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Spectral characteristics of the responses of primary auditory-nerve fibers to frequency-modulated signals

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The spectral responses of cat single primary auditory nerve fibers to sinusoidal frequency-modulated acoustic signals applied to the ear are examined. Period histograms were constructed from the neural spike-train data, and the frequency spectrum was determined by Fourier transforming these histograms. Several clusters of spectral components were present. The lowest-frequency cluster consists of components at DC, at the modulation frequency, and at its harmonics. In the next cluster, components surround the carrier frequency and are separated from it by the modulation frequency and its harmonics. Higher-frequency clusters surround frequencies that are twice and three times the carrier frequency. The components in each cluster are separated from the multiples of the carrier frequency by the modulation frequency and its harmonics. The magnitudes of the spectral components were investigated for carrier frequencies located below, at, and above the unit characteristic frequency, and for different signal levels, modulation frequencies, and modulation indices. The components at the modulation frequency and its harmonics were strong and present over a wide range of signal levels, carrier frequencies, modulation frequencies, and nerve-fiber characteristics. The presence of components at the modulation frequency indicates that a demodulation process is occurring. This process may be significant for speech recognition.

Auditory-nerve fiber; Frequency modulation; Neural coding; Spectral characteristics

Introduction

The importance of modulated signals to the auditory system has been established by observations that many mammalian nerve cells in higher auditory centers fire preferentially to frequency-modulated (FM) and amplitude-modulated (AM) signals applied to the ear (Suga, 1964). This has been seen in studies carried out with FM signals at the cochlear nucleus (Erulkar et al., 1968; Fernald and Gerstein, 1972; Møller, 1969, 1974), superior olivary complex (Watanabe and Ohgushi, 1968), inferior colliculus (Nelson et al., 1966; Suga, 1969), medial geniculate nucleus (Watanabe, 1972), and auditory cortex (Whitfield, 1957; Whitfield and Evans, 1965; Suga, 1965). The responses of primary auditory nerve fibers to sweep tones have been examined by Britt and Starr (1976) and by Sinex and Geisler (1981). Sweep tones are FM stimuli with a carrier frequency that is linearly swept in time. A detailed review and bibliography reporting a number of auditory psychophysical and neural studies, that have made use of FM and AM stimuli, has been provided by Kay (1982).

The objective of our study is to examine the spectral responses of single primary auditory nerve fibers to sinusoidal FM acoustic signals applied to the ear.

Period histograms were constructed from the neural spike-train data, and the frequency spectrum was determined by Fourier transforming this period histogram. In some cases, Fourier transforms were constructed directly from the nerve-spike train. The spectrum in both these cases was found to be similar. Analog experiments were also conducted to examine the low-frequency spectral components contained in the nerve-spike train. Preliminary results were reported earlier (Khanna and Teich, 1988).

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Theory

Frequency-modulated (FM) signals

Frequency modulation is achieved by varying the frequency of a sinusoidal wave f_c (the carrier) by a modulation signal f_m. The degree of modulation is indicated by the modulation index β which is the ratio of the peak frequency deviation Δf of the carrier frequency to the modulation frequency f_m. The theory of frequency modulation is well developed and discussed in detail in the information transmission literature (e.g., Schwartz, 1980).

The individual time behavior of the carrier and modulation waves, and the FM signal are illustrated in Figs. 1(a)–(c). The carrier frequency is 996 Hz, the modulation frequency is 98 Hz, and the modulation index is 5. In this case the peak frequency deviation is 490 Hz. The instantaneous frequency of the FM signal varies between 506 Hz and 1486 Hz during each modulation cycle (Fig. 1(c)). The Fourier spectrum of each of the individual waves is a single frequency, as shown in Figs. 1(d) and 1(e).

The magnitude of the FM spectrum (Schwartz, 1980) is easily calculated (Fig. 1(f)). It is centered at the carrier frequency f_c. The sidebands are separated from it by multiples of the modulation frequency f_m. The sideband amplitudes decrease sharply outside a region $\pm\Delta f$ from the carrier.

The dependence of the FM signal and its spectrum on the modulation index β, for one modulation frequency, is illustrated in Fig. 2. Time functions for an FM signal with a carrier frequency of 3 kHz, a modulation frequency of 98 Hz, and modulation indices of 1, 10, and 20, are shown in

