

# Auditory nerve representation of a complex communication sound in background noise

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A population study of auditory nerve responses in the bullfrog, *Rana catesbeiana*, analyzed the relative contributions of spectral and temporal coding in representing a complex, species-specific communication signal at different stimulus intensities and in the presence of background noise. At stimulus levels of 70 and 80 dB SPL, levels which approximate that received during communication in the natural environment, average rate profiles plotted over fiber characteristic frequency do not reflect the detailed spectral fine structure of the synthetic call. Rate profiles do not change significantly in the presence of background noise. In ambient (no noise) and low noise conditions, both amphibian papilla and basilar papilla fibers phase lock strongly to the waveform periodicity (fundamental frequency) of the synthetic advertisement call. The higher harmonic spectral fine structure of the synthetic call is not accurately reflected in the timing of fiber firing, because firing is "captured" by the fundamental frequency. Only a small number of fibers synchronize preferentially to any harmonic in the call other than the first, and none synchronize to any higher than the third, even when fiber characteristic frequency is close to one of these higher harmonics. Background noise affects fiber temporal responses in two ways: It can reduce synchronization to the fundamental frequency, until fiber responses are masked; or it can shift synchronization from the fundamental to the second or third harmonic of the call. This second effect results in a preservation of temporal coding at high noise levels. These data suggest that bullfrog eighth nerve fibers extract the waveform periodicity of multiple-harmonic stimuli primarily by a temporal code.

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## INTRODUCTION

The manner in which complex acoustic signals are coded and transformed by the ear is an issue fundamental to understanding and modeling information processing in the auditory system. A large corpus of work exists on the peripheral processing of pure tone stimuli; this research has provided valuable clues on how acoustic information is represented by neural activity, but it is insufficient for predicting neural coding of the types of spectrally and temporally complex signals listeners must cope with in their natural environments. Several different laboratories have approached this problem by measuring activity of mammalian peripheral fibers to various kinds of synthetic speech sounds, both at ambient levels and in the presence of background noise (e.g., Carney and Geisler, 1986; Deng and Geisler, 1987; Delgutte and Kiang, 1984a,b,c,d; Geisler and Gamble, 1989; Kiang and Moxon, 1974; Palmer, 1990; Palmer *et al.*, 1986; Sachs *et al.*, 1983, 1988; Sachs and Young, 1979; Young and Sachs, 1979). A variety of processing schemes based on these data have been proposed to account for the neural representation of speech sounds, but whether some predominantly spectral, predominantly temporal, or combined spectral-temporal ap-

proach best describes all the data is still not settled (Delgutte, 1984; Deng and Geisler, 1987; Palmer, 1990; Sachs *et al.*, 1988; Secker-Walker and Searle, 1990; Shamma, 1985; Young and Sachs, 1979).

In our laboratory, we are approaching this issue from a somewhat different comparative perspective, by studying the functional properties of the peripheral auditory system in a particular species to acoustic stimuli that mimic biologically relevant sounds used by that species. This neuroethological approach allows comparisons of behavioral and physiological data from the same species and, because it is conducted with animals specialized for acoustic communication, may yield new insights on the neural processing of complex sounds. Anuran amphibians are excellent animals for conducting neuroethological analyses of sound processing. Many species of anurans have evolved a distinctive, stereotyped vocal repertoire used in regulation of social and reproductive behaviors. The spectral and temporal properties of these vocal signals have been studied both in terms of their acoustic parameters and their biological significance, and thus can be readily used in both behavioral and neurophysiological experiments as a means of examining auditory information processing. The male bullfrog, *Rana catesbeiana*, for example, employs a distinctive, species-specific vocalization to attract females for purposes of mating and to advertise to other males the occupation of a calling site (Capranica, 1968; Wiewandt, 1969). This advertisement call,

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the “jug-o’-rum” familiar to many people who have encountered these animals in their natural environments, consists of a number of harmonically related frequencies with a waveform periodicity ranging in different animals from about 90 to 110 Hz (Capranica, 1965). This vocalization shares certain acoustic features with human vowel sounds; both types of sounds are quasiperiodic with a relatively low fundamental frequency and possess a well-defined spectral envelope reflecting the resonance characteristics of the vocal tract.

Both the spectral and the temporal properties of anuran vocalizations are important for species identification and for distinguishing different functional categories of vocalizations within a species’ repertoire (Capranica, 1965; Gerhardt, 1988). Waveform periodicity can be a particularly important cue in communication for many species. For example, the advertisement calls of two sympatric species of treefrog vary in their periodicities, and behavioral experiments have shown that females of these species discriminate between these vocalizations primarily by these differences in periodicity (Gerhardt, 1978, 1988). Similarly, in playback experiments, males of several species discriminate between sounds, whether synthetic calls or noise bursts, that vary in their envelope periodicity (Allan and Simmons, 1991; Capranica, 1965; Rose and Capranica, 1984). Temporal cues are also important for discrimination of conspecific advertisement calls from conspecific aggressive calls in several species (Gerhardt, 1978; Schwartz, 1987).

The peripheral neural mechanisms underlying these behavioral discriminations are still under study. The anuran inner ear is unique among vertebrate inner ears in consisting of two separate organs specialized for the reception of sounds. The mechanical structure of these organs differs from that of the mammalian cochlea; for example, neither papilla contains a basilar membrane. The amphibian papilla (AP) is the larger of the two organs. In the bullfrog, the AP is innervated by approximately 1500 afferent fibers from the posterior branch of the eighth nerve; there is some efferent innervation as well, but its source is unknown (Wilczynski and Capranica, 1984). Each afferent fiber can innervate from 1–15 hair cells (Lewis *et al.*, 1982). The characteristic frequencies (CF) of these fibers range from about 100 to 1000 Hz, and, although the AP contains no basilar membrane, fibers innervating this organ are arranged in a tonotopic fashion, with lower CFs represented in the rostral portion and higher CFs represented in the caudal portion (Lewis *et al.*, 1982). Typically, AP fibers are broadly tuned, with  $Q_{10}$  values of about 0.5 to 4.0, comparable to tuning curve widths of mammalian fibers in the same frequency range (Feng *et al.*, 1975). The high-frequency slopes of these tuning curves are sharper than the low-frequency slopes. Only those fibers with CFs below about 500 Hz show two-tone suppression and then only to tones with frequencies above the CF (Zakon and Wilczynski, 1988). Amphibian papilla fibers phase lock to simple sinusoids up to frequencies of 700 to 900 Hz (Freedman *et al.*, 1988; Narins and Hillery, 1983), and to the envelope of amplitude modulated sounds up to frequencies of 300 to 500 Hz (Feng *et al.*, 1991; Simmons, 1992).

The second of the two auditory organs, the basilar pa-

pilla (BP), operates as a resonant organ in which, in an individual animal, all afferents (numbering approximately 300–500) have approximately the same CF. Basilar papilla fibers innervate from 1–4 hair cells; there is no known efferent innervation (Wilczynski and Capranica, 1984). BP fibers have higher CFs and tend to have higher thresholds, higher rates of spontaneous activity, and are more broadly tuned than AP fibers; they also do not show two-tone suppression. Across many species, the BP is tuned to a narrow, species-specific range that generally matches the higher range of dominant frequency components in the advertisement call of that species; the tuning of the BP can also vary with the animal’s size, sex, and geographic location (Zakon and Wilczynski, 1988). In the bullfrog, for example, the BP is tuned to frequencies between 1000 to 2000 Hz (Feng *et al.*, 1975; Freedman *et al.*, 1988), and the high-frequency spectral peak in the male bullfrog’s advertisement call is broadly centered around 1400 to 1500 Hz (Capranica, 1968). Also, BP fibers do not synchronize to simple sinusoids at fiber CF, but they will phase lock to sinusoids whose frequencies are below CF, as long as these frequencies are below about 900 Hz (Narins and Hillery, 1983).

Even though the AP and BP are tuned to different frequency ranges, fibers from these two organs respond remarkably uniformly to synthetic species-specific advertisement calls presented in quiet (ambient) conditions (Schwartz and Simmons, 1990). Regardless of its CF, rate of spontaneous activity, or papilla of origin within the inner ear, the synchronized responses of an individual eighth nerve fiber are dominated by the fundamental frequency (waveform periodicity) of the synthetic call. Both AP and BP fibers synchronize strongly to the fundamental frequency of the synthetic call, while phase locking less strongly or not at all to the harmonic frequency in the call closest to fiber CF (even though these fibers will phase lock to low-frequency sinusoids). That is, firing is “captured” by the fundamental frequency, and the higher harmonic spectral fine structure of the synthetic call is not represented in the synchronized responses of the population of fibers. This robust and homogeneous extraction of waveform periodicity is seen at stimulus intensities ranging from 70 to 100 dB SPL. These results are consistent with models of pitch extraction based on temporal coding mechanisms using measurements of the time intervals between major peaks in the stimulus envelope (Licklider, 1951; Schouten *et al.*, 1962).

