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Periodicity extraction in the anuran auditory nerve

I. “Pitch-shift” effects

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Abstract. 1. Activity of individual eighth nerve fibers in the bullfrog, *Rana catesbeiana*, was measured in response to complex, multiple-frequency stimuli differing in both frequency composition and harmonic structure. Stimuli were chosen to parallel types of stimuli producing “pitch-shift” effects in humans.

2. The fundamental frequency of harmonic stimuli can be extracted from the autocorrelation of fiber firing, whether the fundamental is physically present in the stimulus or is a “missing” fundamental. The spectral fine-structure of harmonic stimuli is not robustly represented in fiber temporal response. These effects are seen in both AP and BP fibers.

3. The pseudoperiod of inharmonic stimuli is represented by synchronization to successive high-amplitude peaks in the stimulus envelope. Temporal responses to stimuli with high center frequencies are similar regardless of whether their frequency components are harmonically or inharmonically related. Responses remain dominated by the envelope periodicity, and no “pitch-shift” is signaled. In response to stimuli with low center frequencies, temporal responses signal a “pitch-shift” between harmonic and inharmonic complexes. Both AP and BP fibers show these effects.

4. These data suggest that bullfrog peripheral fibers extract the periodicity of complex stimuli by time-domain rather than frequency-domain coding.

Key words: Auditory nerve – Autocorrelation – Bullfrog – Complex signals – Periodicity pitch – Temporal processing

Introduction

For human listeners, a salient perceptual characteristic of sounds is their pitch. Pitch is a psychological attribute of a sound which is related to certain physical, acoustic

parameters. Simple sinusoids have a tonal pitch related to their frequency. Complex sounds, made up of several frequencies or harmonics that are integer multiples of a common, low fundamental frequency, also have a pitch called residue or periodicity pitch. The periodicity pitch of a complex sound is related to the fundamental frequency of that complex. In order to perceive a periodicity pitch, the fundamental frequency need not actually be present in the complex stimulus; a sound consisting of only high harmonics of a low fundamental frequency will still be perceived as having a pitch described by that low fundamental frequency (Fletcher 1934; Schouten 1940). For these stimuli with “missing fundamentals”, the perceived pitch corresponds approximately to the rate of repetition of the signal envelope (the waveform periodicity) or the frequency spacing between successive harmonics. That is, either a temporal or a spectral cue can be used to extract the residue pitch.

Theories of pitch perception have dominated the history of auditory research, and the identification of the mechanisms by which the auditory system defines complex sounds as having a particular periodicity pitch remains a matter of great debate and active research. Models of the neural representation of pitch in the peripheral auditory system have been proposed using primarily frequency-domain (spectral) codes, primarily time-domain (periodicity) codes, or some combination of frequency- and time-domain codes (“duplex” theories) converging onto a common pitch dimension (de Boer 1976; Goldstein 1973; Lazzaro and Mead 1989; Licklider 1951; Loeb et al. 1983; Moore 1989; Meddis and Hewitt 1991; Patterson 1987; Schouten et al. 1962; Wever 1949; Wightman 1973). Models of the central extraction of pitch from these peripheral patterns of activity can also be based on either frequency-domain or time-domain processing (Goldstein 1973; Langner 1981; Srulovicz and Goldstein 1983; Wightman 1973).

Both physiological and psychophysical data can be marshalled in support of (or in opposition to) either frequency or timing mechanisms for pitch extraction (de Boer 1976; Javel and Mott 1988; Moore 1989). It has

proven very difficult to isolate instances of pitch and pitch-like phenomena that can unambiguously be attributed to either place or periodicity information. (By “pitch-like”, or periodicity, phenomena, we refer to those percepts in animals that may be analogous to periodicity pitch perception in humans.) This is because, in most vertebrates, both place and timing information exist in the auditory periphery and could reasonably serve as a basis for pitch extraction. In the mammalian auditory periphery, the known tonotopic organization of the basilar membrane (Békésy 1960) is the basis for place coding. The basilar membrane performs a spectral analysis of sounds, representing different acoustic frequencies by excitation of different places along its length. The residue pitch of complex signals could be extracted from these patterns of spectral activity by a central processing mechanism. Timing information exists in the ability of auditory nerve fibers to discharge in a synchronized fashion to particular phases of sound waves (Rose et al. 1967). The time interval between bursts of synchronized activity could provide the cue for pitch (Wever 1949). Both types of codes can account for some aspect of either tonal or periodicity pitch perception in humans (Moore 1989; but note that tonal pitch and periodicity pitch need not necessarily be based on the same neural processing mechanism; Hall and Soderquist 1978).

One way in which to distinguish the contribution of the shape of the spectrum of a complex sound from that of its envelope periodicity to the perception of residue pitch is to examine the representation of pitch-like (periodicity) phenomena in an animal species where one or the other of these cues might be less well-developed and thus more easily separated than in other vertebrates. The auditory system of anuran amphibians (frogs and toads) is an example of a system where place cues are less well-developed than in mammals, and time-domain cues might be paramount in the extraction of pitch-like effects.

Anurans possess two organs in their inner ear which are specialized for processing of airborne sounds. Neither organ contains a basilar membrane. The larger of the two organs, the amphibian papilla (AP), is tonotopically organized; low frequencies (below about 400 Hz) are represented in the rostral patch, and high frequencies (up to about 1000 Hz) are represented in the caudal patch (Lewis et al. 1982). The basis for the tonotopy of the AP is not well-understood; it may be imparted by some sort of traveling wave mechanism, possibly supported by the overlying tectorial membrane, or by electrical resonances of the hair cells (Hillery and Narins 1984; Pitchford and Ashmore 1987). The details of the tonotopy of the AP are still to be worked out, and it is not clear whether perceptual performance of anurans is in fact based on this kind of spectral representation (Freedman et al. 1988; Moss and Simmons 1986; Simmons 1988a). The other organ, the basilar papilla (BP), is not organized on a place principle; instead, it operates as a simply-tuned resonant organ in which, in an individual animal, all of the innervating fibers have approximately the same characteristic frequency (CF). BP fibers are tuned to higher frequencies than AP fibers, and their tuning encompasses the range

of high-frequency energy found within the vocal repertoire of a particular species. Across different species, the CFs of BP fibers typically lie in a species-typical range between 1000–4000 Hz (see review in Zakon and Wilczynski 1988).

Although a particular CF can be identified for both AP and BP fibers, these fibers are broadly tuned in the frequency domain. As quantified in the auditory periphery of several different anuran species, frequency tuning, measured in terms of the frequency response to simple sinusoids at 10 dB above threshold (Q_{10dB} values), ranges from about 0.5 to 8.0 (see review in Zakon and Wilczynski 1988). These values are comparable to those measured in the mammalian auditory periphery in the same frequency range (Wilczynski and Capranica 1984). It is within this low frequency range that the tuning of mammalian peripheral fibers does not well account for human acuity in distinguishing tonal pitch, but where temporal processing may account for perception of residue pitch (Moore 1989). The tuning of mammalian fibers begins to sharpen at frequencies above about 1000 Hz (Kiang 1965), while in anurans it remains broad up to the upper limit of BP tuning. In fact, BP fibers tend to be more broadly tuned than AP fibers (review in Zakon and Wilczynski 1988). AP and BP fibers are also broadly tuned as measured by their ability to resolve individual frequencies against masking noise (Ehret and Capranica 1980; Freedman et al. 1988). In the bullfrog, BP fibers have higher critical ratios for detecting tones in noise than AP fibers (Freedman et al. 1988).