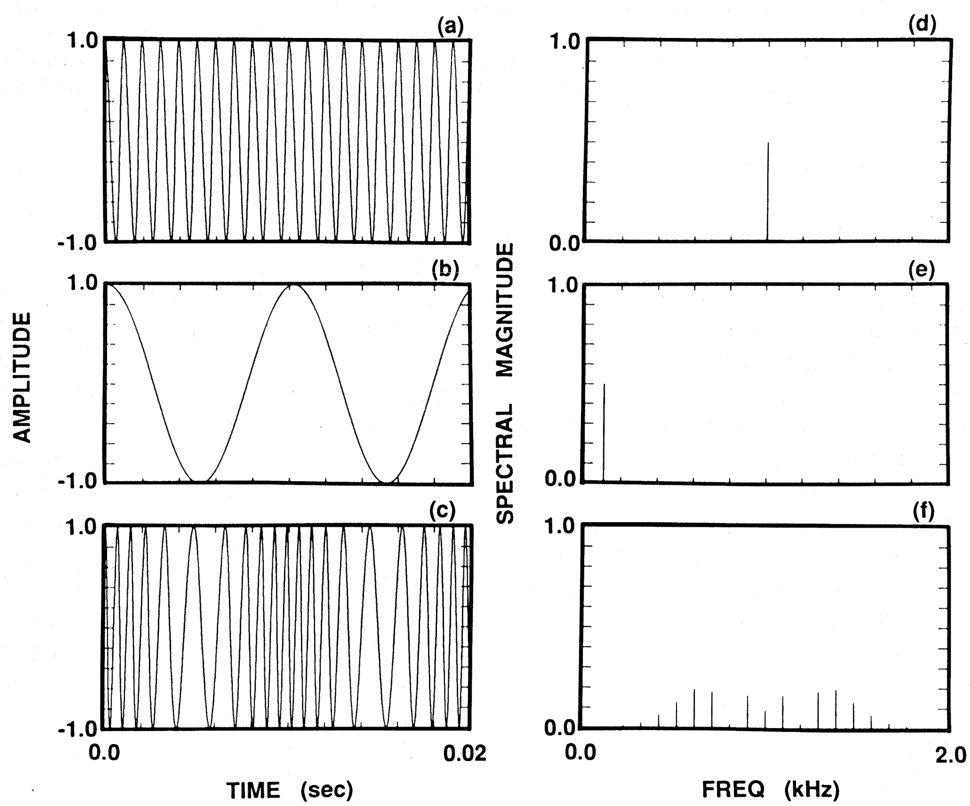

Fig. 1. Time course [(a) and (b)] and spectrum [(d) and (e)] of two cosinusoidal waves used to produce an FM wave by angle modulation. The time course of the FM wave is shown in (c) and its spectrum is shown in (f). The carrier frequency in (a) was 996 Hz and the modulation frequency in (b) was 98 Hz. The spectrum of the FM signal is symmetrical about the carrier frequency. It consists of an infinite series of components with Bessel-function magnitudes that are separated by the modulation frequency.

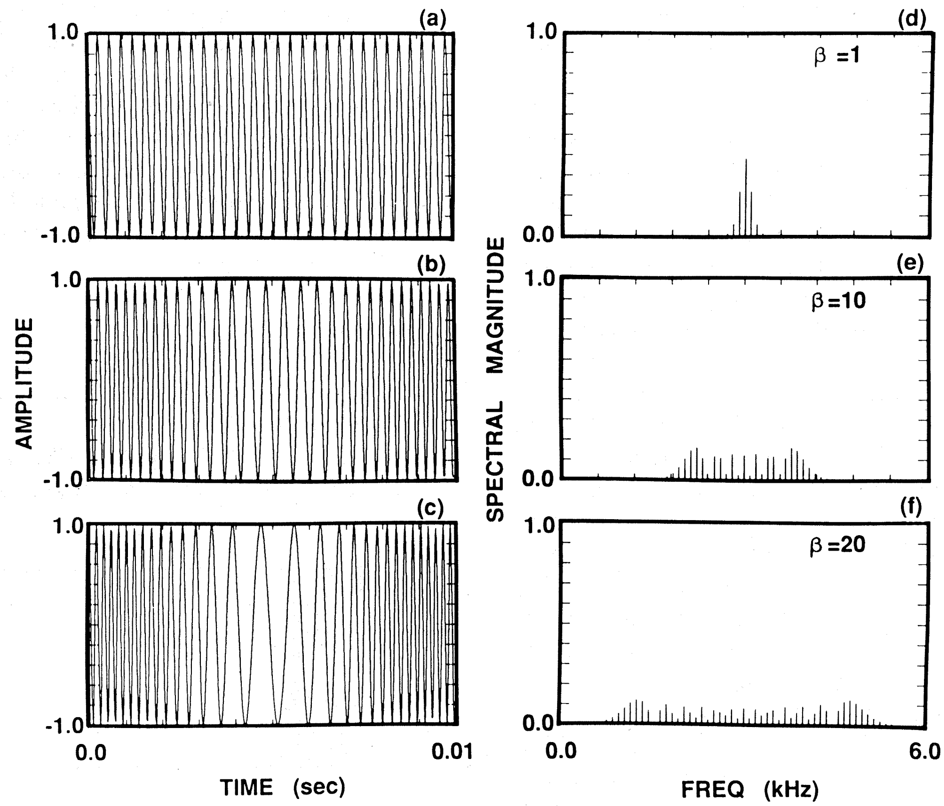

Fig. 2. Time course [(a), (b) and (c)] and spectrum [(d), (e) and (f)] of an FM signal with increasing peak deviation Δf (increasing β) when the carrier frequency (3 kHz) and modulation frequency (98 Hz) are fixed. (a) and (d): $\beta = 1$ ($\Delta f = 98$ Hz). (b) and (e): $\beta = 10$ ($\Delta f = 980$ Hz); (c) and (f): $\beta = 20$ ($\Delta f = 1960$ Hz). The major portion of the FM spectrum is contained in the bandwidth $2\Delta f$.

Figs. 2(a)–(c), respectively. The corresponding spectra are shown in Figs. 2(d)–(f). For $\beta = 1$ the peak deviation Δf is 98 Hz and only two sidebands are present on each side of the carrier. At $\beta = 10$, the peak deviation is 980 Hz and the spectrum extends 1400 Hz below and above the carrier frequency. Finally, for $\beta = 20$, the peak deviation is 1960 Hz and the spectrum extends from about 500 Hz to about 5500 Hz. As β increases, the number of significant sidebands increases while the magnitudes of the spectral components decrease.