The representation of acoustic features in complex vocalizations in the bullfrog’s eighth nerve thus differs in important respects from the representation of features of other complex vocalizations, synthetic speech, in the mammalian auditory nerve. The detailed formant structure of synthetic vowel sounds is generally represented in the discharge patterns of mammalian eighth nerve fibers (Delgutte and Kiang, 1984a; Sachs *et al.*, 1988; Young and Sachs, 1979). Fiber responses are not typically dominated by synchronized firing to the fundamental frequency of the vowel; instead, the synchronized response of a particular fiber is influenced by the position of fiber CF relative to the formant spectrum of the vowel (Delgutte and Kiang, 1984a; Palmer, 1990; Palmer *et al.*, 1986). That is, fibers with CFs close to

one of the formants in the vowel spectrum typically synchronize to this formant, and show little or no envelope modulation related to the fundamental period of the vowel (Miller and Sachs, 1984). Fibers with CFs between the formant frequencies can show these envelope modulations (Delgutte and Kiang, 1984a; Miller and Sachs, 1984; Palmer, 1990; Palmer *et al.*, 1986; Young and Sachs, 1979). The synchronized responses of a particular fiber are also influenced by the fiber's rate of spontaneous activity and the intensity level of the stimulus, as well as by fiber CF. Low spontaneous rate fibers can show strong synchronization to low harmonics of the fundamental frequency of nasal consonant-vowel syllables, particularly when fiber CF is close to one of the low formant peaks in the sound and when the sound is presented at low intensities; high spontaneous rate fibers show such effects only when fiber CF is between formant peaks (Deng and Geisler, 1987). Pitch extraction models based on these data include combined temporal-place processing (the distribution of synchronized activity across the fiber array) as well as purely temporal processing mechanisms (Delgutte, 1984; Miller and Sachs, 1984; Secker-Walker and Searle, 1990; Palmer, 1990).

Studies of the encoding of synthetic speech sounds by the mammalian auditory periphery have suggested that different components (rate or phase locked responses) of fiber discharge patterns can be affected differently by background noise (Delgutte and Kiang, 1984d; Geisler and Gamble, 1989; Kiang and Moxon, 1974; Sachs *et al.*, 1983), and the results of these noise experiments have proven useful in evaluating different coding strategies for the neural representation of speech. The present study extends our previous results in anurans (Schwartz and Simmons, 1990) by examining how the extraction of the waveform periodicity of a synthetic advertisement call by single auditory nerve fibers is affected by background noise. Noise affects both the rate and the synchronized responses of anuran peripheral fibers to simple sinusoids (Freedman *et al.*, 1988; Narins and Wagner, 1989), but its effects on the coding of more complex stimuli have not been studied. Because background signals of conspecific, heterospecific, and abiotic origin can interfere with acoustically mediated mating behavior in anurans, some mechanism must exist in the auditory system to reject these extraneous signals while maintaining efficient coding of both spectral and temporal features of biologically relevant signals. Here, we investigate whether the simple code for periodicity extraction observed under quiet conditions also operates under conditions of background noise.

## I. METHODS

### A. Surgical and recording procedures

Adult bullfrogs (150–350 g), obtained from a commercial supplier, were anesthetized by intramuscular injections of sodium pentobarbital (Abbott; 100 mg/kg) for both surgery and recording. The eighth nerve was exposed via a ventral approach through the roof of the mouth. The animal was wrapped in moist gauze to aid cutaneous respiration and positioned on a vibration isolation table (Newport Research Corp.) in a sound attenuating chamber (Industrial Acous-

tics). Experiments were conducted at temperatures of 20 °C–22 °C.

Activity of single eighth nerve fibers was recorded with glass micropipettes filled with 3 M KCl. Electrode impedances ranged from 20–40 M $\Omega$ . The micropipettes were advanced into the posterior branch of the nerve close to its emergence from the otic capsule using a Kopf Model 607 hydraulic microdrive. Action potentials were amplified by a WPI DAM 80 AC differential amplifier (gain of 1000, filtered at 0.01–3 kHz) and by a Rockland model 442 filter (gain of 20 dB, filtered at 0.3–3 kHz). They were displayed on an oscilloscope (Tektronix 922R), monitored over a loudspeaker, and recorded on one channel of a TEAC quadrophonic tape recorder for subsequent analysis.

### B. Stimulus generation and calibration

Synthetic advertisement calls were digitally constructed by Fourier synthesis on an IBM PC/XT computer with a Data Translation model DT 2801A board at a sampling rate of 10 kHz. The signal consisted of 21 harmonics of 100 Hz summed in sine phase, with a low-frequency peak (first “formant”) at 200 Hz, a dip in spectral energy at 500 Hz, and a broad high-frequency peak (second “formant”) centered at 1400 Hz. The energy at the high-frequency peak was 10 dB down from that at the low-frequency peak. The power spectral density at the fundamental frequency of 100 Hz was at least 20 dB less than the height of the predominant spectral peak at 200 Hz. The time waveform and amplitude spectrum of the synthetic call are shown in Fig. 1. Call duration was 800 ms and rise-fall time was 10 ms. The amplitudes and frequencies of the harmonics, the waveform periodicity, and stimulus duration were chosen to conform to those in the natural vocalization (Capranica, 1965), and to the stimulus used in our previous work (Schwartz and Simmons, 1990). The signals were low-pass filtered at 5 kHz (Krohn-Hite 3550), attenuated (Coulbourn S85-05 electronic attenuator), and transmitted to the first channel of a mixer/amplifier (Coulbourn S82-24). During an experiment, the synthetic call and a computer-generated pulse coincident with its onset were simultaneously recorded on two channels of the tape recorder.

Noise was generated by a Coulbourn S81-02 noise generator, low-pass filtered at 6 kHz (Krohn-Hite 3550), attenuated (Hewlett-Packard 350D), and transmitted to the second channel of the mixer/amplifier. The acoustic signals (synthetic call plus noise) were then passed through a Rane GE27 equalizer, amplified (Harmon-Kardon PM645 stereo amplifier) and presented ipsilateral to the exposed nerve using a Beyer DT-48 earphone enclosed in a specially constructed brass housing. Also inserted in this housing was a calibrated 1-mm probe tube attached to a Brüel & Kjær 4134  $\frac{1}{2}$ -in. condenser microphone and 2209 sound level meter for monitoring the sound pressure level of the stimuli at the animal's tympanum. A tapered rubber tube attached to the housing was placed close to, but not touching, the edges of tympanum and was sealed with silicone grease to form a closed system. The frequency response of the sound delivery system was calibrated at the beginning of each experimental

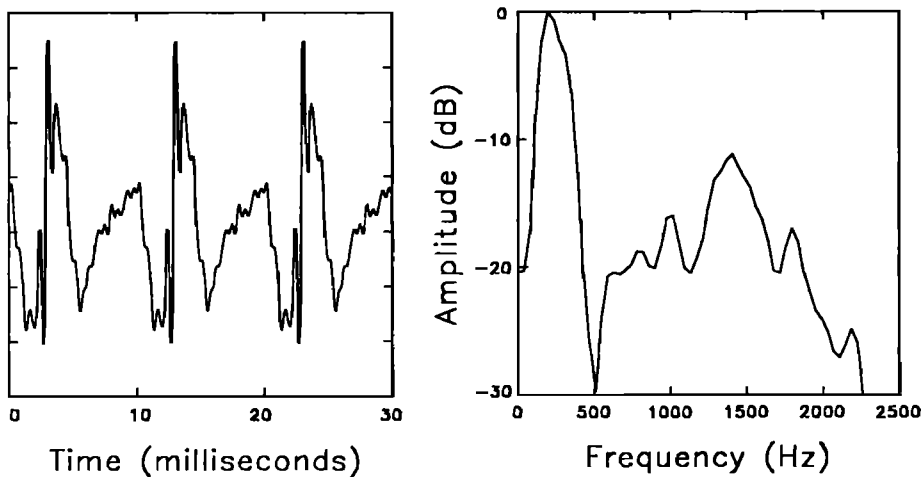


FIG. 1. Amplitude-time display (left) and Fourier spectrum (right) of three periods of the synthetic advertisement call. The call was digitally sampled at a rate of 20 kHz with an R/C electronics interface board in an IBM PC/AT computer and the spectrum was computed with ILS programs from Signal Technology, Inc.

session. Spectra, computed on line with ILS software from Signal Technology, Inc., were corrected for the frequency response of the earphone and the probe tube and were adjusted with the stereo equalizer to be flat ( $\pm 3$  dB) over the range of 100–3000 Hz (see Fig. 2). Loudspeaker distortion products were at least 55 dB down from the first harmonic at the frog's ear. Amplitudes of both the synthetic call and the background noise are expressed as rms amplitudes (dB SPL re:  $20 \mu\text{Pa}$ ).