The relevance of the frog system to the understanding of the neural bases of residue pitch effects lies in this unique organization of the anuran inner ear. Comparing neural coding in fibers innervating the two different inner ear organs allows one to deduce, in the same animal, the relative contribution to sound perception of a primarily temporal (BP) to a primarily spectral or mixed spectral/temporal (AP) processing mechanism. Previous research on the coding of periodicity in the anuran auditory periphery has demonstrated that eighth nerve fibers are particularly sensitive to the amplitude envelope of complex sounds (Feng et al. 1991; Rose and Capranica 1985; Schwartz and Simmons 1990; Simmons et al. 1992a, b). It has been demonstrated in several species of anurans that BP fibers do not phase lock to simple sinusoids at fiber CF (Freedman et al. 1988; Narins and Hillery 1983). Yet, both AP and BP fibers synchronize strongly to the envelope of modulated noise bursts up to modulation rates of 300 to 500 Hz (Feng et al. 1991; Simmons et al. 1992c). Moreover, in the bullfrog (*Rana catesbeiana*), both AP and BP fibers phase lock to the low fundamental frequency of multiple-harmonic complex sounds, even when the frequency components of these sounds are close to fiber CF (Schwartz and Simmons 1990; Simmons et al. 1992a, b). Specifically, the waveform periodicity of a synthetic, phase-coherent version of the bullfrog's advertisement call is preferentially extracted from the timing of fiber firing, and the spectral fine-structure (the distribution of harmonics) is not reflected in fiber temporal response (Schwartz and Simmons 1990). This is because firing is “captured” by the

fundamental frequency. This precise signalling of waveform periodicity is related to the "peakiness" of the stimulating waveform: It is affected by background noise (Simmons et al. 1992a) and by changes in the phase spectrum of the signal that alter its shape from an impulse-like to a noise-like waveform (Simmons et al. 1992b). AP and BP fibers are affected in the same way by these manipulations. This similarity of the synchronized responses of fibers from the two different inner ear organs suggests that both organs are encoding periodicity by a similar mechanism, and that this mechanism is based on temporal rather than spectral ("place") processing. Even though the tonotopic organization of the AP does provide a possible basis for periodicity extraction by frequency coding, the data suggest that this organ, as well as the BP, is in fact encoding periodicity by a time-domain mechanism.

The present experiment was designed to further explore the mechanisms of periodicity extraction in the bullfrog's peripheral auditory system by analyzing fiber responses to complex stimuli with different spectral shapes and that vary in their harmonic structure. Previous research on complex periodicity extraction in the bullfrog's auditory periphery (Schwartz and Simmons 1990; Simmons et al. 1992a, b) used signals with only one periodicity (that present in a conspecific vocalization) and with the fundamental frequency present. In this experiment, the periodicity of the signals does not represent one present in a conspecific vocalization, and for some signals, the fundamental frequency is not physically present. Further, this experiment was designed to parallel psychoacoustic work on "pitch-shift" effects.

The "pitch-shift" effect was first described in a series of experiments on human perception of the pitch of amplitude-modulated (AM) tones (de Boer 1956; Schouten et al. 1962). When the carrier and the modulation frequencies of AM tones are harmonically-related, then listeners report a periodicity pitch associated with the modulation frequency. For example, if the carrier frequency is 2000 Hz and the modulation frequency is 200 Hz, the perceived pitch is 200 Hz. This pitch can either be extracted from the envelope of the AM tone, which repeats every 5 ms, or from the 200 Hz frequency spacing between the carrier and the sidebands produced by the modulation process. The perceived pitch could result from temporal coding, achieved by synchronization to the waveform envelope directly (Schouten et al. 1962). Or, it could result from frequency coding, whereby fibers respond most vigorously to either the carrier or sideband frequencies; a central processing mechanism could then extract the periodicity of the signal by measuring time intervals between these spectral patterns (Goldstein 1973). When the carrier is shifted in frequency so as not to be harmonically related to the modulation frequency (2040 Hz modulated by 200 Hz), listeners report a shift in the perceived pitch (from 200 to 204 Hz) that is related to the change in the temporal fine-structure of the waveform (de Boer 1956; Schouten et al. 1962). The frequency spacing between carrier and sidebands in the inharmonic AM complex remains at the frequency of the modulating tone (200 Hz in this example), but it no

longer corresponds to the perceived pitch. Rather, the perceived pitch of the inharmonic complex is better approximated by the average rate of repetition of the waveform envelope, which is slightly higher than 200 Hz. The fact that in inharmonic stimuli the time intervals between high-amplitude peaks in the envelope can vary from cycle to cycle corresponds to the perception of the pitch of such stimuli as rougher and less well-defined than the pitch of harmonic stimuli (de Boer 1976). "Pitch-shifts" have also been observed in response to other multiple-frequency stimuli consisting of a variable number of harmonics (Patterson 1973; Patterson and Wightman 1976). These effects have been interpreted as suggesting that pitch is determined by a timing mechanism that is sensitive to the temporal fine-structure of the waveform (Schouten et al. 1962), although alternative explanations are possible (de Boer 1976; Gerson and Goldstein 1978; Moore 1989; Patterson and Wightman 1976). The robust nature of the phenomenon indicates its importance in understanding the neural bases of pitch perception, and in motivating models of pitch.

Methods

Adult bullfrogs (200–400 g) were anesthetized by intramuscular injections of sodium pentobarbital (Nembutal; 100 mg/kg) for both surgery and recording. The animal was placed ventral-side-up on a cork platform, and the eighth nerve was exposed via an incision in the roof of the mouth. For recording, the animal was placed on a vibration isolation table (Newport Research Corp.) in a sound attenuating chamber (Industrial Acoustics). The chamber was maintained at a temperature of 20–22° C. The animal was kept moist during the experiment to aid cutaneous respiration. A typical recording session lasted 4–6 h.

Acoustic stimuli were digitally generated on an IBM PC/XT computer equipped with a Data Translation DT2801A board. Sampling rate was 10 kHz. Stimulus duration is 300 ms and rise/fall time is 10 ms. Six different complex stimuli, each with three equal-amplitude frequency components, were generated. For 3 of these stimuli, the frequency components are harmonically-related, while in the remaining 3 stimuli, the frequency components are inharmonically related but with the same frequency spacing between the individual components. Harmonically-related stimuli consist of 3 successive equal-amplitude harmonics of 200 Hz, with center frequencies (f_c) of 400 Hz, 800 Hz, and 1600 Hz, summed together in sine phase. All of these stimuli have a waveform periodicity of 200 Hz and for 2 of these stimuli, 200 Hz is a "missing fundamental." Center frequencies were chosen to lie within the frequency response range of both AP (f_c 400 and 800 Hz) and BP (f_c 1600 Hz) fibers. Stimulus waveforms are shown in Fig. 1. Note that the harmonic stimuli have well-defined periodic envelope maxima or peaks which repeat exactly every 5 ms or 200 Hz. To generate inharmonic stimuli, the center frequencies of the harmonic complexes are shifted upwards by 77 Hz while keeping the frequency spacing between components at 200 Hz. These stimuli have f_c s of 477, 877, and 1677 Hz. For these stimuli, the periodicity of the envelope remains at 200 Hz, but the temporal fine-structure of the waveform differs from that in the corresponding harmonic stimuli; that is, peaks in the waveform do not repeat exactly every 5 ms but vary over successive lobes of the envelope. For the stimulus f_c 477 Hz, for example, successive high-amplitude peaks in the envelope repeat from cycle-to-cycle over the range of 3.98 to 6.38 ms, with an average over many cycles varying from 197 to 203 Hz. The "pseudoperiod" of the inharmonic stimuli can be derived from the average time interval over which the waveform approximately repeats (de Boer 1976).