Demodulation of an analog FM signal

There are many ways in which an FM signal can be demodulated (Schwartz, 1980). In one simple scheme, an FM signal is converted into an AM signal by passing it through a system whose transfer function varies with input frequency. Examples are an RC filter and a simple tuned circuit whose center frequency is different from the carrier frequency. The modulation signal can then be recovered by means of an AM demodulator, as discussed in the companion paper (Khanna and Teich, 1989). Such simple FM demodulation schemes generally introduce distortion into the FM-to-AM conversion process.

The tuned behavior of the cochlea, together with the asymmetric deflections of the hair-cell stereocilia bundles (Flock, 1984), could provide the requisite apparatus for FM demodulation in the inner ear.

Methods

The methods used in carrying out the experiments reported here were identical to those discussed previously and in the companion paper on AM signals (Teich and Khanna, 1985; Khanna and Teich, 1989).

To generate the FM signals, the carrier frequency was modulated by a sinusoidal wave. The modulation frequency was varied over a broad range (from 5 to 98 Hz) and the modulation index β ranged from 1 to 40. Carrier frequencies below, at, and above the CF of the nerve fiber were used.

In most cases, period histograms were constructed by averaging the nerve-spike data (Teich and Khanna, 1985). The period histogram was Fourier transformed to obtain the spectrum. For the data presented in Figs. 3–7 and 9–11, the histograms consisted of 4096 bins, each of 50 μs duration, so that one pass across the period histogram represented 204.8 ms. Data shown in these figures were collected for 30 s, corresponding to 146 repetitions. Since a typical unit fires at roughly 100 spikes/s there were some 20 spikes per pass of the period histogram. The values of the spectral magnitude at DC, representing the total number of spikes in the histogram, is therefore about 3000 in these figures. The period of a modulation frequency of 100 Hz is 10 ms so that at 100 spikes/s there is an average of one nerve spike produced per modulation cycle.

In some experiments no averaging was used, in which case 1.024 s (2048 bins of 0.5 ms duration each) of nerve-spike data were collected. The data presented in Fig. 8 are therefore simply Fourier transforms of the 1-μs monophasic pulses generated by the nerve-spike train (Teich and Khanna, 1985).

Results

Full spectrum of the period histogram in response to FM signals

The spectral responses of a primary nerve fiber to an FM signal applied well-below, below, at, and above the unit CF, are illustrated in Figs. 3–6, respectively. These data are all from the same unit (CF 2299 Hz, threshold 10 dB SPL). The stimulus was a sinusoidally modulated FM signal with a modulation frequency of 98 Hz, a modulation index of 5, a peak deviation of 490 Hz, and a stimulus level of 50 dB SPL.

The spectral magnitudes of the input signals are shown in part (a) of each of these figures. The spectral components are symmetrically arranged around the carrier frequency and exhibit the characteristic Bessel-function-sideband shapes, examples of which are shown in Figs. 1 and 2. Plots of the spectral magnitudes of the period histograms obtained from the neural response are shown in part (b) of each figure.

Response well below CF

The results obtained with a carrier frequency f_c at 996 Hz, which is well-below the CF of the unit, are shown in Fig. 3.

The spectrum of the applied FM signal, which is centered at the carrier frequency f_c, is illustrated

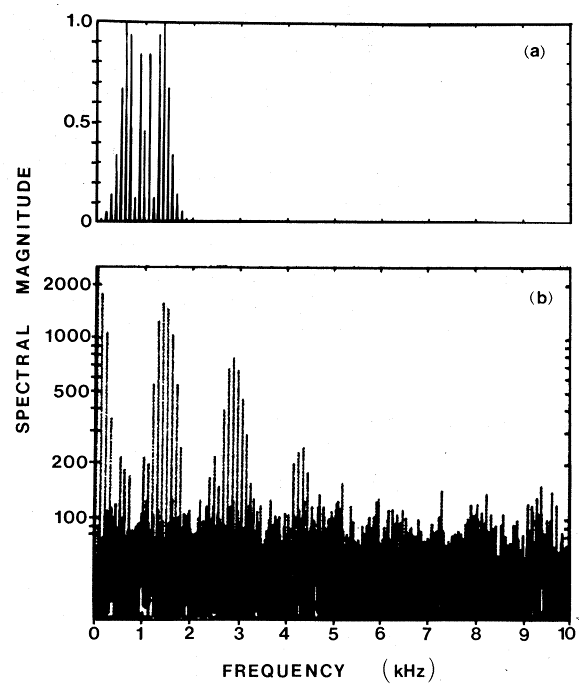

Fig. 3. (a) Spectrum of the FM signal applied to the ear. The stimulus SPL was 50 dB, the carrier frequency was 996 Hz, the modulation frequency was 98 Hz, and the modulation index was 5. Spectral magnitude is displayed as a function of frequency. Note that the spectral components are distributed symmetrically about the carrier frequency. (b) Spectrum of the period histogram for a unit with a CF of 2299 Hz and a threshold of approximately 10 dB SPL. Four clusters of frequency components can be seen above the noise floor. These are at the baseband and at multiples of the carrier frequency. The spectrum of the histogram differs considerably from that at the input.

in Fig. 3(a). It exhibits 16 sidebands of appreciable magnitude (Schwartz, 1980), eight on either side of the carrier. The spacing between the sidebands is at the modulation frequency $f_m = 98$ Hz.