### C. Procedure

A frequency-modulated sweep (0.05–3 kHz, sweep rate 1 per s, presented at 80 dB SPL) generated by one Wavetek model 182 function generator sweeping another was used as a search stimulus. Once an auditory fiber was encountered, its CF, threshold at both CF and to the synthetic call, and sharpness of tuning at 10 dB above threshold at CF were determined audiovisually. The relatively low spontaneous rates of anuran eighth nerve fibers make such determinations straightforward. The synthetic call was then presented

at a level of either 70 or 80 dB SPL, levels which approximate those at which bullfrogs vocalize in their natural environment (Megela-Simmons, 1984), and repeated at a rate of 1/2 s for 40–60 repetitions. This constituted the no noise baseline. After a 30–60 s period of no stimulation, continuous background noise was added, and responses to at least 40 additional repetitions of the call embedded in the noise were then recorded. Noise levels ranged from 60–90 dB SPL rms. Because the noise waveform was allowed to vary between stimulus presentations, this procedure may reduce the effects of noise on the responses to the call (Geisler and Gamble, 1989; Sachs *et al.*, 1983). Each change in noise level was preceded by a 30–60 s period of no stimulation. The intensity of the synthetic call was then changed, and responses to the call alone and to a range of noise levels were again recorded. If an individual fiber could be “held” long enough, then its spontaneous rate and saturation rate to both CF tone bursts and to the synthetic call were also measured.

### D. Data analysis

Peri-stimulus-time (PST) histograms, period histograms, and the autocorrelation functions of the spike trains were calculated with an IBM PC/AT computer and R/C Electronics isc-67 data acquisition board and software. Data were sampled at a rate of 20 kHz (50- $\mu\text{s}$  bin width). PST histograms were calculated over the 800-ms duration of the stimulus (call + noise interval) and for a 800-ms interval before stimulus onset (noise alone interval). Total spike counts in each interval, and spike counts in consecutive 50-ms epochs within the stimulus + noise interval were calculated from these histograms. These data were used to compile plots of spike discharge rate (Sachs and Young, 1979) over fiber CF at ambient noise levels and for each noise condition. In such plots, an individual data point represents the number of spikes evoked by the call (call + noise) for an individual fiber. These data points are then averaged across CFs using a triangular weighting function with a 0.25-oct. base. Because saturation rate could not be obtained for all fibers in the sample, spike counts used in the rate profiles were not normalized with respect to this measure.

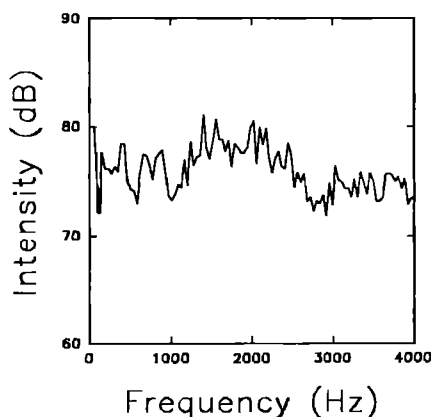


FIG. 2. Spectrum of the background noise, measured with a calibrated probe tube in the earphone housing and Brüel and Kjaer 4134  $\frac{1}{4}$ -in. microphone. The spectrum of the noise was calculated as described for the synthetic call itself.

Period histograms were constructed over the fundamental period (10 ms) of the synthetic call. Vector strength to the 100-Hz fundamental (Goldberg and Brown, 1969) was calculated from these histograms, and its statistical significance was calculated using the Rayleigh test of circular data (Mardia, 1972). Fourier transforms of the period histograms were performed using ILS signal-processing software, and used to calculate the synchronization index for an estimation of phase locking to higher harmonics in the synthetic call (Johnson, 1980).

## II. RESULTS

### A. Basic response properties

Data presented here are based on the responses of 125 single eighth nerve fibers to the call presented in quiet (ambient) conditions, and in at least one level of background noise. Because all fibers could not be held long enough to complete the entire protocol, sample sizes differ for the different noise conditions.

Basic response properties of fibers recorded in this study are consistent with those previously reported for bullfrog eighth nerve fibers (Feng *et al.*, 1975; Freedman *et al.*, 1988); we therefore presume that the data were not obviously affected by the different types of anesthesia used in these studies. Fiber CFs range from 100 to 1636 Hz, and thresholds at CF vary between 5–61 dB SPL. Here, CF and tone threshold are positively related ( $r_s = 0.37$ ,  $p < 0.0001$ ). The spontaneous activity of this sample of fibers ranges from 0–28 spikes/s, and is also positively correlated with CF ( $r_s = 0.5$ ,  $p < 0.0001$ ). Sixty-eight percent of the fibers in our sample have no spontaneous activity. On the basis of both anatomical and physiological data (Feng *et al.*, 1975; Freedman *et al.*, 1988; Lewis *et al.*, 1982), we categorize those fibers with CFs less than 1000 Hz as originating from the AP, and those with CFs greater than 1000 Hz as originating from the BP. In the frequency region around 1000 Hz, fibers are categorized as either AP or BP on the basis of their sharpness of tuning (BP fibers are typically more broadly tuned), level of spontaneous activity (BP fibers typically have higher rates of spontaneous activity), and CF distribution (all BP fibers in an individual frog tend to have the same CF, and BP fibers are typically encountered more superiorly in the eighth nerve than AP fibers; Zakon and Wilczynski, 1988). Fibers innervating the AP are divided into AP low and AP mid groups on the basis of their CFs (cutoff frequency of 450 Hz). Because of the relative uniformity in fiber responses to the synthetic call, particularly for fibers with CFs above about 500 Hz (see below), it is unlikely that any errors in fiber classification appreciably affect our conclusions.

Fiber thresholds to the synthetic advertisement call and the distribution of these thresholds are shown in Fig. 3. Call threshold is positively correlated with CF ( $r_s = 0.41$ ,  $p < 0.0001$ ). Call thresholds range from 18–75 dB SPL; this results in “sensation levels” (dB above call threshold) for individual fibers that ranged from 5–72 dB above call threshold. Here, AP low fibers have on average lower thresholds than other fibers, probably reflecting the

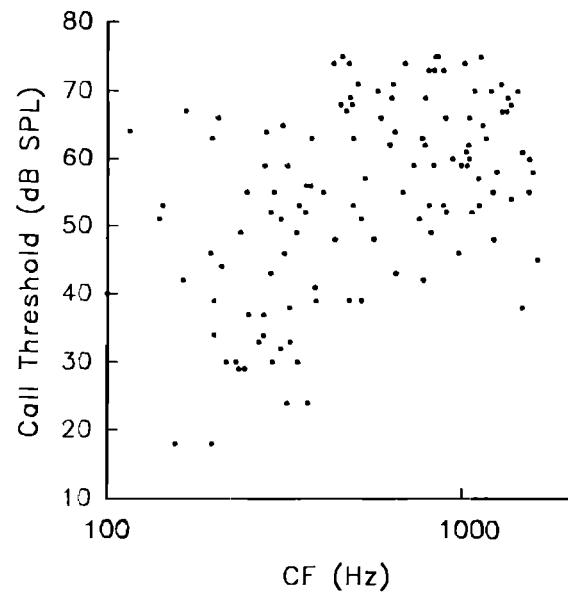


FIG. 3. Threshold (dB SPL) to the synthetic advertisement call across fiber CF. Only fibers with call thresholds of 75 dB SPL or less were used in this study.

concentration in spectral energy in the synthetic call in this low-frequency range. A range of thresholds is apparent at each CF group, however.