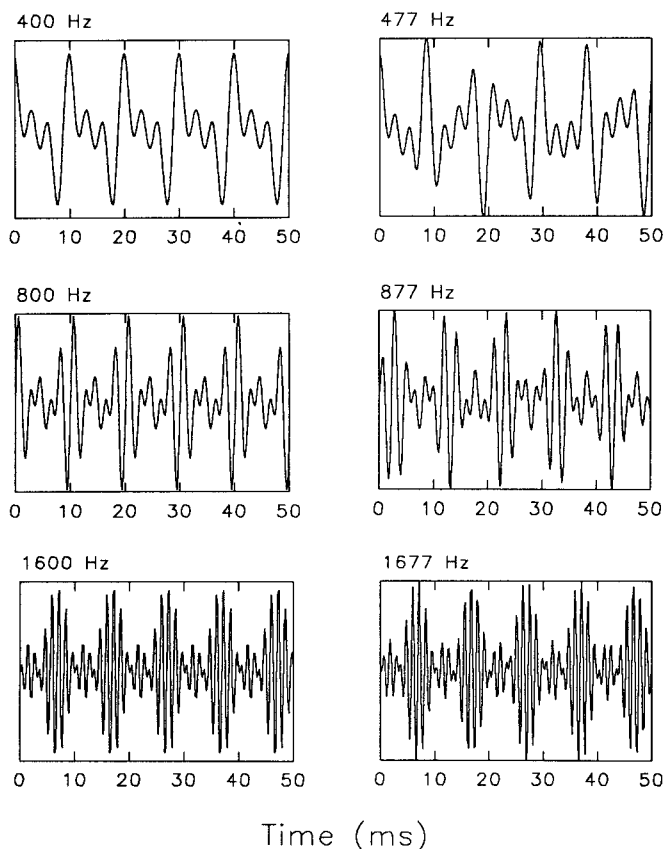


Fig. 1. Waveforms of the synthetic stimuli used in the experiment. The 3 harmonic complexes are in the left column and the 3 inharmonic complexes are in the right column. All stimuli consist of 3 equal-amplitude components summed in sine phase, and are specified by their center frequencies (f_c), as indicated by each waveform. Harmonic stimuli are, from top to bottom, left column: f_c 400 Hz (with component frequencies of 200, 400, and 600 Hz); f_c 800 Hz (component frequencies of 600, 800, and 1000 Hz); and f_c 1600 Hz (component frequencies of 1400, 1600, and 1800 Hz). All of these stimuli have an envelope periodicity of 200 Hz. Inharmonic stimuli are, from top to bottom, right column: f_c 477 Hz (component frequencies of 277, 477, and 677 Hz); f_c 877 Hz (component frequencies of 677, 877, and 1077 Hz); and f_c 1677 Hz (component frequencies of 1477, 1677, and 1877 Hz)

The stimuli were low-pass-filtered (Krohn-Hite model 3550) at 5 kHz, attenuated (Coulbourn S85-08 electronic attenuator), passed through a stereo equalizer (Rane), and amplified (Harmon/Karden PM 645). They were presented ipsilateral to the exposed nerve using a Beyer DT48 earphone enclosed in a custom-built coupler. The coupler also contained a Brüel and Kjaer model 4134 $\frac{1}{2}$ " condenser microphone, used in conjunction with a Brüel and Kjaer model 2209 sound level meter for calibration and for monitoring the intensities of the stimuli during an experiment. A rubber tube extending from the tip of the coupler was positioned close to the tympanum and sealed around its edges with a thick coating of silicone grease to form a closed acoustic system. The frequency response of the coupling system was measured at the start of each recording session using a Data Translation DT2801 interface board, and spectra were computed using ILS programs from Signal Technology, Inc. A Rane stereo equalizer was used to maintain the frequency response of this system within 3 dB over the range of 20–5000 Hz.

Activity of single eighth nerve fibers was recorded with glass micropipettes (impedances of 30 to 60 M Ω) filled with 3 M KCl. The electrodes were advanced into the posterior branch of the eighth

nerve using a Kopf model 607 hydraulic microdrive. Spike activity was amplified using a WPI DAM 80AC differential amplifier (gain of 1000, filtered from 0.1 to 3 kHz) and a Rockland 442 filter (gain of 20 dB, filtered from 0.3 to 3 kHz). This was then displayed on an oscilloscope (Tektronix 922R), monitored over a loudspeaker, and recorded on one channel of a TEAC quadrophonic tape recorder for subsequent analysis. The acoustic stimuli and a computer-generated pulse coincident with stimulus onsets were simultaneously recorded on two other channels of the tape recorder.

A frequency-modulated sweep (50 Hz–3 kHz, sweep rate 1/s, presented at a level of 80 dB SPL) generated by one phase-locked Wavetek function generator (model 182) sweeping another was used as a search stimulus. Once an auditory fiber was encountered, its CF, threshold at CF, and frequency response at 10 dB above CF (Q_{10}) were estimated audio-visually. The complex stimuli were then presented by computer in a random order. Each stimulus was presented for 40–60 repetitions at a repetition rate of 1/s. The intensity of all stimuli was kept at a level of 10 dB above the rate threshold for the complex stimulus whose center frequency was closest to fiber CF. This means that, for a given fiber, all stimuli were presented at the same intensity (which varied in absolute, but not relative, levels across fibers). Spontaneous activity was also recorded.

For off-line analysis, spike activity was passed through a window discriminator and digitized with an IBM PC/AT computer and R/C Electronics series 200 data acquisition board and accompanying software. Data were sampled at a rate of 20 kHz (50 μ s bin width). Post-stimulus-time (PST) histograms, period histograms, and the autocorrelation functions (ACFs) of the spike trains were calculated using custom-written software. Period histograms were compiled over the 200 Hz frequency spacing between components in the complex sounds, at the period of each frequency component in the complex, and at the period of fiber CF. Vector strength was calculated from these histograms to provide a measure of phase-locking to these components. The statistical significance of phase-locking was determined using the Rayleigh test of circular data (Mardia 1972). The ACF provides information about periodicities in the response without using the stimulus as a reference, as is the case in analyses based on period histograms. The ACF plots the distribution of time intervals between successive nerve spikes; a periodic ACF implies that fibers are phase-locking systematically to some component in the stimulus. Fourier transforms of the ACFs were also calculated (3 Hz binwidths). These indicate the components to which the fiber is synchronizing.

Results

Data are presented from 47 individual eighth nerve fibers, recorded from 9 animals (both right and left ears), that responded to at least one pair of harmonic and inharmonic stimuli with similar center frequencies. Fiber CFs ranged from 98 to 1380 Hz, with thresholds at CF ranging from 18 to 75 dB SPL, and $Q_{10\text{dB}}$ values ranging from 0.5 to 4.4. Fiber spontaneous activity ranged from 0 to 16 spikes/s. These characteristics are comparable to those previously recorded in the bullfrog eighth nerve (Freedman et al. 1988; Schwartz and Simmons 1990; Simmons et al. 1992a, b).

Fiber CF and the center frequency of the multiple-component sound are important factors determining the timing of fiber responses. Typical results for a low CF fiber, in the form of ACFs and their Fourier spectra, are presented in Fig. 2. This fiber has a CF of 374 Hz and presumably originates from the rostral patch of the AP. The ACF for the f_c 400 Hz complex is periodic with peaks occurring every 5 ms. The power spectrum of this ACF

