamic range according to the formula

$$R_{Norm} = \frac{R_{t+No} - R_{No}}{R_{\theta+50} - R_{sp}} \tag{2}$$

where R_{t+No} is total driven rate, R_{No} is driven rate to the noise alone, $R_{\theta+50}$ is driven rate to a BF tone 50 dB above the fiber's threshold, and R_{sp} is the fiber's SR. Figure 9 shows that the amplitude of the tone-evoked response increased with the intensity of the test tone. A straight line fit to pass through the ordinate describes the data points.

Temporal responses. Figure 10 shows synchronized rate responses for the same population of fibers shown in Figure 8. Large peaks in the moving averages indicate strong phase-locking at all three suprathreshold S/Ns. The intensity of the test tone determined the amplitude of synchronized rate for fibers in the region of 1 kHz as well as the amount of spread of synchrony to fibers with BFs above 1 kHz. In general, phase-locking spread more rapidly to high SR fibers than to low and medium SR fibers, which is attributable to the lower thresholds of high SR fibers.

Discussion

The results of this study show that selected auditory nerve fibers in the cat exhibit tone-evoked rate and temporal responses in the presence of continuous broadband noise at S/Ns near behavioral detection thresholds over a wide range of moderate to high noise levels. Results are consistent with reports that some auditory nerve fibers exhibited rate or temporal responses to BF tones in noise at S/Ns near behavioral detection threshold (Abbas, 1981; Young, 1984). At moderate to high noise levels, the rate representation occurs among low and medium SR fibers. High SR fibers, in contrast, are saturated by high intensity noise. Strong phase-locking occurs among fibers with BFs near test tone frequency regardless of SR, and phase-locking spreads to fibers with successively higher BFs as test tone level is raised.

Relation to previous auditory nerve studies. As was discussed in the introduction, the wider overall operating range of low and medium SR fibers is attributable to the higher and more widely dispersed thresholds and wider dynamic ranges (including sloping saturation) that the low and medium SR groups exhibit and to dynamic range shifts which, in particular, render low and medium SR fibers resistant to saturation by high intensity noise (Costalupes et al., 1984). Because of their higher thresholds and wider dynamic ranges, low and medium SR fibers also responded less vigorously to the noise background and thereby exhibited larger rate increases than did their high SR counterparts.

The effects of broadband noise on rate behavior of auditory nerve fibers also account for the noise level-dependent decline in the amplitude of the tone-evoked response among low and medium SR fibers, summarized in Figure 5. Noise dominates the low level response of fibers and raises the threshold for tone-evoked response (Rhode et al., 1978). Noise-evoked rate monotonically increases as noise intensity is raised. Two-tone suppression of the tone-evoked response by the noise shifts dynamic range to higher intensities

(Narins, 1984), which retards saturation by the noise. However, because the effectiveness of the noise in obscuring the tone-evoked response proceeds at a somewhat faster rate than dynamic range shift (approximately 0.6 dB of shift/1-dB increase in noise intensity (Costalupes et al., 1984)), smaller rate increases occur at successively higher noise levels.

The low absolute rate thresholds and narrower dynamic ranges of high SR fibers suggest that these fibers may be especially important in determining absolute sensitivity of hearing in quiet. The overall operating ranges of cells in the cochlear nucleus, conversely, could be extended if cells received convergent input from fibers representing different SR groups. There is evidence, for instance, that fibers of different SR types converge to form end bulbs of Held in the anteroventral cochlear nucleus. It has been shown that fibers associated with each SR group terminate in end bulb of Held complexes (Rouiller et al., 1983). The cells of these complexes are believed to derive their SR from auditory nerve fibers (Koerber et al., 1966). Goldberg and Brownell (1973), however, failed to isolate end bulb cells with low SR. Therefore, these cells may derive their SR from convergent input from low, medium, and high SR fibers. Evidence of extended dynamic ranges among cochlear nucleus cells has been described by Gibson et al. (1985), who suggested that cochlear nucleus cells exhibit resistance to saturation by noise that was comparable to that observed for low and medium SR fibers. Finally, Rouiller et al. (1983) reported that simple synapses associated with low and medium SR fibers were found in the cochlear nucleus in greater numbers than those associated with high SR fibers. They suggest that low and medium SR fibers may exert a greater influence in coding information that is averaged across SR groups.