### B. Analysis of discharge rates

Figure 4 shows average rate profiles to the synthetic call at intensities of 70 dB SPL (left column) and 80 dB SPL (right column), under both ambient (no noise) conditions and at background noise levels of 60–90 dB SPL rms. These plots show the distribution of call-evoked activity across fiber CF. At a call intensity of 80 dB SPL in the no noise condition, the average line representing total firing rate is somewhat bimodal in shape: There is a peak in the rate profile at low CFs, a dip in the function in the mid-CF range, and another broad peak in a high frequency region around 800–1600 Hz. Both low-frequency-sensitive fibers with CFs lower than about 400 Hz and high-frequency-sensitive fibers with CFs above about 800 Hz show on average similarly high rate responses to the synthetic call. This probably reflects the concentration in spectral energy in the synthetic call in these frequency regions. Fibers with CFs near 500 Hz, where there is a dip in the call spectrum, typically have lower rate responses than fibers with lower or higher CFs; however, these differences in rate responses are not statistically significant. Moreover, the fine structure of the response profile does not precisely match that of the call spectrum. The high-frequency peak in the response profile is centered around 1000 Hz, rather than at 1400 Hz as in the call spectrum, and this high-frequency peak is as high as the low-frequency peak, a pattern not seen in the spectrum of the call, where the high-frequency peak is 10 dB down from the low-frequency peak (Fig. 1). Average rate to the call decreases as noise level increases, but the overall shape of the response profile persists at noise levels as high as 90 dB SPL rms. This indicates that some fibers were not saturated or masked at

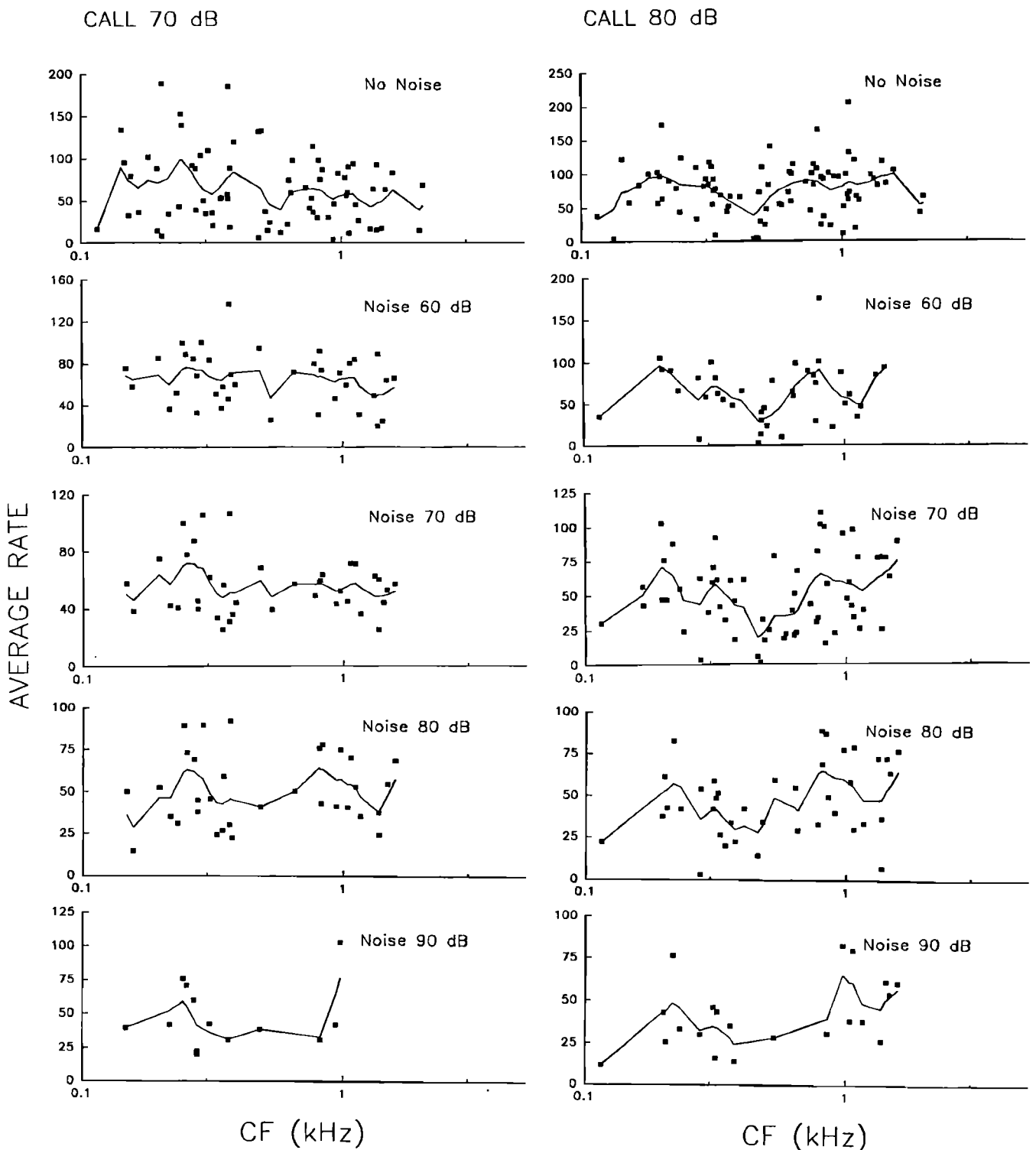


FIG. 4. Average rate profiles, plotting spikes/s against fiber CF, of the sample of recorded fibers in response to the synthetic call at intensities of 70 dB SPL (left column) and 80 dB SPL (right column), both under no noise and noise conditions. Each data point represents spike counts from one fiber with a particular CF. The continuous line represents an average based on a triangular weighting function with a 0.25-oct. base. Note the differences in the scale of the y axis between the different plots.

these high noise levels. The relatively small sample size at high noise levels makes interpretation of these rate profiles problematic.

At a call intensity of 70 dB SPL in the no noise condition, the shape of the response rate profile again does not reflect the detailed spectral structure of the call spectrum. At

noise levels of 60 and 70 dB SPL rms, the rate profiles tend to become flatter in shape. The small number of data points at the higher noise levels makes those plots difficult to interpret.

Examples of PST histograms to the synthetic call presented at 80 dB SPL are shown in Fig. 5. The shapes of these

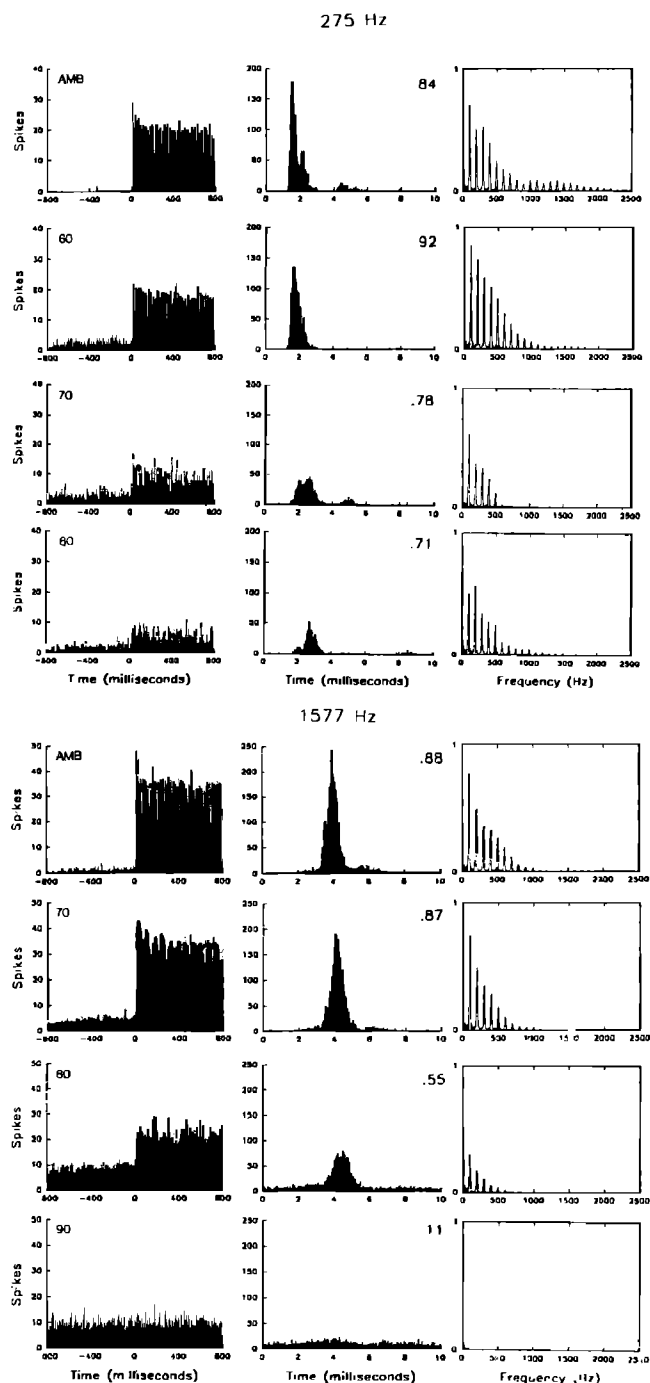


FIG. 5. Responses of two auditory-nerve fibers (CFs 275 Hz, top, and 1577 Hz, bottom) to the synthetic advertisement call in ambient (no noise) conditions and under different levels of background noise. Plotted are PST histograms (left), period histograms (middle), and Fourier transforms of period histograms (right). PST histograms are compiled to show both the interstimulus (noise alone) interval from  $-800$  to  $0$  ms, and the stimulus (call + noise) interval from  $0$  to  $800$  ms. Period histograms are compiled over the period (10 ms) of the synthetic call. The number at the upper right of the period histograms is the vector strength to the 100-Hz fundamental frequency of the call. Call intensity is 80 dB SPL. The noise level (60-, 70-, 80-, or 90-dB SPL rms) is indicated by the number shown in the top left corner of each row of histograms. Call thresholds are 37 dB SPL (top) and 58 dB SPL (bottom).