The fast Fourier transform (FFT) of the period histogram is shown in Fig. 3(b). Four groups of spectral components rise above the noise floor. The leftmost cluster represents baseband components, which appear at DC and at the first 7 multiples of $f_m = 98$ Hz, i.e., at $f = nf_m$ where $0 \leqslant n \leqslant 7$. The spectral magnitude is greatest at the modulation frequency of 98 Hz and progressively decreases as the harmonic number increases. The spectral components in the second group occur at the carrier and upper sideband frequencies of the applied signal, i.e., at $f = f_c + nf_m$ where $0 \leqslant n \leqslant 8$. The third cluster of spectral components generally mimics the asymmetry of the second group, but begins somewhat above $2f_c$. The fourth cluster begins quite a bit above $3f_c$. The magnitudes of the clusters generally decrease with increasing frequency.

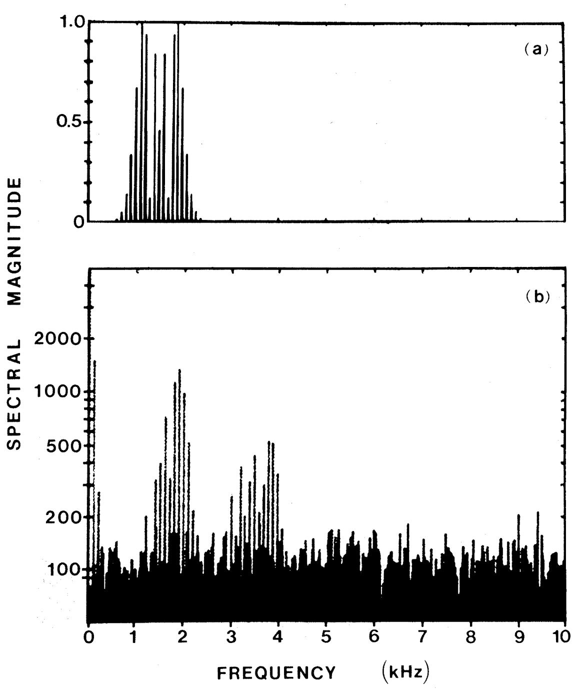

Fig. 4. (a) Spectrum of the FM signal applied to the ear. The nerve fiber, signal level, modulation frequency, and modulation index were the same as described in Fig. 3, but the carrier frequency was changed to 1499 Hz. (b) The spectrum of the period histogram shows three clusters of frequency components, at the baseband and at multiples of the carrier frequency.

Response below CF

The results obtained with a carrier frequency f_c at 1499 Hz, which is below the CF of the unit, are shown in Fig. 4. The spectrum of the applied FM signal, illustrated in Fig. 4(a), is similar to that shown in Fig. 3(a) but is translated up in frequency as a result of the higher carrier frequency. The spacing between the sidebands is again at the modulation frequency (98 Hz).

The Fourier transform of the period histogram is shown in Fig. 4(b). In this case three groups of spectral components are evident. The leftmost cluster represents baseband components, which appear at DC and at the fundamental and second harmonic of the modulation frequency.

The second group has spectral components principally at the carrier and upper sideband frequencies of the applied signal, but there are a few components that fall below the carrier frequency as well. The third cluster of spectral components occurs at twice the carrier frequency and its upper sidebands.

Response at CF

The spectrum of the period histogram is shown in Fig. 5 for the same unit with identical conditions except that the carrier frequency was at the CF of the unit. The input spectrum is therefore similar to that shown in Fig. 3(a), but its center frequency is at 2299 Hz.

The Fourier transform of the period histogram shown in Fig. 5(b) exhibits 3 groups of spectral components: at the baseband, centered at the carrier frequency (2299 Hz), and centered at twice the carrier frequency (4598 Hz). The spacings of all frequency components are at the modulation frequency (98 Hz).

The baseband components occur at DC and at the modulation frequency and its harmonics. The amplitudes of the second and third harmonic components are larger than that of the fundamental. This occurs only when the carrier frequency is close to the CF of the unit. The cluster of components centered at the CF closely resembles the spectrum of the applied FM signal. The third cluster of components, aside from being smaller in magnitude, has a somewhat different character from the second cluster. For example, the central spectral component at 2299 Hz in the second

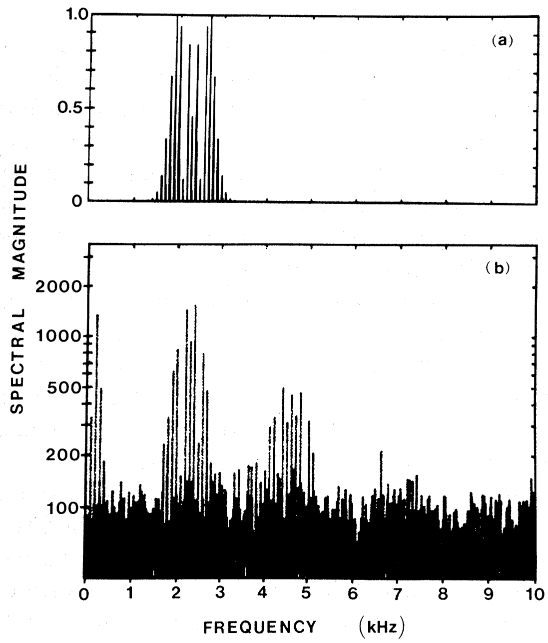

Fig. 5. (a) Spectrum of the FM signal applied to the ear. The nerve fiber, signal level, modulation frequency, and modulation index were the same as described in Fig. 3, but the carrier frequency was increased to 2300 Hz. (b) The spectrum of the period histogram shows three clusters of frequency components, at the baseband and at multiples of the carrier frequency.

cluster is smaller than its two surrounding sidebands.