Effects arising from efferent projections to the cochlea, about which little is known at present, may prove to be important. Efferent fibers to the outer hair cells project primarily to the high frequency (basal) end of the cochlea (Ishii and Balogh, 1968). Studies by Wiederhold (1970) showed that stimulation of efferent fibers shifts the dynamic ranges of auditory nerve fibers to higher intensities. Thus, activation of auditory efferents by broadband noise may reduce tone- and noise-evoked rates of high BF fibers, thereby reducing rate variability and improving detectability of the tone signal in noise.

Comparison with psychophysical studies. Tone-evoked rate responses among low and medium SR fibers were restricted to a range of BFs in the region of the test tone frequency. Moreover, insofar as each fiber generally showed either a rate increase or a decrease at each of the tone levels tested, the spatial rate representation shown in the population profile was to a first-approximation constant as overall intensity was varied. The spatial representation of the rate response exhibited filter properties that can be compared with psychophysically determined peripheral filtering properties. Psychophysical studies show that the noise power required to mask a test tone is independent of noise bandwidth within a restricted range of frequencies surrounding the frequency of the test tone. The constant power bandwidth is known as the *critical band* and is believed to reflect frequency resolution of the cochlea. A comparable measure, the *critical ratio*, is derived from detection threshold for tones in broadband noise. Critical ratios differ from critical bands by a constant decibel separation for frequencies above 250 Hz (see Costalupes, 1983, for the cat) and are believed to reflect the same mechanism. However, since a tone is detectable when its power is roughly 4 dB less than the power of the noise, critical ratios give a spurious estimate of the width of the psychophysical peripheral filter. Comparisons of neural and psychophysical bandwidths will therefore be made using critical bandwidths. The case for rate coding will be strengthened if it can be shown that rate responses occur over a range of BFs comparable to that of critical bands obtained from behaving cats.

Neural bandwidths were determined for each experiment by using the population profile that had the greatest number of low and medium SR fibers in the region of the test tone frequency. The upper edge of the bandwidth was the arithmetic mean of the highest BF showing a tone-evoked rate increase and the BF of the nearest fiber not showing a rate increase (usually this fiber showed rate suppression). The lower limit was the similar arithmetic mean of the lowest BF showing a rate increase in the region of the test tone and the nearest BF showing no rate increase. Bandwidth was defined as the difference between these two means. Table I shows that neural critical bands derived from the rate responses of low and medium SR fibers to tones in noise were comparable to psychophysical critical bands for both 1- and 8-kHz test tones. In view of the presumed cochlear origin of two-tone suppression (Sellick and
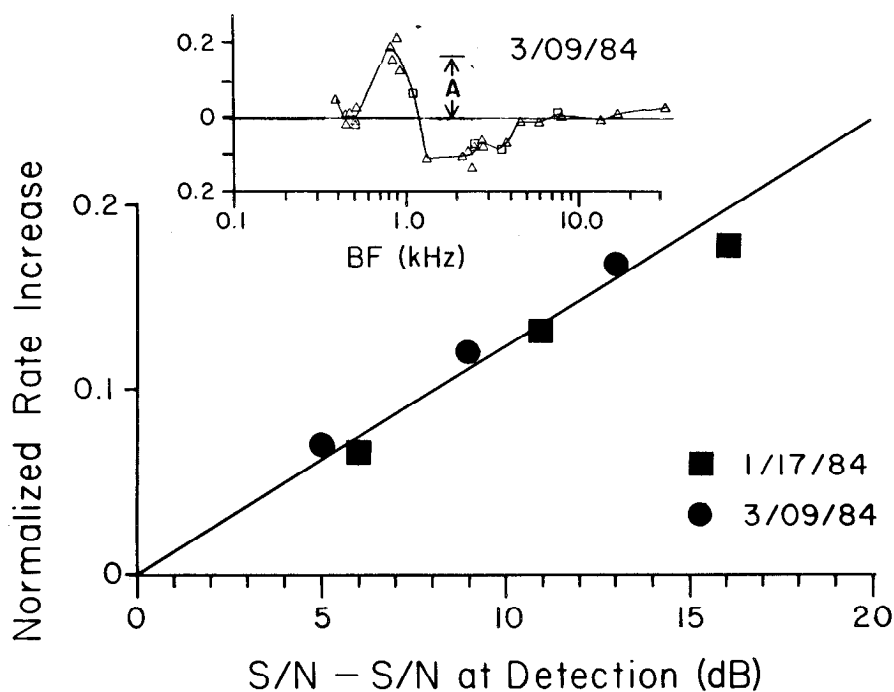

Figure 9. Normalized peak amplitudes in the region of 1 kHz as a function of stimulus S/N. The *abscissa* indicates decibels above the mean behavioral detection threshold. The *straight line* was fit by eye. *Inset:* Normalized rate change profile for a population of low and medium SR fibers. Response amplitude at the peak of the moving average is indicated by *A*.