histograms in the no noise condition are “primarylike;” only two fibers in our sample show a phasic “on” response to the call. As noise level increases, the PST histogram becomes relatively “flatter” in shape, that is, the onset peak becomes

smaller as compared to the steady-state rate; this is paralleled by an increase in spike rate in the interstimulus (noise alone) interval. At “masked” levels (1577 Hz fiber in 90-dB SPL rms noise), the number of spikes in the interstimulus interval and in the stimulus interval are equal. Changes in PST histogram shapes with increasing background noise were quantified by calculating a ratio of onset rate to steady-state rate, formed by dividing spike rate in the first 50 ms of the response by spike rate in the final 50 ms of the response (as previously used in studies of adaptation of anuran eighth nerve fibers to tone bursts; Megela and Capranica, 1981). In the no noise condition, the mean “rate ratio” in response to the call at 80 dB SPL is 3.44; PST histogram shape is not correlated with fiber CF. “Rate ratio” declines as background noise increases, reaching a mean of 1.48 at the highest noise level tested (90 dB SPL rms). These changes are statistically significant (Kruskal-Wallis test,  $X = 33.53$ ,  $df = 4$ ,  $p < 0.001$ ). For the 70-dB SPL stimulus, rate ratio decreases from 1.99 to 1.05 over the same range of noise levels ( $X = 23.94$ ,  $df = 4$ ,  $p < 0.001$ ).

### C. Analysis of synchronized responses

Period histograms and their Fourier transforms are presented in Fig. 5 for two individual fibers. One fiber has a CF of 275 Hz, close to the low-frequency spectral peak in the call, and presumably innervates the rostral portion of the AP. The other fiber has a CF of 1577 Hz, close to the high-frequency spectral peak in the call, and presumably innervates the BP. Call intensity was 80 dB SPL, and background noise varied as indicated in the figure. The synchronized responses of these fibers are remarkably stereotyped and consistent, given their different tuning characteristics and origin within the inner ear. That is, both fibers phase lock to the fundamental frequency of the call, as indicated by the single-peaked period histogram, even though the CFs of these fibers are close to one of the higher harmonics (the third and the fifteenth) and two of the “formant” peaks (200 and 1400 Hz) in the call. For these fibers, as well as for many others in our data set, this selective coding of the fundamental frequency, rather than of the major spectral peaks in the call, is apparent at all noise levels tested, until the fiber temporal response is “masked” (at 90 dB SPL rms for the CF 1577 Hz fiber). The Fourier transforms of these single-peaked period histograms show a primary peak at 100 Hz, followed by a series of progressively smaller peaks, extending up to frequencies of 500 Hz or higher. The shape of the period histogram is thus reflected in the smoothly decaying shape of the Fourier transform. The higher frequency peaks in the Fourier transform are at harmonic multiples of the frequency of the primary peak; they may represent rectifier distortion products or rectifier-type nonlinearities (Young and Sachs, 1979) on one hand, or responses to higher harmonics in the call on the other hand (the higher frequencies present in the call are also at harmonic multiples of the fundamental frequency). Any deviations from a smoothly decaying curve in the Fourier transform probably include true fiber synchronization to that particular harmonic frequency, as in the responses of fiber 275 Hz in ambient conditions.

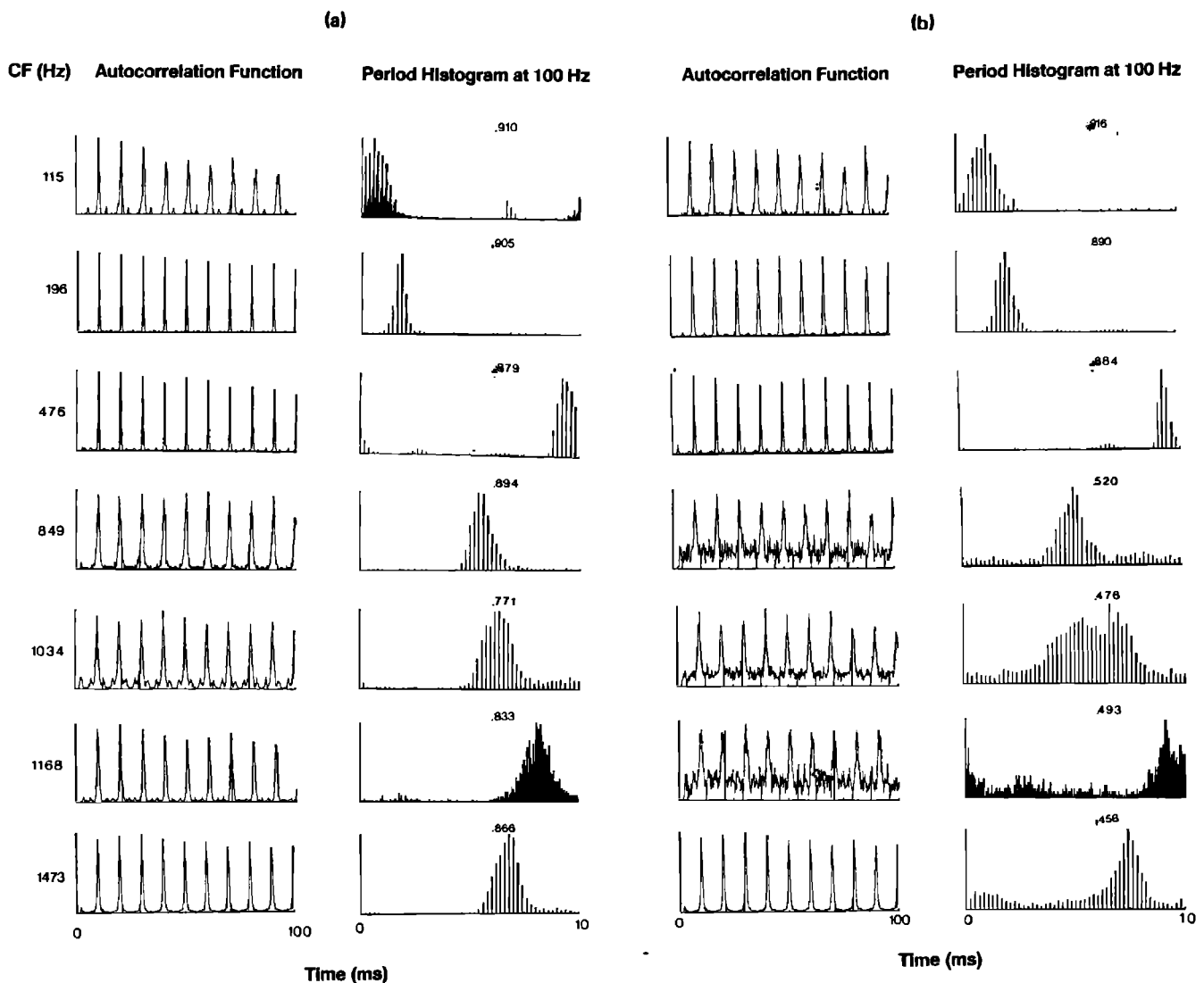


FIG. 6. Autocorrelation functions and period histograms to the 100-Hz fundamental frequency of 7 individual fibers in response to the synthetic call presented at 80 dB SPL in no noise (a) and at a background noise level of 80-dB SPL rms (b). Fiber CFs are as indicated; call thresholds are 64, 43, 74, 75, 62, 65, and 61 dB SPL, respectively. The number above each period histogram is the vector strength to the fundamental frequency.

The synchronized responses to these other harmonics are small compared to that to the fundamental frequency.

The "capture" of fiber synchronized response by the fundamental frequency, rather than by the higher harmonic structure, of the synthetic call is further documented in Fig. 6. Plotted here are the autocorrelation functions for fibers with CFs ranging from 115–1473 Hz and the period histograms to the 100-Hz fundamental frequency in the call, at call intensities of 80 dB SPL presented in quiet [Fig. 6(a)], and at a noise level of 80 dB SPL rms [Fig. 6(b)]. In the no noise condition, all of these fibers show periodic autocorrelation functions, with time intervals between peaks in these functions varying around 10 ms. This indicates that the fibers are responding in a periodic fashion to the fundamental frequency, as supported by the high vector strengths to this component in the period histograms. The autocorrelation function of the fiber with CF 115 Hz also contains small secondary peaks midway between the large peaks, indicating that this fiber is also responding to the second harmonic in the call. Synchronization to the call harmonic closest to fiber

CF is largely absent, particularly for fibers with CFs of 476 Hz and above. The pattern of response seen under no noise conditions is largely preserved under background noise [Fig. 6(b)]. The similarities in fiber temporal responses measured using the autocorrelation function and the period histogram analyses show that these data are not biased by the particular method of data analysis used.