374 Hz

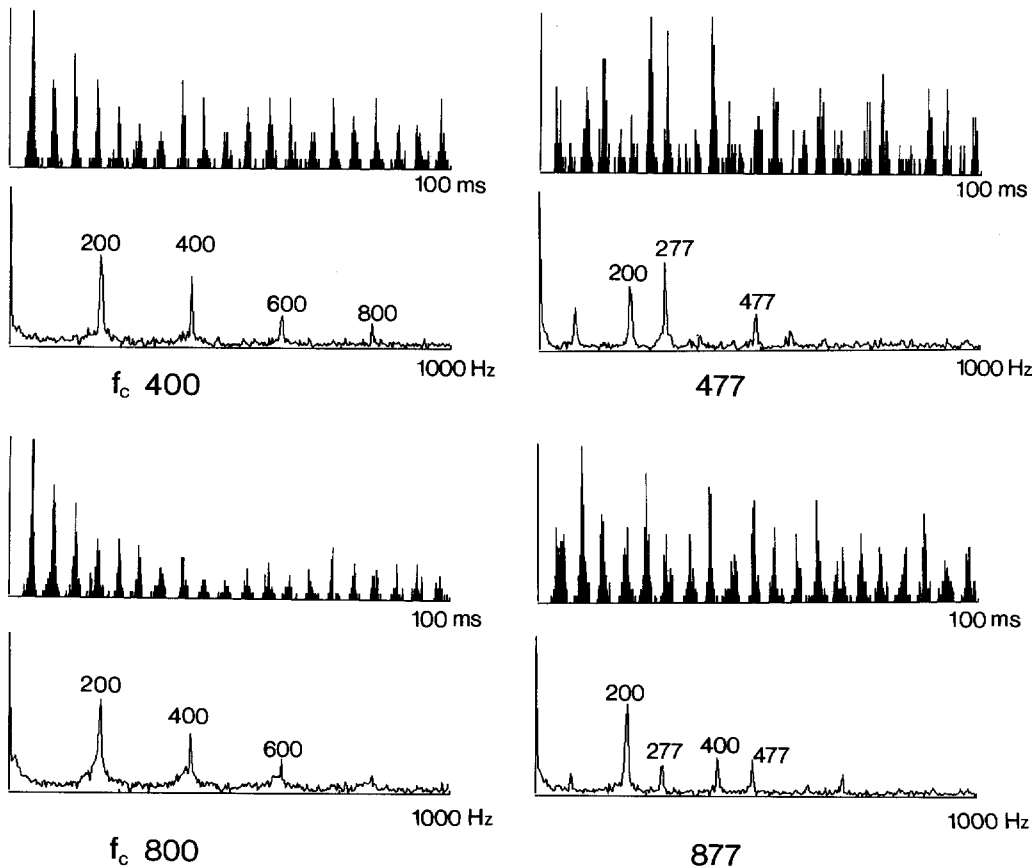


Fig. 2. Autocorrelation functions (ACFs) and power spectra for a fiber with CF 374 Hz, in response to stimuli f_c 400, 477, 800, and 877 Hz. The frequency position of the major peaks in the power spectra are indicated

has a predominant peak occurring at 200 Hz (which corresponds to both the waveform periodicity and the lowest harmonic present in the sound), and shows other progressively smaller peaks at its harmonics of 400, 600, and 800 Hz (note that there is energy in the stimulus at 400 and 600 Hz, but not at 800 Hz). The ACF for the f_c 477 Hz complex is choppy and has a different overall shape than the one for the f_c 400 Hz complex. The power spectrum of this function has its maximal peak at 277 Hz, the lowest frequency component in the complex stimulus; smaller peaks occur at the 200 Hz envelope period and at the 477 Hz center frequency of the complex. These differences in the timing of fiber firing to these two different complex sounds are not apparent in the rate responses of this fiber; the total number of spikes is the same (see Fig. 8). The ACFs for the stimuli with f_c 800 and 877 Hz are also periodic, and also differ from each other. The power spectrum of the ACF in response to the stimulus with f_c 800 Hz is similar to that for the stimulus with f_c 400 Hz: The highest peaks in the power spectra are at the 200 Hz periodicity, and at the first two harmonics of this frequency. The power spectrum of the ACF in response to the stimulus with f_c 877 Hz has peaks at the 200 Hz envelope pseudoperiod, 277 Hz, 400 Hz, and 477 Hz. In contrast to the power spectrum in response to the stimulus with f_c 477 Hz, the predominant peak in the power spectrum to the stimulus with f_c 877 Hz is at

the 200 Hz envelope pseudoperiod. This particular fiber did not respond to the complexes with f_c s 1600 and 1677 Hz at this particular stimulus intensity.

Figure 3 shows firing patterns for a fiber with a CF of 978 Hz; this fiber presumably originates from the caudal part of the AP. The ACFs and power spectra for the 3 harmonic complexes are on the left, and those for the 3 inharmonic complexes are on the right. The ACFs for the 3 harmonic complexes are periodic, with well-defined peaks approximately every 5 ms. The power spectra of these ACFs show maximal peaks at 200 Hz, the envelope periodicity of the complexes, and at harmonics of this frequency (600 Hz for f_c 400 Hz; 600 and 800 Hz for f_c 800 Hz; and 400 Hz for f_c 1600 Hz). Note the absence of dominant peaks at the sidebands and center frequencies of the signals with f_c 800 and 1600 Hz. Responses to the inharmonic complexes with f_c 877 and 1677 Hz also are periodic, and show peaks in their power spectra at the 200 Hz envelope pseudoperiod and at its second harmonic of 400 Hz. Again, the power spectra of ACFs do not show peaks at the sidebands or center frequencies of these complexes, even when these frequencies are close to fiber CF and within the region of synchronization to simple sinusoids. The power spectrum in response to the complex with f_c 1677 Hz is identical to that for f_c 1600 Hz. The ACFs for the stimuli with f_c 400 and 477 Hz are also periodic, but their power spectra

978 Hz

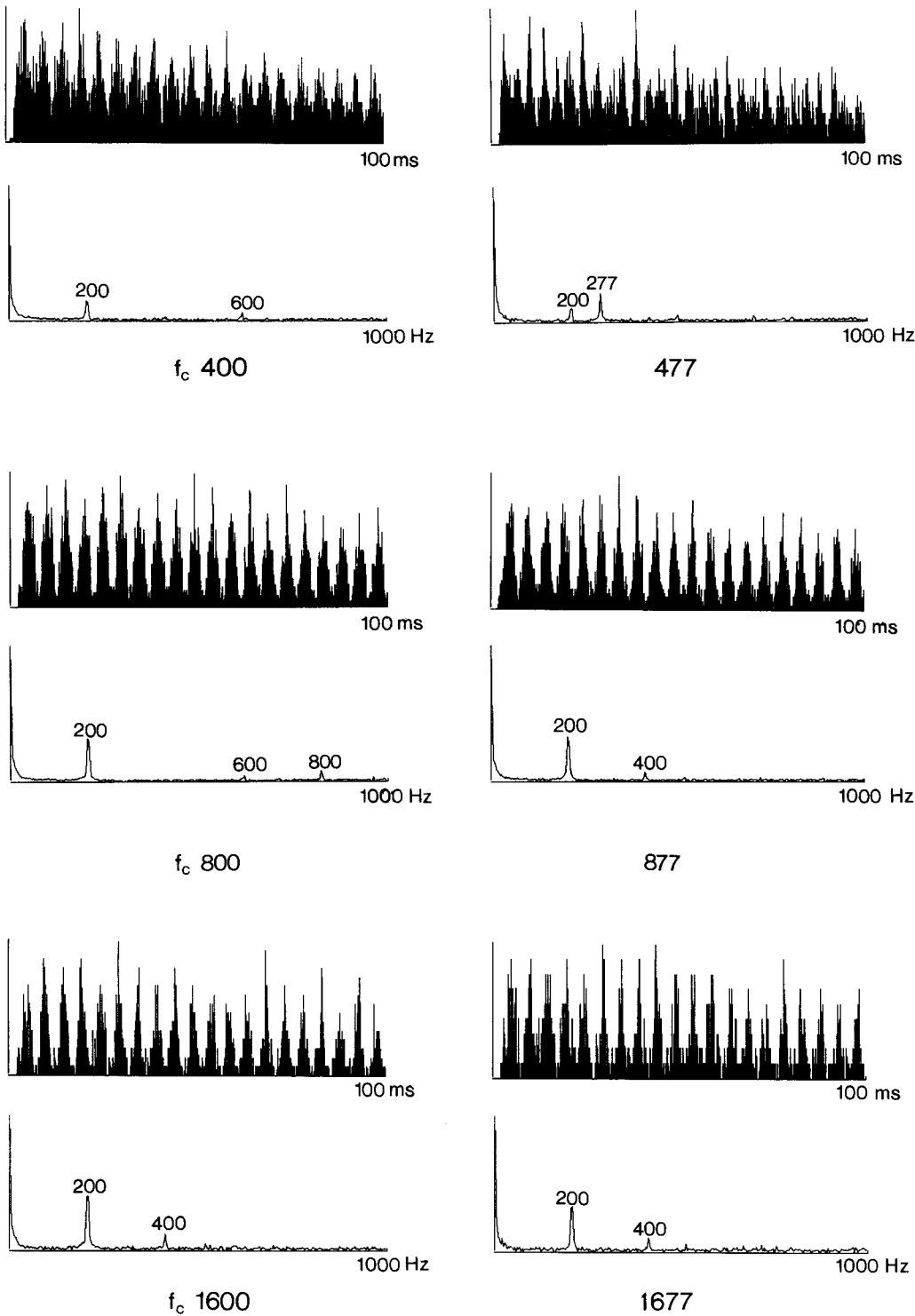


Fig. 3. ACFs and power spectra for a fiber with CF 978 Hz, in response to stimuli f_c 400, 477, 800, 877, 1600, and 1677 Hz

differ from each other. The power spectrum in response to the harmonic complex shows a predominant peak at 200 Hz, representing both the waveform periodicity and one of the frequency components present in the sound, while the power spectrum in response to the inharmonic complex shows a predominant peak at 277 Hz, corresponding to the low frequency sideband of this stimulus.