Response above CF

Results obtained with a carrier frequency f_c at 2500 Hz, which is above the CF (2299 Hz) of the unit, are presented in Fig. 6. The spectrum of the applied FM signal is shown in Fig. 6(a).

The Fourier transform of the period histogram is shown in Fig. 6(b). Three groups of spectral components are observed. The leftmost cluster shows baseband components at the modulation frequency and its first four harmonics. The middle group has spectral components principally at the carrier and lower sideband frequencies, but there some smaller components that fall above the carrier frequency as well. The third cluster of spectral components occurs at twice the carrier frequency and its lower sidebands. The asymmetry in these sidebands is in the opposite direction to that observed when the carrier frequency was below CF.

The asymmetry between the lower and upper sidebands is similar to that observed for AM stimulation at a carrier frequency above the CF of the unit (Khanna and Teich, 1989; Fig. 8).

Widths of the spectral-component clusters

The increasing width of the successive spectral-component clusters is illustrated in Fig. 7 for a unit with a CF of 1196 Hz (the frequency tuning curve (FTC) for this unit is shown in Fig. 9(a)). The stimulus was a sinusoidally modulated FM signal with a carrier frequency of 1499 Hz at a level of 60 dB SPL. The modulation frequency was 19.5 Hz and the modulation index was 20. The third group of spectral components (which lies between 2.3 and 3.2 kHz) is wider than the second group (which lies between 1.1 and 1.8 kHz). This effect does not occur for AM stimulation.

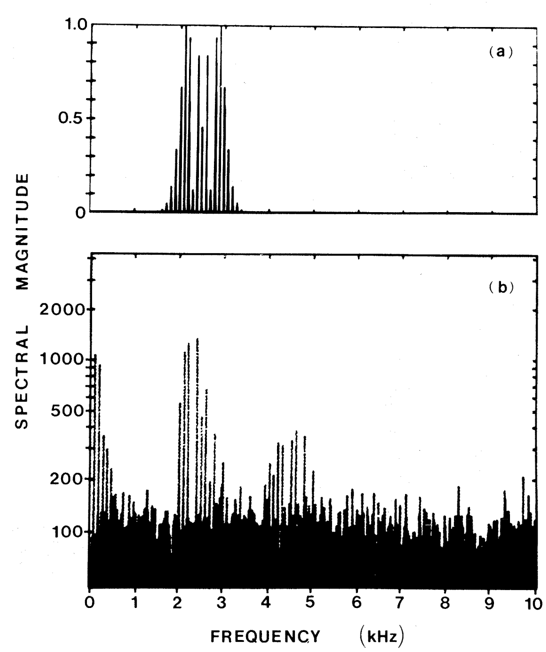

Fig. 6. (a) Spectrum of the FM signal applied to the ear. The nerve fiber, signal level, modulation frequency, and modulation index were the same as described in Fig. 3, but the carrier frequency was set at 2500 Hz. (b) The spectrum of the period histogram shows three clusters of frequency components, at the baseband and at multiples of the carrier frequency.

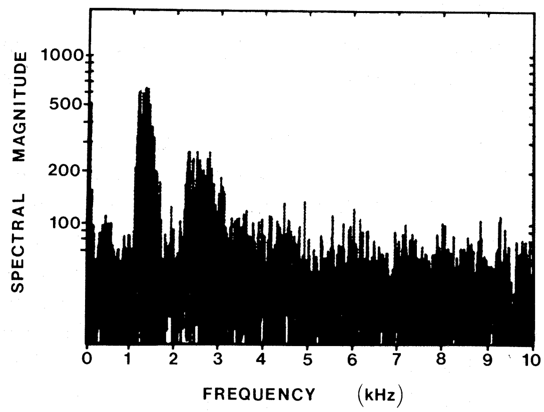

Fig. 7. Spectrum of the period histogram in response to an FM signal for a unit with a CF of 1196 Hz. The carrier frequency was 1499 Hz at a level of 60 dB SPL, the modulation frequency was 19.5 Hz, and the modulation index was 20. The width of the successive clusters of frequency components is seen to increase.

Full spectrum of the nerve-spike train in response to FM signals

As pointed out in Section III, the data presented in Figs. 3–7 and 9–11 are Fourier transforms of period histograms. Each histogram represents 146 repetitions of the stimulus. Averaging of this kind is often performed to enhance the signal-to-noise ratio.

It is important to ascertain how this averaging process affects the observed spectrum. A series of experiments were carried out to determine if the various spectral clusters will be observable when there is no averaging.

The stimulus was a sinusoidally modulated FM signal. The carrier frequency was 500 Hz, the modulation frequency was 9.8 Hz, and the modulation index was 40. The unit CF was 500 Hz. The nerve spikes were collected in 2048 bins, each of 0.5 ms duration, so that the duration of the entire nerve-spike sequence collected was 1.024 s. Since there was no averaging in this case, the data presented in Fig. 8 are simply Fourier transforms of the nerve-spike train. The stimulus level was decreased from 90 dB SPL to 50 dB SPL in 10 dB steps. The total number of nerve spikes collected at each level was between 50 and 100.