Figure 7 plots mean vector strength to the 100-Hz fundamental frequency of the call for fibers grouped by CF, at call intensities of 70 dB SPL (left) and 80 dB SPL (right). Vector strength to the fundamental frequency does not vary significantly with fiber CF or call intensity in no-noise or low-noise (60 dB SPL rms) conditions (all tests were performed using the Kruskal-Wallis nonparametric statistic). That is, there are no significant differences in the phase locking ability of the three groups of fibers in these conditions. At higher noise levels, differences between fibers are found primarily in the noise level at which synchronization to the fundamental disappears. At a call intensity of 80 dB SPL, AP low fibers continue to phase lock to the fundamental



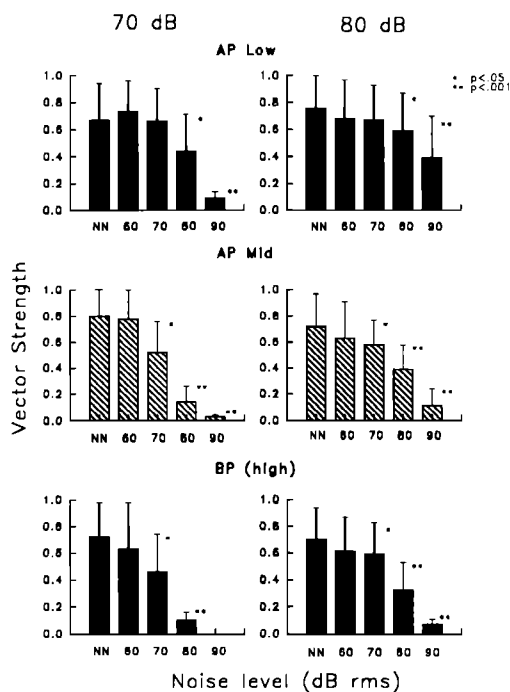


FIG. 7. Vector strength (mean  $\pm$  standard deviation) to the 100-Hz fundamental frequency of the synthetic call for fibers grouped by CF at call intensities of 70 dB SPL (left column) and 80 dB SPL (right column). Noise level is indicated on the x axis. Here, NN is the no noise condition. Statistical significance of the differences in vector strength was tested using the nonparametric Kruskal–Wallis test. Significant differences indicate differences between no noise and noise conditions for each group of fibers at one particular call intensity.

frequency at all levels of background noise tested, although the absolute value of the calculated vector strength declines (vector strength at 80 and 90 dB SPL rms are significantly lower than in no noise conditions). These fibers exhibit stronger phase locking to the fundamental than either AP mid or BP fibers at noise levels of 80 or 90 dB SPL rms. Vector strength of AP mid and BP fibers does not differ significantly from each other at any noise level, even though the distribution of spectral energy in the call is lower in this mid-frequency than in the high-frequency range. Fibers in these groups show on average no statistically significant synchronization to the fundamental frequency at noise levels of 90 dB SPL rms. Similar patterns are seen in response to the synthetic call presented at 70 dB SPL (Fig. 7, left). At this call intensity, there are no differences in synchronization between the three groups of fibers in no noise and low noise conditions. At noise levels of 70 and 80 dB SPL rms, AP low fibers show stronger synchronization to the fundamental than AP mid or BP fibers. At 90 dB SPL rms, vector strength to the fundamental is close to 0 for AP low and AP mid fibers; BP fibers were not tested in this condition.

Although most of the fibers in our sample encode the fundamental frequency of the synthetic call in their temporal patterns of discharge in both ambient and low to moderate noise conditions, the remaining fibers instead phase lock to one of the higher harmonics in the call. These effects are particularly obvious in high (80 or 90 dB SPL rms) noise conditions. Period histograms of the responses of these fibers show multiple peaks, and the number of these peaks and the

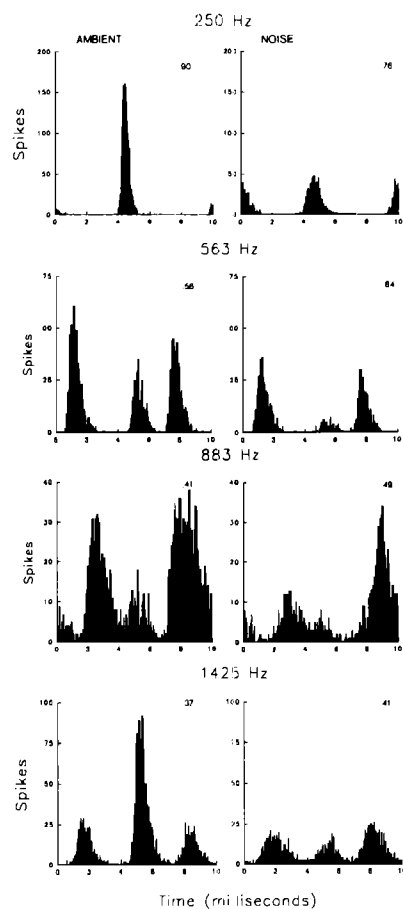


FIG. 8. Period histograms for four fibers showing synchronization to harmonics other than the first. Stimulus intensity is 80 dB SPL in all cases. Responses in the no noise condition are graphed on the left and responses at a noise level of 80 dB SPL rms are graphed on the right. The number at the top right of each histogram is the synchronization index to that particular harmonic, as calculated from Fourier transforms of the period histograms.

time interval between them is an indication of the harmonic number to which the fiber is synchronizing (Sachs *et al.*, 1988); this was confirmed by computing the Fourier transform of the period histograms and the autocorrelation of the spike trains. Some examples of the variability in synchronization are shown in Fig. 8. The fiber with the CF of 250 Hz phase locks to the fundamental frequency of the call in the no noise condition (Fig. 8, left), but at a noise level of 80 dB SPL rms, the fiber synchronizes instead to the second harmonic (Fig. 8, right). For this fiber, noise apparently produces a shift in synchronization from the fundamental to the major spectral peak in the call. This fiber has a CF midway between the second and third harmonic of the call fundamental frequency; recall that the second harmonic is the first “formant” of the call. The fiber with CF of 563 Hz phase locks to the third harmonic of the call in no noise conditions, but to the second harmonic at a noise level of 80 dB SPL rms; the fiber does not synchronize to the sixth harmonic of the call, which is the harmonic closest to its CF. The fiber with CF of 883 Hz shows a similar pattern, synchronizing to either the second or third harmonics rather than to either the fundamental frequency or the ninth harmonic, which is the call component closest to its CF. Finally, the fiber with CF of 1425 Hz synchronizes to the third harmonic of the call, and

not to the fourteenth (second "formant"), the component closest to its CF.

None of the fibers in our data set synchronizes to any harmonic in the call higher than the third at any noise level, even when fiber CF is close to one of these higher harmonics. Figure 9 plots the proportion of fibers synchronizing to the first three harmonics in the synthetic call at different background noise levels. These data were quantified by computing a synchronization index for the highest (primary) peak in the Fourier transforms of the period histograms; a fiber was defined as synchronizing to that harmonic of the call represented by this peak only when the synchronization index is statistically different from 0. Because some fibers do not show significant phase locking at all noise levels, the proportions in Fig. 9 do not always add up to 1.0. At ambient noise levels, 89% of all fibers in our sample, regardless of their CF, synchronize to the first harmonic (fundamental frequency) of the call. Only 12% of the sample synchronize to the second harmonic (the first "formant") and only 9% to the third harmonic. Whether a fiber synchronizes to the second or third harmonic has no apparent relation to its CF; both AP and BP fibers in our sample show these effects, and there is no correlation between fiber CF and the harmonic number to which phase locking occurs. (Note, however, the small number of fibers synchronizing to any harmonic other than the first.) There is little difference in the relative proportion of fibers synchronizing to one of these three harmonics at noise levels of 60 or 70 dB SPL rms. At higher noise levels, the proportion of fibers synchronizing to the first harmonic begins to decline. This is due to one of two effects: The

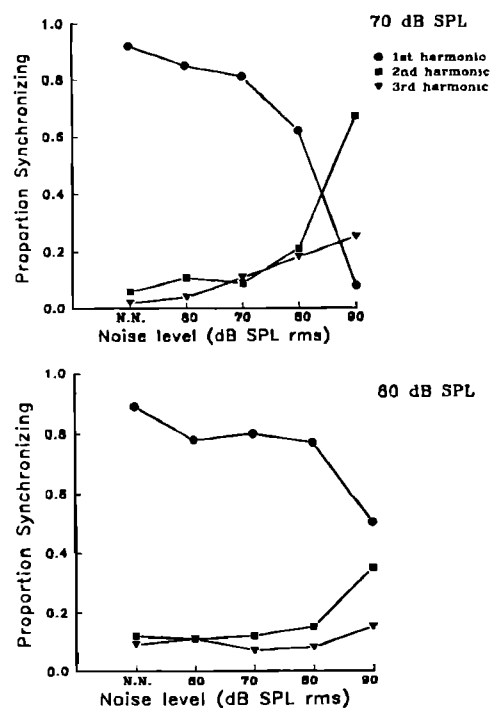


FIG. 9. Proportion of fibers synchronizing to different harmonics in the synthetic call as a function of background noise level, for call intensities of 70 dB SPL (top) and 80 dB SPL (bottom).

fiber begins synchronizing to the second or third harmonic rather than to the first, or the fiber no longer phase locks at all and values of the synchronization index are statistically insignificant from 0.