Examples of responses from a fiber with a CF of 1248 Hz, which presumably originates from the BP, are shown in Figure 4. This fiber responds rather similarly to all of the harmonic stimuli, regardless of their center frequencies. Even in response to those stimuli with components close to the CF of this fiber (f_c 1600 and 1677 Hz), there are no peaks in the power spectra at this

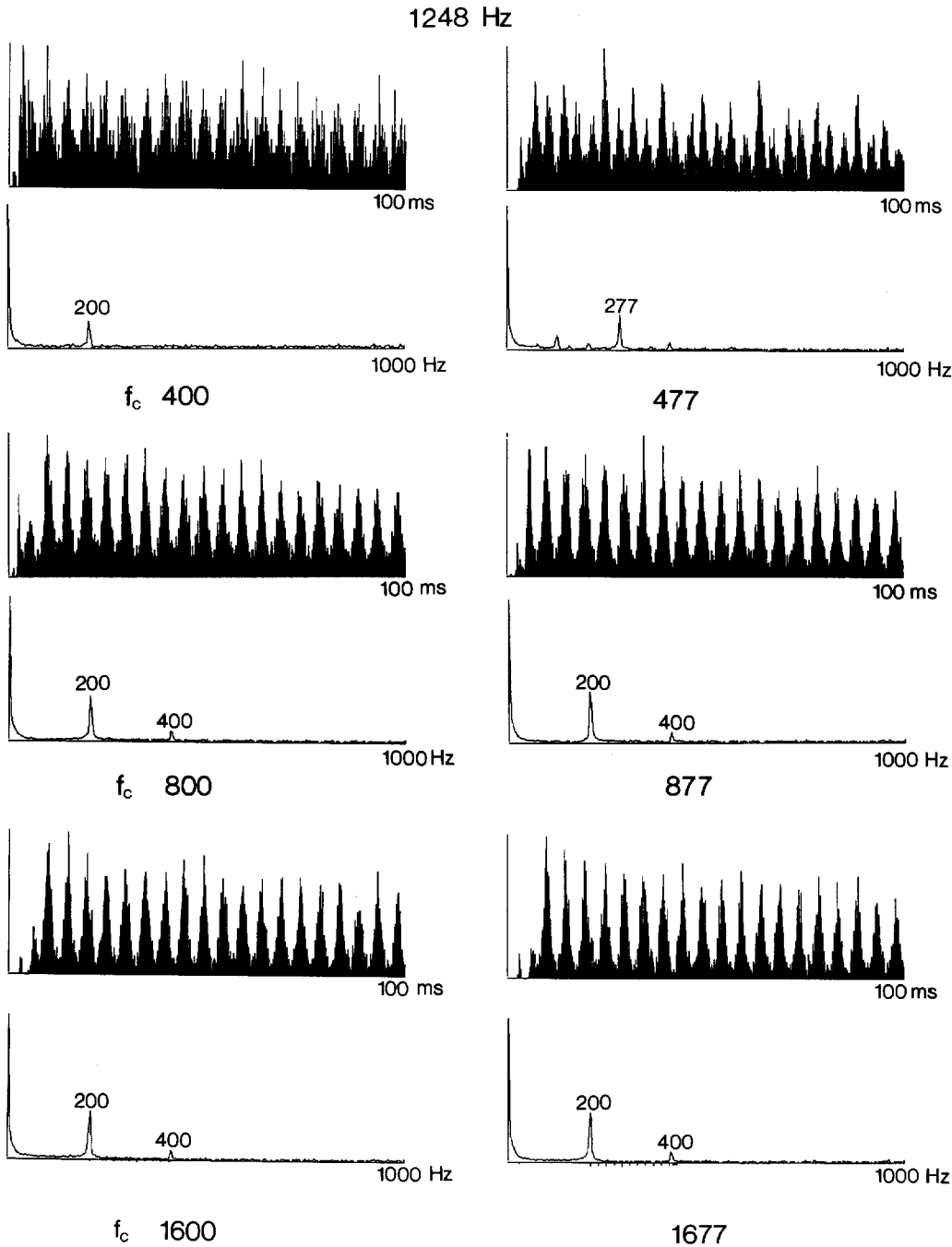


Fig. 4. ACFs and power spectra for a fiber with CF 1248 Hz, in response to stimuli f_c 400, 477, 800, 877, 1600, and 1677 Hz

frequency. This is consistent with the inability of such high-frequency-sensitive fibers to phase-lock to simple sinusoids at their CFs (Freedman et al. 1988; Narins and Hillery 1983). The ACFs and the power spectra are identical for the stimuli with f_c 800, 877, 1600, and 1677 Hz. The responses to the stimuli with f_c 400 and 477 Hz differ. The power spectrum of the response to the stimulus with f_c 400 Hz shows only one peak, at the 200 Hz waveform periodicity, while that for the stimulus with f_c 477 Hz has a maximal peak at 277 Hz, the lowest frequency component in the complex sound.

A summary of the data based on ACFs for all fibers in our sample is presented in Fig. 5. Here, we plot, for

each stimulus separately, the identity of the highest peak in the Fourier transform (FFT peaks) of the ACF to that stimulus against fiber CF. Only peaks with normalized heights (peak amplitude divided by the dc value) of 0.1 or higher were included in the analyses; peaks smaller than this are often undistinguishable in the response, and are not statistically significant. Fibers whose response patterns showed no peaks higher than this cutoff were considered to be nonperiodic (NP). Most (at least 80%) fibers in our sample respond to the stimuli in a periodic fashion. The dominant peak in the Fourier transforms of the ACFs for the majority of fibers (69 to 89%) is at 200 Hz for all of the harmonic stimuli (Fig. 5, left col-

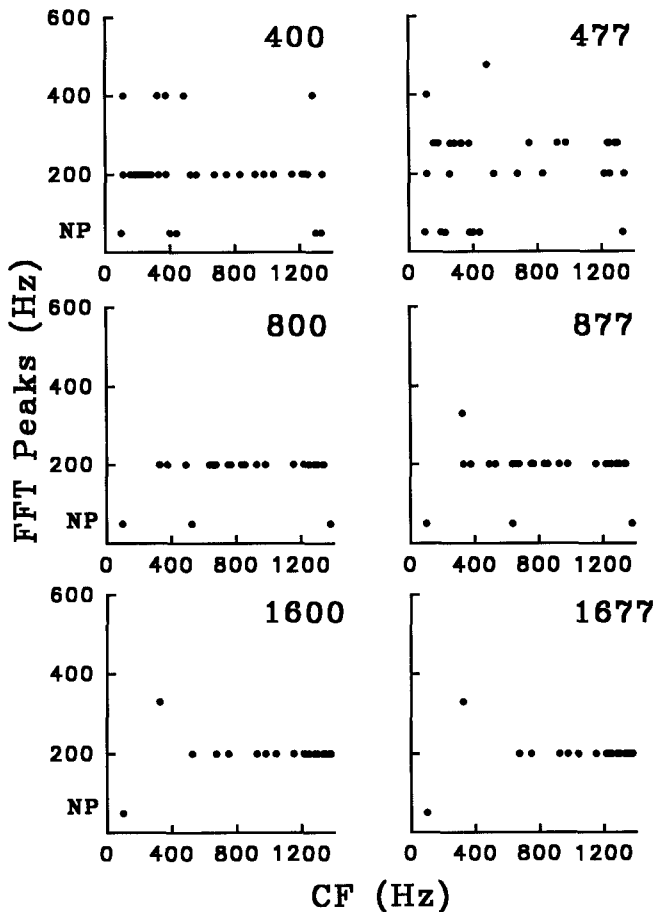


Fig. 5. Dominant peak in the Fourier transforms (FFT peaks) of the ACFs plotted against fiber CF for each stimulus. f_c indicated at the top of each individual graph

umn). This is also true for the responses of fibers to the inharmonic stimuli with f_c 877 and 1677 Hz; here, between 83 and 89% of fibers show a dominant FFT peak at 200 Hz. It is only for the low frequency inharmonic complex (f_c 477 Hz) that the dominant peak in the Fourier transform shifts to the 277 Hz low frequency sideband of the complex for a large proportion (45%) of the fibers. Although this shift in the dominant component is most often seen in responses of low CF fibers, it is not restricted to them.