TABLE I

Neural and psychophysical critical bandwidths

	1 kHz		8 kHz	
Neural	Exp. 8/17/83	450 Hz	Exp. 7/27/83	1890 Hz
	Exp. 1/17/84	476 Hz	Exp. 3/16/84	1610 Hz
	Exp. 3/09/84	526 Hz	Exp. 6/12/84	1330 Hz
Psychophysical	Pickles (1975)[a]	350 Hz	Pickles (1975)[a]	1520 Hz
	Pickles (1979)[a]	418 ± 50 Hz		
	Pickles (1979)[b]	436 ± 78 Hz		

[a] Masking by noise of variable bandwidth.
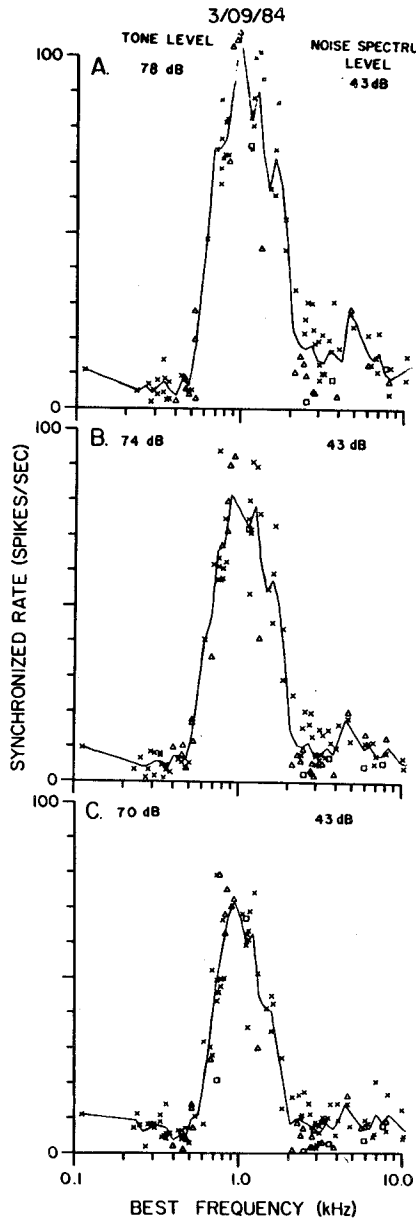[b] Masking by rippled spectrum noise.

Figure 10. Synchronized rate profiles for 1-kHz test tone in 43-dB spectrum level noise at three S/Ns. Data are from same experiment shown in Figure 7. *Symbols* are described in the legend to Figure 2.

medium SR fibers in the presence of moderate to high intensity background noise levels for behavioral suprathreshold S/Ns. Temporal information is also present and cannot be ruled out as a basis for encoding information used in detecting tones in noise. The rate representation among low and medium SR fibers, however, was found over a range of S/Ns that was similar to those of behavioral detection thresholds and was confined to a tonotopic region similar to those of behavioral critical bandwidths. These properties are consistent with a neural coding scheme based on average rate information in the discharge patterns of auditory nerve fibers.

Further studies should consider whether average rate responses of auditory nerve fibers account for the representation of spectrally complex sounds such as speech. Studies using steady-state synthesized vowels revealed that low SR fibers maintained a robust representation of first formant frequencies at high overall sound levels (Sachs and Young, 1979; Sachs et al., 1983). Rate changes among fibers with BFs in the region of second and third formant frequencies, which are important for correct identification of vowel sounds, were also noted in some circumstances. The role of two-tone suppression in either enhancing or suppressing representation of second and third formant frequency information is of particular interest. A description of the representation of spectrally complex sounds such as vowels in the rate responses of low and medium SR fibers using behaviorally relevant sound levels would contribute greatly to testing the general usefulness of a rate-coding scheme.

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Russell, 1979), the spatially restricted rate representation supports the view that psychophysical critical bands reflect cochlear resolution and provides further support for a rate-place coding scheme.

Concluding remarks. The results of this study show that rate information is present in the tone-evoked responses of low and

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