#### D. Comparison of rate and temporal responses

Figure 10 shows the relation of rate and temporal coding in representing the synthetic call under conditions of high levels of background noise. Shown in this figure are PST and period histograms of responses of four individual fibers to the synthetic call presented at 80 dB SPL against background noise of 80 or 90 dB SPL rms. At these noise levels, PST histograms are flat in shape, with equivalent numbers of spikes in the stimulus (call + noise) and interstimulus (noise alone) intervals. This indicates that fiber rate responses are masked (Freedman *et al.*, 1988). Yet, period histograms still show significant phase locking, with the calculated vector strength statistically different from 0. All

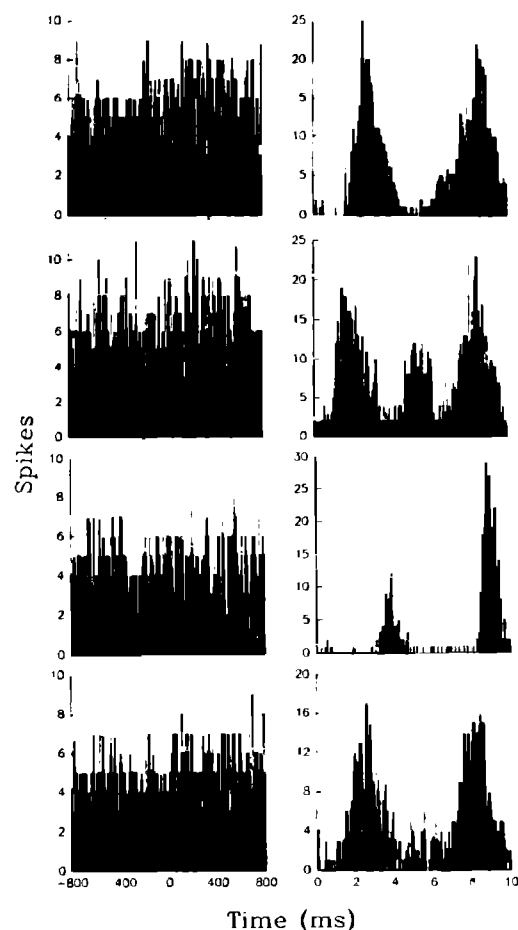


FIG. 10. PST and period histogram responses of four fibers at high levels of background noise. CFs and call thresholds are, from top to bottom, 200 Hz, 34 dB SPL; 309 Hz, 65 dB SPL; 518 Hz, 51 dB SPL; and 1545 Hz, 60 dB SPL. For all fibers, call intensity is 80 dB SPL and noise intensity is 80 dB SPL rms, except for the fiber with CF 200 Hz, where noise intensity is 90 dB SPL rms. The synchronization index and the dominant harmonic in the period histogram are 0.60 (second harmonic); 0.36 (third harmonic); 0.80 (second harmonic); and 0.45 (second harmonic). All of these indices are significantly different from 0. With the exception of the fiber with CF 309 Hz, all of these fibers phase lock to the fundamental frequency of the call under no noise and low-noise conditions.

four of the fibers shown in Fig. 10 show significant synchronization to the second or third harmonic in the call under these high noise levels; three of these four fibers phase lock to the fundamental frequency of the call under no noise and low noise conditions (see also fiber 250 Hz in Fig. 8). These data indicate that, at least for some fibers, synchronized firing is captured by the dominant component in the call (the second harmonic; the amplitude of the third harmonic is smaller but still relatively high) under high noise levels; but synchronized firing is still not captured by the component in the call closest to fiber CF. Our data set contained few unambiguous examples in which synchronization to the fundamental frequency was more resistant to noise masking than the corresponding rate responses; however, the large (10 dB) increments in noise level may have resulted in such effects being missed.

### III. DISCUSSION

The results of this study suggest that temporal discharge patterns of bullfrog eighth nerve fibers do not accurately encode the detailed formant structure of a synthetic, species-specific advertisement call either in quiet (ambient) or noisy conditions. The spectral fine structure of the synthetic call is not coded by different patterns of synchronization across fibers with different CFs; instead, the majority of fibers, regardless of their CF, show a homogeneous pattern of synchronization, phase locking preferentially to the fundamental frequency (waveform periodicity) of the call, particularly under no noise or low noise conditions. Firing is captured by the fundamental frequency, even though this is effectively a "missing" fundamental (its amplitude is about 20 dB down from the major spectral peak in the call). This is true even for those fibers whose CFs are close to one of the spectral peaks in the call. It also holds for fibers with CFs in the frequency region around 500 Hz, where there is a dip in the call spectrum; these fibers have relatively lower rate responses than fibers with other CFs, but still exhibit equally good synchronization to the waveform periodicity. The dominance of the fundamental frequency on response synchrony has been found consistently in over 300 individual fibers studied in the no noise condition, from this and previous studies (Schwartz and Simmons, 1990; Simmons and Ferragamo, 1989). Moreover, this extraction of the periodicity of the synthetic call is relatively immune to changes in stimulus intensity (Schwartz and Simmons, 1990; Fig. 7) and persists at low to moderate levels of background noise (Fig. 9).

Background noise of the type and level used in this study has two main effects on fiber temporal response: Noise can simply reduce the magnitude of synchronization to the fundamental frequency, such that vector strength begins to approach 0 and fiber temporal responses become "masked;" or noise can produce a shift in synchronization from the fundamental frequency to the second or third harmonic. Many fibers synchronize to the fundamental frequency of the call at all noise levels tested; what varies is the magnitude of the calculated vector strength. Within this group of fibers, AP low fibers retain their synchronization ability at higher noise

levels than either AP mid or BP fibers (Fig. 7). A few fibers synchronize to the second or third harmonic of the call both under ambient and noisy conditions, until their temporal responses are masked. The second effect of the noise is illustrated in Figs. 9 and 10. Here, noise produces a shift in phase locking, from the fundamental frequency (in no noise or low noise conditions) to either the second (first "formant") or the third harmonic of the call (at high noise levels). This shift in phase locking serves to increase the dynamic range for phase locking at noise levels where rate responses are masked. In no case, however, is synchronization seen to any harmonic higher than the third, even for those BP fibers which are spectrally tuned to high frequencies. Some fibers do not show masking of either rate or temporal responses at any noise level tested. This may be due to the relatively high thresholds of some fibers to the call (Fig. 3); the relatively small number of fibers tested under high noise levels; or because noise intensity was probably not incremented in small enough steps to accurately judge the signal-to-noise ratio for masking in all fibers. The relative preservation of temporal responses over rate responses has also been observed in other studies (Delgutte and Kiang, 1984d; Freedman *et al.*, 1988; Narins and Wagner, 1989; Sachs *et al.*, 1983), even though different types of noise were used in some of this earlier work.

Those fibers which synchronize to the fundamental frequency only, those which synchronize only to the second or third harmonics, and those which shift their synchronization with increasing background noise do not differ in any obvious way on the various parameters we recorded (CF, threshold, spontaneous rate, sharpness of tuning). The small number of fibers that synchronize to harmonics other than the fundamental, in either quiet or noisy conditions, however, makes any quantitative comparisons difficult. In an individual animal in a given recording session, all three types of fibers were encountered, so it is highly unlikely that these differences in discharge synchrony are due to extraneous factors such as variability in anesthetic level, surgical technique, or stimulus calibration.

Narins and Wagner (1989) showed that the response area of a fiber as defined by its frequency-tuning curve is not necessarily the same shape or width as the fiber's "phase-locking existence region." Both AP and BP fibers phase lock to low-frequency tones, and the frequency region of strongest phase locking to these simple sinusoids is typically below about 500 Hz (Narins and Wagner, 1989). These results are consistent with those reported here, in that both AP and BP fibers synchronize to low-frequency harmonics of the call, while not synchronizing, or synchronizing much less, to higher harmonics closest to fiber CF. What is interesting, however, is that even though these fibers should be capable of synchronizing to any of the low (below the seventh) harmonics in the call, their synchronized firing is captured by the low-amplitude fundamental frequency, and not by the dominant second harmonic. The frequency of the fundamental does not consistently lie within the tuning curves of the high-frequency-sensitive fibers in our sample at the call intensities employed here. This implies that the "phase-locking existence region" of fibers to multiple-harmonic sounds

is broader than that to simple sinusoids. Presumably, these fibers are extracting the fundamental from the high-frequency harmonics in the call that lie within their tuning curves; their broad tuning curves mean that several harmonically related components are being passed through at once, and therefore discharges are being modulated at the period of the common fundamental (Horst *et al.*, 1986; Miller and Sachs, 1984). The effective filter width for the anuran auditory system's analysis of complex sounds is therefore broader than predicted on the basis of individual frequency threshold curves, as also noted in mammalian data (Palmer *et al.*, 1986; Deng *et al.*, 1987).