The fibers that do not show a dominant peak at either 200 Hz, or at 277 Hz for the f_c 477 Hz complex, respond to the stimuli in one of two ways. First, some fibers synchronize strongly to the frequency component in the complex closest to fiber CF. For example, in response to the stimuli with f_c 877, 1600 and 1677 Hz, the fiber with CF 330 Hz signals in its ACF the 330 Hz CF. This is shown in Fig. 5 as a FFT peak at 330 Hz. Another fiber, with CF 490 Hz, responds to the f_c 400 Hz complex with a dominant peak at the 400 Hz carrier frequency, and to the f_c 477 Hz complex with a peak at the 477 Hz carrier frequency. These peaks are the stimulus components closest to fiber CF. This is also seen in the responses of two other fibers with CFs close to 400 Hz; their responses to the complex with f_c 400 Hz also reflect a dominant

peak at the 400 Hz center frequency. In response to the complex with f_c 477 Hz, these fibers show a dominant peak in the FFT at 277 Hz. These effects are for some fibers a result of the particular stimulating intensity used here; at higher intensities, the responses of some fibers become more typical, shifting to signal a dominant peak corresponding to the envelope periodicity. The effects of stimulus intensity were not examined for enough fibers, however, to quantitatively examine this. Note that two other fibers show a dominant FFT peak at 400 Hz for the f_c 400 Hz complex. One fiber has a CF of 110 Hz and the other has a CF of 1280 Hz. These points are anomalous, and the two fibers were not held long enough to further examine their response properties.

Second, some fibers do not respond to the stimuli in a periodic fashion, and no dominant peak can be identified in the Fourier transforms of their ACFs. This is also a result of stimulus intensity; although spike rate is above spontaneous level, insufficient spikes are evoked to produce sufficiently-good synchronization to meet our criteria of a significant peak in the power spectrum of the response. This is true for the responses of the fiber with CF 1300 Hz in response to the complexes with f_c 400 and 477 Hz; for the fiber with CF 1330 Hz in response to the complex with f_c 400 Hz; and for the responses of the fiber with CF 1380 Hz in response to the complexes with f_c 800 and 877 Hz.

Another factor contributing to nonperiodic responses lies in a comparison of the adaptation properties of these fibers with their synchronizing ability. Anuran peripheral fibers show a variety of adaptation patterns in response to single tone bursts (Megela and Capranica 1981). These patterns range from flat or tonic PST histogram shapes to phasic, onset patterns. This diversity in adaptation patterns to tone bursts is also apparent here in the responses to the complex stimuli. Figure 6 plots the adaptation ratio, calculated from PST histogram shapes to the complex stimuli, against the dominant FFT peak in the ACF of responses to each stimulus. The adaptation ratio is formed by dividing the number of spikes in response to the first 20 ms of the stimulus epoch by the number of spikes in the last 20 ms of the stimulus epoch. A ratio of 1 indicates a flat or tonic response; an onset responder will have no spikes in the last 20 ms of the stimulus epoch. Adaptation ratios of about 4 and above (up to onset responses) indicate a "primary-like" response (Megela and Capranica 1981). Figure 6 shows that fibers showing nonperiodic responses and fibers responding maximally to the stimulus component closest to CF rather than to the waveform periodicity are more likely to have high rather than low adaptation ratios. For example, the fiber with CF 98 Hz (Fig. 5) does not respond in a periodic fashion to any of the stimuli. Its adaptation ratio in response to the two complexes with low f_c s shows an onset response, and in response to the other stimuli its adaptation ratio is high, ranging from 9 to 26. Those fibers (see Fig. 5) synchronizing best to the stimulus component closest to CF also have adaptation ratios of 4 and above, indicating "primary-like" or onset responses. Some BP fibers (CFs 1300 and 1380 Hz) show flat PST histogram shapes (adaptation ratios between 1

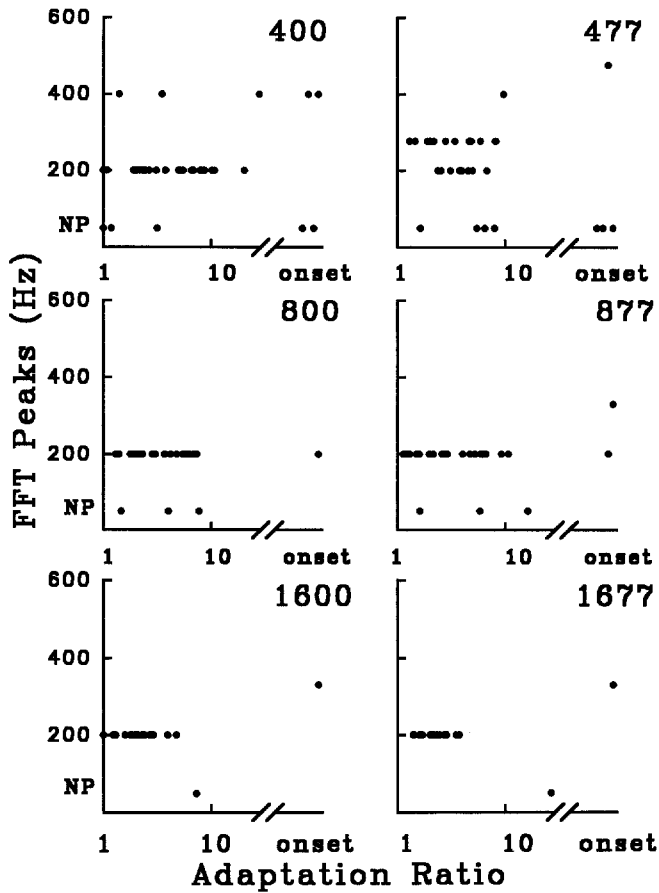


Fig. 6. Dominant peak in the Fourier transforms of the ACFs plotted against fiber adaptation ratio for each stimulus. Adaptation ratios of 30 or above were considered onset responses

and 2) but still do not respond to some stimuli (f_c 400, 477, 800, and 877 Hz) in a periodic fashion, even though these fibers do extract the 200 Hz envelope periodicity of the stimuli f_c 1600 and 1677 Hz. These effects may be related to stimulus intensity, but enough data were not gathered to examine the interactions between intensity and adaptation properties quantitatively over a large sample of fibers.