The Fourier spectra obtained are illustrated in Fig. 8(a)–(e). Spectral magnitude is shown as a

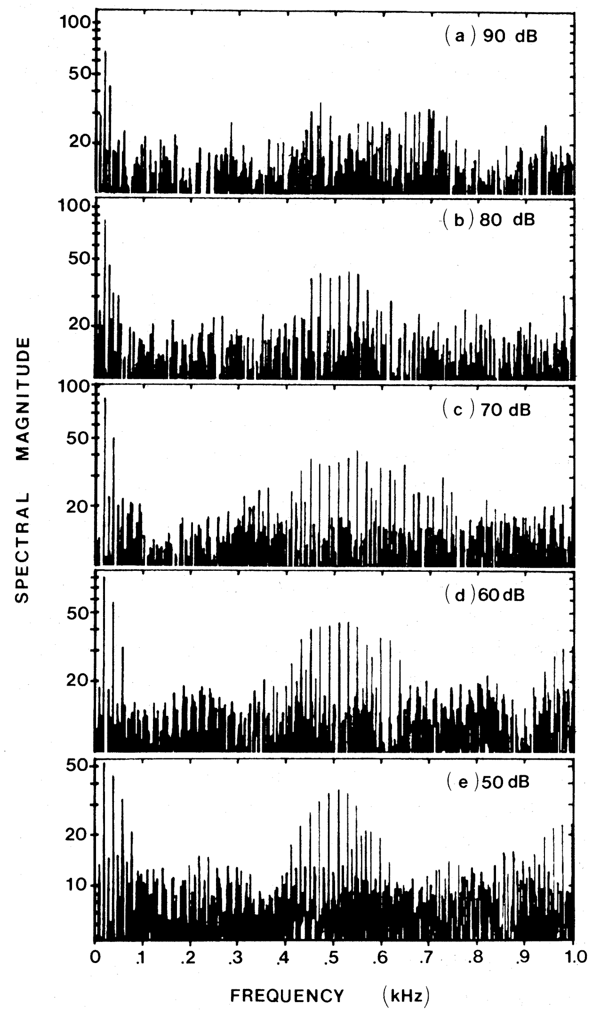

Fig. 8. Spectrum of a 1.024-s segment of the nerve-spike train from a unit with a CF of 500 Hz. The carrier frequency was 500 Hz, the modulation frequency was 9.8 Hz, and the modulation index was 40. The stimulus levels were: (a) 90 dB SPL, (b) 80 dB SPL, (c) 70 dB SPL, (d) 60 dB SPL, and (e) 50 dB SPL. Three groups of spectral components can be observed above the noise. The first group consists of components at DC, at the modulation frequency, and its harmonics (note that even-order harmonics are enhanced). The second group consists of lower- and upper-sideband components centered at the carrier frequency. The third group consists of lower-sideband components centered at twice the carrier frequency; the upper sideband components cannot be seen since they lie beyond the maximum frequency measured. The spectral components within each group are separated from each other by the modulation frequency fm. Since no averaging was carried out on the signal, it is clear that the nerve-spike train contains baseband, carrier, and sideband frequency components. It is important to note that baseband components are present at all stimulus levels.

function of frequency from DC to 1 kHz. Three groups of spectral components are evident above the noise. The first group consists of components at DC as well as at the modulation frequency (9.8 Hz) and its harmonics. The second group consists of lower- and upper-sideband components centered at the carrier frequency. The third group consists of lower-sideband components centered at twice the carrier frequency. Because the frequency scale extends only up to 1 kHz, the corresponding upper sidebands cannot be seen. The spectral components within each group are separated from each other by the modulation frequency.

At the lowest stimulus level used in this experiment (50 dB SPL) the modulation frequency and seven of its harmonics appear in the baseband group of spectral components (Fig. 8(e)). The spectral magnitudes of the even harmonics ($2f_m$, $4f_m$, $6f_m$, and $8f_m$ are substantially larger than those of the odd harmonics (the second harmonic is about four times larger than the fundamental). This occurs when the carrier frequency is centered at the CF of the nerve fiber (see also Fig. 5).

The alternation of magnitudes between the even and odd components is also seen in the second and third clusters of spectral components centered at the carrier frequency and at twice the carrier frequency. The average magnitude of the components in a cluster decreases as the cluster frequency increases.

At 60 dB SPL (Fig. 8(d)), only six baseband components can be discerned, and the magnitudes of the harmonics of the modulation frequency decrease with harmonic number at a rate steeper than that seen in the spectrum at 50 dB SPL. The spectrum surrounding the carrier frequency appears to be comparatively flatter and more asymmetrical, with a greater number of components appearing on the high frequency side.

At 70 dB SPL (Fig. 8(c)), only four baseband components can be seen. The spectral magnitude of these components is nearly double that of the corresponding components at 50 dB SPL (Fig. 8(e)), principally because the total number of neural spikes (represented by the spectral magnitude at DC) has doubled. The asymmetry of the spectrum around the carrier is even more prominent. The magnitude of this group of components is less than half that of the 2nd harmonic of the modulation frequency. The cluster of spectral components at twice the carrier frequency has virtually disappeared.