The data presented here suggest that identifying dominant components in Fourier spectra of fiber temporal responses (Deng and Geisler, 1987; Shamma, 1985) is not always sufficient for identifying spectral peaks in the call, particularly in ambient or low noise levels; this is because, under these conditions, adjacent frequency channels respond to the same dominant component, the fundamental frequency. At high noise levels, such a dominant component scheme would identify the major spectral peak at 200 Hz, and the somewhat smaller peak at 300 Hz; the high-frequency information in the call would still be missed. This scheme may be sufficient for estimating the periodicity or "pitch" of the call. Whether this finding is specific to the particular synthetic call used here is still under investigation; a stimulus with different relative amplitudes or phases of the same harmonic components conceivably might elicit a different pattern of synchronized activity. This appears unlikely, however, because, except under high noise levels, the synchronized firing of fibers is not captured by the dominant energy peak at 200 Hz but by the relatively small amplitude fundamental, suggesting that relative amplitude of the higher harmonics might not be crucial in influencing fiber synchronization. More direct tests of this possibility have not been reported, though. The restricted range of phase locking of anuran eighth nerve fibers to simple sinusoids (Freedman *et al.*, 1988; Narins and Hillery, 1983) and to modulated tones and noise (Feng *et al.*, 1991; Simmons, 1992) in itself implies that synchronization must be limited to low harmonics. Changing the phase relations of the harmonics in the call would result in changing a very peaky waveform into a flatter one, and this might result in less peaky period histograms (Deng *et al.*, 1987). Such phase manipulations in fact do produce more heterogeneity in fiber responses (Simmons and Ferragamo, 1989); these effects will be reported in a separate publication. The present investigation leaves unanswered the question of how different spectral patterns are encoded in the eighth nerve; but they suggest that unless these spectral differences result in differences in the periodicities of complex sounds, different spectral patterns are likely transmitted by differences in rate rather than in temporal responses. The relative resistance of temporal responses to noise masking suggests that, under biologically realistic levels of background interference, information about the waveform periodicity and the low harmonics is preserved, while high-frequency information is lost.

The pattern of synchronization to the synthetic advertisement call reported here is strikingly different from that

reported in studies of mammalian peripheral responses to synthetic speech sounds. If the filtering mechanisms of the auditory periphery of anurans and mammals were equivalent, one would expect the output of anuran peripheral filters to be dominated by the high-amplitude harmonic in the synthetic call closest to the center frequency of a particular filter ("strong-component capture," Deng and Geisler, 1987; Deng *et al.*, 1987), an expectation which clearly does not hold. Temporal discharge patterns of mammalian fibers in response to synthetic speech or other multiple harmonic signals under ambient noise conditions are not typically dominated by the fundamental frequency of the stimulus. Rather, patterns of synchronization across the fiber array are complex, and are related to fiber CF, spontaneous rate, the relationship of fiber CF to the formant frequencies in the speech sound, the relative height of energy peaks in multitone complexes, and the level of the sound (Carney and Geisler, 1986; Delgutte and Kiang, 1984a; Deng and Geisler, 1987; Deng *et al.*, 1987; Miller and Sachs, 1984; Palmer *et al.*, 1986; Young and Sachs, 1979). The complex nature of synchronized responses in the population of fibers reflects the encoding of spectral fine structure, as well as the fundamental frequency, of complex, multiple-harmonic stimuli (Horst *et al.*, 1986). The effects of background noise on the encoding of these types of sounds vary with fiber CF (Delgutte and Kiang, 1984d; Geisler and Gamble, 1989; Miller and Sachs, 1984; Sachs *et al.*, 1983). Sachs *et al.* (1983) reported that noise primarily reduces the amplitude of synchronization to particular frequency components in synthetic vowels; fibers with CFs away from the major formants in the vowel are most affected, and their firing is captured by the noise. Fibers with CFs above the first two formant frequencies show reduced synchrony at noise levels where fibers with lower CFs, which typically phase lock to the closest formant frequency, still show significant phase locking. Delgutte and Kiang (1984d) similarly showed that noise suppresses synchronized responses primarily of those fibers whose CFs are far from formant frequencies. The temporal discharge patterns of fibers with CFs near the formant frequencies, which are dominated by these formant frequencies, are little affected by noise (at least at the levels used in their study). For fibers with CFs far from the formant frequencies, noise shifts the response components from signaling components of the vowel to signaling components of the noise (nonharmonic response components). In general, noise has the strongest effects on the CF regions between the major formant peaks in the stimulus, and in high CF regions. Geisler and Gamble (1989) reported that fibers with CFs near energy peaks in a synthetic consonant-vowel stimulus continue to synchronize to that component in noise; the synchrony of fibers with CFs away from these peaks is captured by the noise. All of these results differ from those reported here in showing clear coding of formant peaks in the speech sound in background noise.

Along with this coding of spectral fine structure, cues for waveform periodicity may also be evident in fiber responses to complex speech sounds and other multiple-harmonic stimuli (Horst *et al.*, 1986; Miller and Sachs, 1984). In response to equal-amplitude, multiple-harmonic stimuli

at low intensities, synchronized responses of fibers show components at the fundamental frequency of these stimuli. The degree of synchronization to this component decreases with increases in stimulus intensity and with increases in the relative amplitudes of one or more harmonics (Deng *et al.*, 1987; Horst *et al.*, 1986). However, information about the fundamental frequency can be retained in the interval histograms of fiber responses (Horst *et al.*, 1986). How these effects might be influenced by noise is unclear. Delgutte and Kiang (1984d) and Miller and Sachs (1984) reported that many of the periodicity cues for coding of the fundamental frequency of synthetic vowels are strongly degraded at moderate noise levels over all CF regions, except near the "place" for the fundamental frequency. Envelope modulations are seen only in fibers whose CFs are not near the formant frequencies, and these modulations decline under conditions of background noise. Therefore, even though cues for periodicity may be present in responses of both anuran and mammalian fibers, the dominance of the periodicity cue and its preservation under at least some noise conditions, as well as the lack of coding of the higher-harmonic spectral fine structure, indicate that the neural code by which periodicity information is transmitted in the anuran auditory periphery is simpler than in the mammalian auditory periphery (even though some sort of temporal processing mechanism might be operating in both cases). Some mammalian cochlear nucleus neurons exhibit a phenomenon called "pitch-period following," in which spike discharges are phase locked to the fundamental frequency of complex periodic stimuli (Kim and Leonard, 1988; Palmer *et al.*, 1986; Sachs *et al.*, 1988). This phenomenon may be analogous to that reported here.

Although the spectral fine structure of the synthetic advertisement call is not encoded by the synchronized responses of the population of fibers, the overall bimodal structure of the call spectrum might be extracted from the rate responses of the fibers, at least at some call intensities. Even in the tonotopically organized AP, higher-harmonic spectral peaks in the call are not consistently coded by peaks of fiber activity at the appropriate place. These data imply that the bimodal nature of the stimulus spectrum, and not the specific distribution of frequencies within the low- and high-frequency groups, is important in mediating vocal behavior in these animals. That is, the actual position of the spectral peaks within the low and high range, whether at 200 and 1400 Hz, or 300 and 1500 Hz, may not be of crucial behavioral importance in evoking calling and may in fact vary between individual animals. Behavioral experiments conducted with bullfrogs (Capranica, 1965) show that a combination of both low-frequency (100–400 Hz) and high-frequency energy (1000–1600 Hz), with a relative frequency dip in a mid-frequency region around 500 Hz, is necessary to evoke vocalizations in response to playbacks of species-specific advertisement calls; the relative heights of the spectral peaks in these regions can vary substantially without significantly influencing the males' responses. Moreover, the exact frequency of the energy peak in the low- and high-frequency regions could vary within these ranges and still elicit vocal responses; what is required is a dip in the spectrum at a mid-frequency region. In some species, amplitude modulated

noise can be just as effective in eliciting vocalizations from male frogs as spectrally structured stimuli (Allan and Simmons, 1991; Rose and Capranica, 1984). Therefore, the temporal fine structure of the stimulus, and by implication the details of the spectrum, may be relatively unimportant in mediating vocal behavior as long as the basic waveform periodicity and the overall bimodal shape of the spectrum are intact.

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