Results of analyses based on period histograms are shown in Fig. 7. This figure graphs the mean vector strength to the 200 Hz envelope periodicity of the complex sounds as calculated from period histograms, for fibers divided into groups by their CFs: AP low fibers (APl) have CFs below about 490 Hz, AP mid fibers (APm) have CFs between 500–1000 Hz, and BP fibers have CFs above 1000 Hz. The group of AP fibers was divided in this way because fibers with CFs above and below about 500 Hz have different nonlinear properties (Capranica and Moffat 1980). With the exception of the responses of APl fibers to the two complexes with high f_c s, all fibers show good phase-locking (statistically-significant vector strengths) to the 200 Hz envelope periodicity of the complexes, regardless of center frequency. Only two AP low fibers respond to the stimuli with f_c 1600 and 1677 Hz at this intensity, and the calculated vector strengths of their responses do not reach

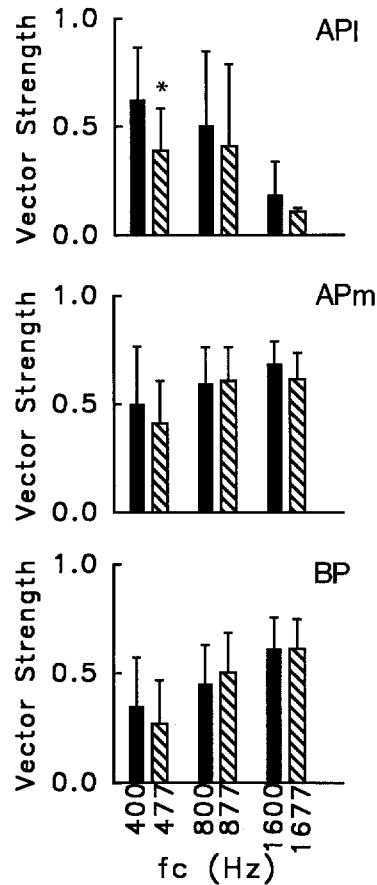


Fig. 7. Vector strength to the 200 Hz periodicity (frequency spacing) of the complex stimuli for fibers grouped by CF. APl (low) fibers have CFs less than 490 Hz, APm (mid) fibers have CFs between 500–1000 Hz, and BP fibers have CFs higher than 1000 Hz. Statistical differences in vector strength, indicated by *, refer to differences between harmonic and inharmonic complexes with similar center frequencies

statistical significance. Fibers in all groups show a trend for lower vector strengths to the inharmonic complex with f_c 477 Hz. This is statistically significant only for the group of AP low fibers, however (t -test for matched pairs; $t(15) = 3.74, P < 0.01$). Across fiber groups, vector strength to 200 Hz differs significantly between APl and BP fibers for the complex with f_c 200 Hz ($t(23) = 2.9, P < 0.01$) and for the two complexes with f_c 1600 ($t(12) = 3.9, P < 0.01$) and 1677 Hz ($t(12) = 5.1, P < 0.01$). Otherwise, the calculated vector strengths between fiber groups are comparable and do not differ significantly.

The rate responses of the sample of fibers to the different stimuli are quantified in Fig. 8, which shows plots of average rate against fiber CF for the stimuli grouped by their center frequencies. Fig. 8A graphs data for the stimuli with f_c 400 and 477 Hz; Fig. 8B graphs data for the stimuli with f_c 800 and 877 Hz; and Fig. 8C graphs data for the stimuli with f_c 1600 and 1677 Hz. Fibers typically show similar rate responses to harmonic and inharmonic stimuli with similar center frequencies, and overall there are no significant differences in rate responses between the harmonic and inharmonic complexes (t -tests for matched pairs; for data in Fig. 8A,

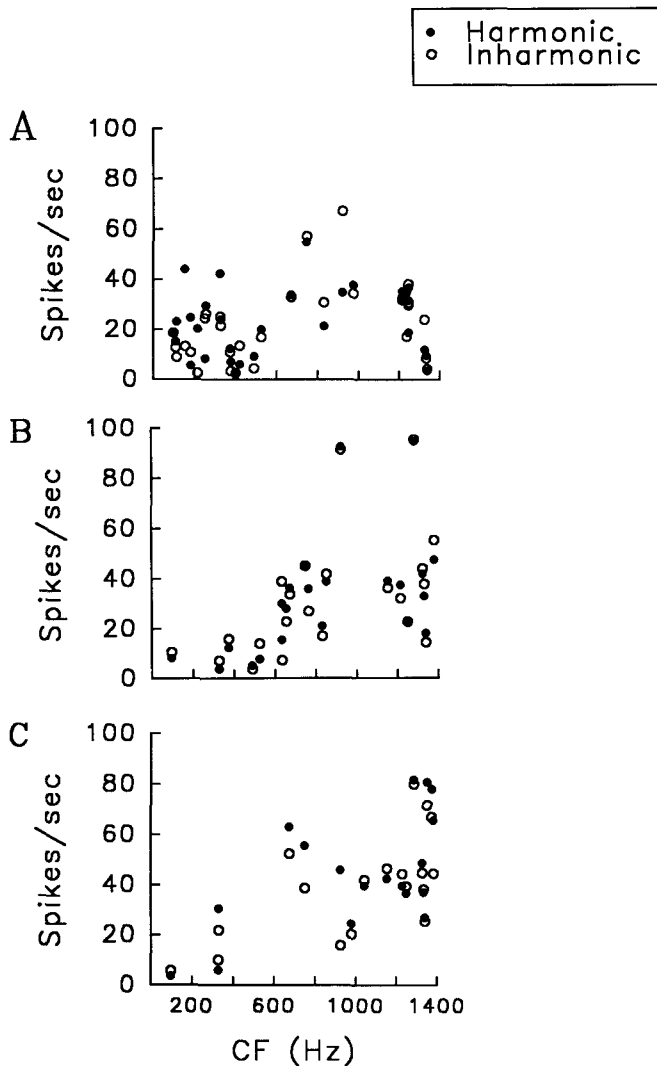


Fig. 8A-C. Spike rate to the harmonic and inharmonic stimuli for those fibers which responded to both types of stimuli. **A** Responses to f_c 400 and 477 Hz. **B** Responses to f_c 800 and 877 Hz. **C** Responses to f_c 1600 and 1677 Hz

$t(29)=0.61$, $P=0.54$; for data in Fig. 8B, $t(18)=1.8$, $P=0.08$; for data in Fig. 8C, $t(24)=0.66$, $P=0.51$.

Discussion

These data suggest that the bullfrog's eighth nerve extracts the periodicity of multiple-frequency stimuli through the timing of fiber firing; the envelope period or pseudoperiod of the complex stimuli could be extracted by an autocorrelation algorithm measuring the time intervals between spike discharges. These data also show that harmonic stimuli made up of different frequency components but with the same waveform periodicity are encoded similarly – by the synchronized responses of individual fibers to the waveform envelope. For example, Fig. 2 shows that the power spectra of the ACFs of the fiber with CF 374 Hz in response to stimuli with f_c 400

and f_c 800 Hz are quite similar. Such similarities in the timing of fiber firing to harmonic complexes with the same fundamental frequency but different spectral components are also apparent in the responses of other fibers with higher CFs (Figs. 3 and 4). Both AP and BP fibers are preferentially extracting, in the timing of their firing, the waveform periodicity of the stimuli, even when the stimuli contain components close to fiber CF. Fibers do not typically synchronize strongly to that stimulus component closest to fiber CF, as would be expected from a mechanism based on spectral coding. These data demonstrate that the “capture” of fiber firing by the fundamental frequency of complex stimuli as described earlier (Schwartz and Simmons 1990; Simmons et al. 1992a, b) does not represent a specialization for processing of the periodicities of biologically-relevant vocal signals and is not restricted to complex signals with the fundamental frequency present in the stimulus spectrum. This argues that temporal processing is a general code for the representation of the periodicity of complex sounds in the bullfrog auditory periphery.

The pseudoperiod of inharmonic signals is also represented in the timing of fiber responses. This may come about by averaging time intervals between peaks in the fine-structure of the waveform close to the envelope crests. The pseudoperiod is not robustly represented by a spectrally-based code, either in the responses of AP or BP fibers. If such a code were operating, we would expect to see synchronization to individual frequency components, which would then serve as a basis for higher-order extraction of the frequency spacing between these components. Only in the case of the stimulus with f_c 477 Hz is the low frequency sideband robustly represented in fiber temporal response.

The data reported here also show that bullfrog peripheral fibers can detect differences in the harmonic structure of complex sounds consisting of low frequency components. As shown in Figs. 2, 3 and 4, all fibers, regardless of their CFs, show a different pattern of temporal response to harmonic and inharmonic complex sounds with f_c of 400 and 477 Hz. Specifically, both the 200 Hz envelope pseudoperiod and the 277 Hz sideband of the inharmonic sounds can be extracted from the power spectra of the ACFs of fiber response. Low CF (Fig. 2) but not mid or high CF (Figs. 3 and 4) fibers also can signal in the timing of their firing the differences in harmonic structure between those stimuli with center frequencies of 800 and 877 Hz. Spectral changes in the complex stimuli are not consistently signaled in fiber response. This relative insensitivity of bullfrog peripheral fibers to changes in the fine-structure of complex stimuli, as compared to changes in stimulus envelope, has also been observed with other manipulations that affect fine structure, such as changes in the phase spectrum (Simmons et al. 1992b). It means that periodicity extraction does not occur in precisely the manner predicted by Schouten's theory, which requires sensitivity to temporal fine-structure (Schouten 1940; Schouten et al. 1962).