At 80 dB SPL (Fig. 8(b)), the magnitude of the component at the modulation frequency remains low and its second harmonic continues to dominate the spectrum. However the relative magnitudes of the odd-order baseband components is increased. The number of spectral components around the carrier is severely reduced compared to that seen at 70 dB SPL.

Finally, at 90 dB SPL (Fig. 8(a)), there is a slight decrease in the magnitudes of the second and third harmonics of the modulation frequency while the components at the carrier frequency essentially disappear into the noise and are no longer seen.

Behavior of the baseband spectral components in response to FM signals for low-CF units

In FM, as in AM, the lowest-frequency components in the FFT spectrum appear at the modulation frequency and its harmonics. It is convenient to use the baseband synchrony index (BSI) as a measure of their strength. This parameter was introduced in the companion AM paper (Khanna and Teich, 1989); it is defined as the ratio of the spectral magnitude at the fundamental modulation frequency to the spectral magnitude at DC. The nth-order baseband synchrony index, BSI(n), represents the ratio of the spectral magnitude at the nth harmonic of the modulation frequency to the spectral magnitude at DC.

Dependence of the baseband synchrony indices on carrier frequency

The baseband synchrony indices for carrier frequencies below, at, and above the CF are presented in Fig. 9 (CF 1196 Hz). The FTC of the nerve fiber is shown in Fig. 9(a). The carrier frequencies used were: 596 Hz (Fig. 9(b)), 1196 Hz (Fig. 9(c)), and 1499 Hz (Fig. 9(d)). The data were obtained for a signal applied at 60 dB SPL, with a modulation frequency of 19.5 Hz and a modulation index of 20. (The full spectrum of the period histogram for this unit at 1499 Hz is shown in Fig. 7.)

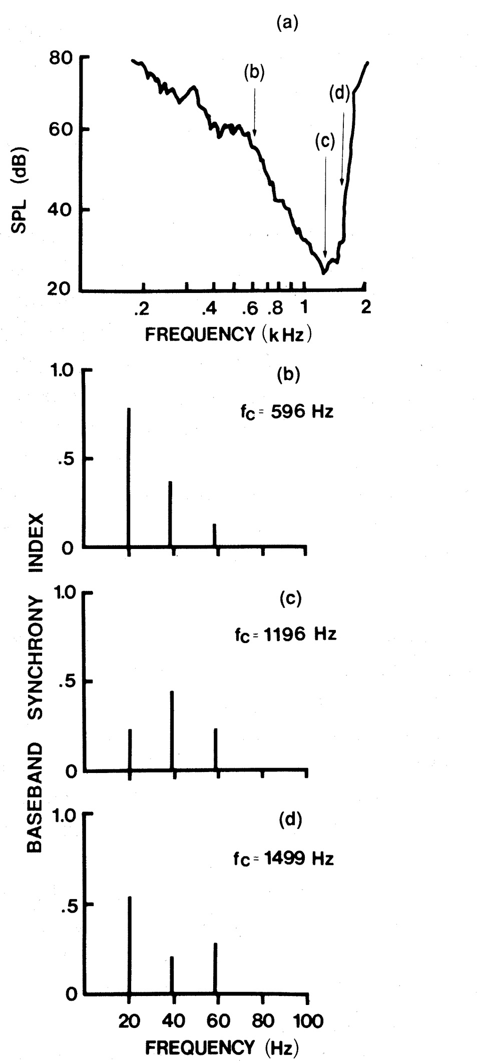

Fig. 9. (a) Frequency tuning curve for a unit with a CF of 1196 Hz. (b)–(d) Baseband synchrony indices (BSIs) for the modulation frequency and its first and second harmonics, for carrier frequencies of 596 Hz, 1196 Hz, and 1499 Hz. The BSIs are defined as the ratio of the spectral magnitudes at the baseband frequencies to the spectral magnitude at DC (see text). The data were obtained for a signal applied at 60 dB SPL, with a modulation frequency of 19.5 Hz and a modulation index of 20. Note that for stimulus frequencies below and above the CF, the BSI at the fundamental modulation frequency is largest, but for a signal at CF, the BSI at the second-harmonic of the modulation frequency is larger than that at the fundamental.

Below CF, the BSI at the modulation frequency, at its second harmonic, and at its third-harmonic were 0.77, 0.37, and 0.12, respectively. At CF, the values were 0.22, 0.44, and 0.22, respectively. Above CF, they were 0.55, 0.20, and 0.28, respectively. The significance of a particular numerical value for the BSI is similar to that for the ordinary synchronization index (SI) discussed by Johnson (1980).

The magnitude of BSI at the second-harmonic of the modulation frequency is greater than that at the fundamental when the stimulus is at CF.

Dependence of the baseband spectral magnitude on modulation frequency

The baseband spectral magnitude and baseband synchrony index were determined for three modulation frequencies in one unit (CF 1800 Hz). The stimulus was below the CF (996 Hz), at an SPL of 60 dB, and the modulation index was 10. Modulation frequencies used were 19.5 Hz, 49 Hz, and 98 Hz. The results are presented in Table I; they show that the baseband spectral magnitude and the BSI increase with modulation frequency. This behavior is dependent on the relationship of the stimulus frequency and the unit CF. As the modulation frequency f_m increases, the peak deviation $\Delta f = \beta f_m$ increases from 195 Hz to 970 Hz so that the stimulus is brought closer to the CF of the unit during the modulation cycle. This has the effect of increasing the response of the unit.