Anuran fibers with CFs above about 700 to 1000 Hz do not synchronize to simple sinusoids presented at or above CF (Freedman et al. 1988; Narins and Hillery

1983), but do phase lock to low frequency (below 500 Hz) sinusoids within their frequency-tuning curves (Narins and Wagner 1989). The absence of synchronization to the components in the complex sounds with frequencies higher than this 500 Hz cutoff, as shown in our data, is another indication of this restricted region of phase locking. The synchronized firing of fibers with higher CFs is not "captured" by those frequency components in the complex sounds closest to the cutoff for pure tone synchronization; instead, for most fibers, the strongest synchronization is seen to the envelope periodicity.

It has previously been suggested (Feng et al. 1991; Rose and Capranica 1985; Schwartz and Simmons 1990; Simmons et al. 1992a, b) that anuran peripheral fibers act as "envelope detectors". In such a model, the fiber would fire to high-amplitude portions of a half-wave rectified version of the stimulus envelope. For the stimulus with f_c 400 Hz, there is a single prominent peak in each repetition of the stimulus envelope. For the stimuli with higher f_c s (800 Hz and 1600 Hz), the high-amplitude peaks occur close together in time and the fine-structure tends to be smoothed (Fig. 1). The responses of both AP and BP fibers to these stimuli (Figs. 2 to 4) seem to be consistent with the operation of a simple envelope detector. The inability of most AP and BP fibers to extract the spectral fine-structure of the inharmonic stimuli might also be explained by such a scheme, given that the tuning of these fibers is so broad that the fine-structure peaks cannot be resolved. On the other hand, it is unclear how a simple envelope detector scheme, without additional assumptions, would predict the "pitch-shift" seen in responses to the inharmonic complex with f_c 477 Hz (Fig. 2).

In modelling these results, other fiber response properties need to be considered. First, as shown in Fig. 6, the adaptation properties of fibers can influence their ability to synchronize to the waveform envelope. Moreover, the known nonlinear properties of anuran peripheral fibers (Capranica and Moffat 1980) may also affect temporal sensitivity. It may be that the sensitivity of low CF fibers to the fine-structure of inharmonic stimuli with low frequency components is affected by two-tone suppression, although why suppression only affects inharmonic stimuli is unclear. One way in which the envelope periodicity of inharmonic stimuli might be preserved is by difference tone excitation. In fact, propagation of difference tones had been originally proposed as underlying residue pitch perception (Helmholtz 1863, quoted in de Boer 1976). It is possible that the fiber responses to both the harmonic and inharmonic signals observed here are due to responses to difference tones. Capranica and Moffat (1980) showed, however, that only AP low fibers exhibit true difference tone sensitivity (when the frequency of the difference tone equals fiber CF). The similarity in temporal responses of AP low with AP mid and BP fibers observed here argues against an argument based on this kind of nonlinearity. In any event, any model of signal processing in the anuran inner ear must therefore refine the envelope detection scheme to incorporate both adaptation and nonlinear effects. One such model, based on responses to simple sinusoids, has been described by van Stokkum and Gielen (1989);

how this model would account for processing of complex stimuli is unknown.

The interpretation of the data presented here is based on autocorrelation analyses and their Fourier transforms. We have no direct evidence that the nervous system actually computes the autocorrelation of the spike trains, and we have no direct evidence that only the dominant component of the Fourier transform is computed and processed by the central auditory system. On the other hand, the peripheral processing scheme described here is consistent with, and could provide the input for, the cross-correlation analyses of complex sound coding in the anuran auditory midbrain presented by Epping and Eggermont (1987) and Eggermont and Epping (1987), although periodicity extraction is not a focus of that work.

Experiments similar to those reported here, comparing responses to harmonic and inharmonic stimuli, have also been conducted in the auditory periphery of several species of mammals (Greenberg 1986; Javel 1980). These studies show that mammalian fibers code both the waveform periodicity and the spectral fine-structure of complex signals. Unlike the results seen in the bullfrog, the firing of mammalian fibers is not typically captured by the fundamental frequency or envelope periodicity of the signal. For example, chinchilla auditory nerve fibers signal both the envelope period and the fine-structure of AM tones in their temporal patterns of firing; for many fibers, synchronization is typically strongest to that stimulus component (carrier or sideband) closest to fiber CF (Javel 1980). Moreover, responses of mammalian fibers to the same stimuli show a diversity of response patterns, related to fiber CF, threshold, stimulus intensity, and sensitivity to two-tone suppression (Javel 1980), as compared with the relatively more homogeneous responses of bullfrog fibers shown here. Mammalian fibers with CFs higher than about 5000 Hz synchronize to the envelope of AM tones with these high carrier frequencies, and the period histograms of their responses do not reflect the fine-structure of such stimuli. Fibers with lower CFs, in the range of sensitivity of bullfrog peripheral fibers, signal both the fine-structure and the envelope periodicity in their temporal responses, at least over a restricted range of intensities (Javel 1980). The representation of the temporal fine-structure of inharmonic stimuli differs from that observed in our data, in that the chinchilla fibers are able to code both lower and upper sideband frequencies.

Greenberg (1986) described temporal responses of cat auditory nerve fibers with "low" CFs (below about 4000 Hz) and "low to medium" (below 18 spikes/s) spontaneous rates to two-component harmonic and inharmonic signals. Such fibers signal in their ACFs the period (or pseudoperiod) and the fine-structure of these sounds. It has been suggested that this subset of fibers, whose spontaneous rates and CFs at least at the lower range are comparable to those of anuran peripheral fibers, are particularly sensitive to waveform periodicity (Greenberg 1986). Interspike interval timing information can play an important role in pitch extraction in the mammalian auditory periphery (Evans 1986; Licklider 1951),

and the patterns of fiber firing have been interpreted as providing a physiological basis for a model of pitch processing based on sensitivity to temporal fine-structure (Javel 1980; Javel and Mott 1988; Schouten et al. 1962). The presence of a pronounced tonotopy and the relatively wider existence range of pure tone synchronization point to a more complicated algorithm for periodicity processing in the mammalian than in the anuran system (Srulovicz and Goldstein 1983; Wightman 1973).

Behavioral evidence implicates envelope periodicity as one important acoustic cue mediating species-specific communication in anurans (review in Gerhardt 1988). The vocalizations of many anuran species have distinct waveform periodicities, and these envelope cues may be used to distinguish between the different functional categories of calls in the vocal repertoire of a particular species, as well as between conspecific and heterospecific vocalizations. Whether frogs can discriminate sounds based on differences in their harmonic structure is unclear. Simmons (1988b) showed that green treefrogs tested in a psychophysical paradigm have different thresholds for detecting harmonic and inharmonic two-component signals in noise. The results of that experiment were interpreted as suggesting that frogs might use the cue of harmonic structure as a means of improving the signal-to-noise ratio for sound detection in a noisy acoustic environment (Simmons 1988b). On the other hand, Gerhardt et al. (1990) showed that such differential sensitivity to harmonic structure is not apparent in the behavior of female green treefrogs tested using a discrimination/recognition paradigm that mimics communication in the natural environment. These differences in results may be due to methodological differences between the two studies; for example, the harmonic and inharmonic stimuli used by Gerhardt et al. (1990) were both presented in series at the same, species-typical repetition rate, which could have itself influenced the females' responses. In the experiment by Simmons (1988b), stimuli were presented singly and aperiodically. How these factors influence sound detection is currently under study. The physiological data presented here suggest that differences in harmonic structure of at least some complex sounds are detectable by eighth nerve fibers. If the responses of peripheral fibers play a role in guiding behavior, then the data leave open the possibility that harmonic structure might be a salient perceptual cue for anurans at least under some listening conditions.

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