Variation of the baseband synchrony indices with modulation index

The baseband synchrony indices are shown for three values of the modulation index in Figs.

TABLE I
DEPENDENCE OF THE BASEBAND SPECTRAL MAGNITUDE AND BSI ON MODULATION FREQUENCY FOR A LOW-FREQUENCY UNIT (CF 1800 Hz)

Modulation frequency (Hz)	Baseband spectral magnitude	Baseband synchrony index (BSI)
19.5	625	0.18
49.0	1228	0.31
98.0	1590	0.45

The carrier frequency was 996 Hz at 60 dB SPL with a modulation index of 10. As the modulation frequency increases, the stimulus is brought increasingly closer to the CF of the unit for brief periods during the modulation cycle, thereby increasing the response of the unit to the modulation frequency and its harmonics (see text).

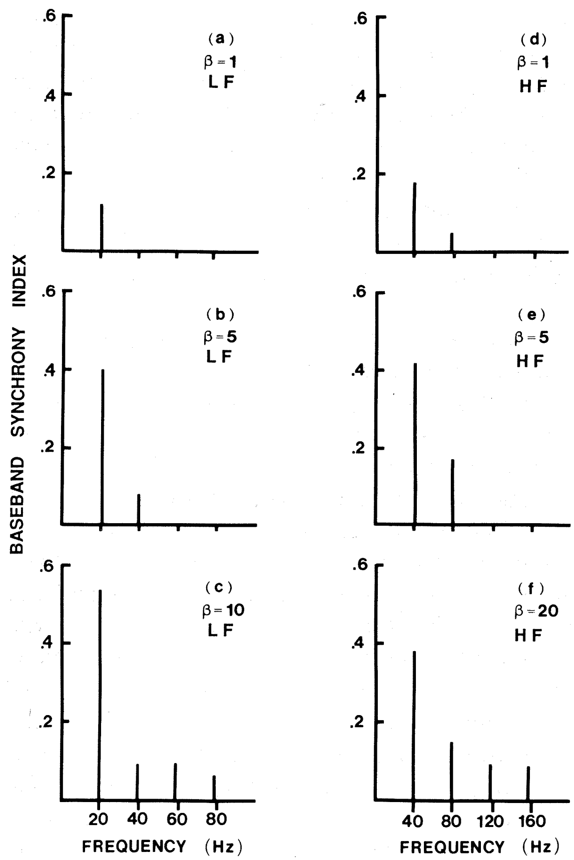

Fig. 10. (a)–(c) BSIs for three values of the modulation index for a low-CF unit (1800 Hz). The carrier frequency was 2099 Hz, with a level of 60 dB SPL, and a modulation frequency of 19.5 Hz. The modulation index β was 1 in (a), 5 in (b), and 10 in (c). The BSIs increase with increasing β. (d)–(f) BSIs for three values of β for a high-CF unit (8800 Hz). The carrier frequency was at 7500 Hz, with a level of 50 dB SPL, and a modulation frequency of 39 Hz. The modulation index β was 1 in (d), 5 in (e), and 20 in (f). The BSIs first increase, and then decrease slightly, with increasing β.

10(a)–(c) (CF 1800 Hz). The stimulus was above the CF (2099 Hz), at 60 dB SPL, and the modulation frequency was 19.5 Hz. The modulation index was 1 in (a), 5 in (b), and 10 in (c).

The BSI at the modulation frequency, and at its second and third harmonics, increase in a nonlinear fashion with increasing β. The BSI increases from 0.12 to 0.53, as β increases from 1 to 10. The number of harmonics seen in the baseband spectrum increases with increasing β.

Behavior of the baseband spectral components in response to FM signals for high-CF units

Variation of the baseband spectral magnitudes with modulation index

The behavior of the baseband synchrony index in response to increasing modulation index for high-CF units is similar to that for low-CF units as considered above. The BSI is shown for three values of β in Fig. 10 (CF 8800 Hz). The carrier frequency was 7500 Hz, at 50 dB SPL, and the modulation frequency was 39 Hz. The modulation index was 1 in (d), 5 in (e), and 20 in (f).

The BSI increases from 0.18 to 0.42, and then decreases to 0.38, as β increases from 1 to 5 to 20, respectively. The number of the harmonics increases with β.

Variation of the baseband spectral magnitudes with signal level for a carrier below CF

The spectral magnitudes of the DC and baseband components are presented as a function of stimulus level in Fig. 11(a) (CF 8.0 kHz). The carrier frequency was 5498 Hz, the modulation frequency was 19.5 Hz, and the modulation index was 20.

The curve marked DC in Fig. 11(a) represents the spike rate. Because of loss of phase-locking at high frequencies, these units do not carry significant temporal information at the carrier frequency or its sidebands. As a consequence, there are no appreciable spectral components at these frequencies. On the other hand, the baseband component at the modulation frequency (curve denoted BB in Fig. 11(a)) is clearly strong and dominant. The magnitude of this component increases with increasing stimulus level, reaching a maximum value at 30 dB SPL, and then decreases at higher levels. Significant spectral components are also present at the second and third harmonics of the modulation frequency (denoted 2BB and 3BB in Fig. 11(a), respectively); these reach their maxima at slightly different stimulus levels.

These same data are presented in terms of the baseband synchrony indices in Fig. 11(b). The BSI at the modulation frequency climbs from a value of 0.16 at 10 dB SPL to a maximum value of 0.56 at 20 dB SPL and then steadily declines to a value

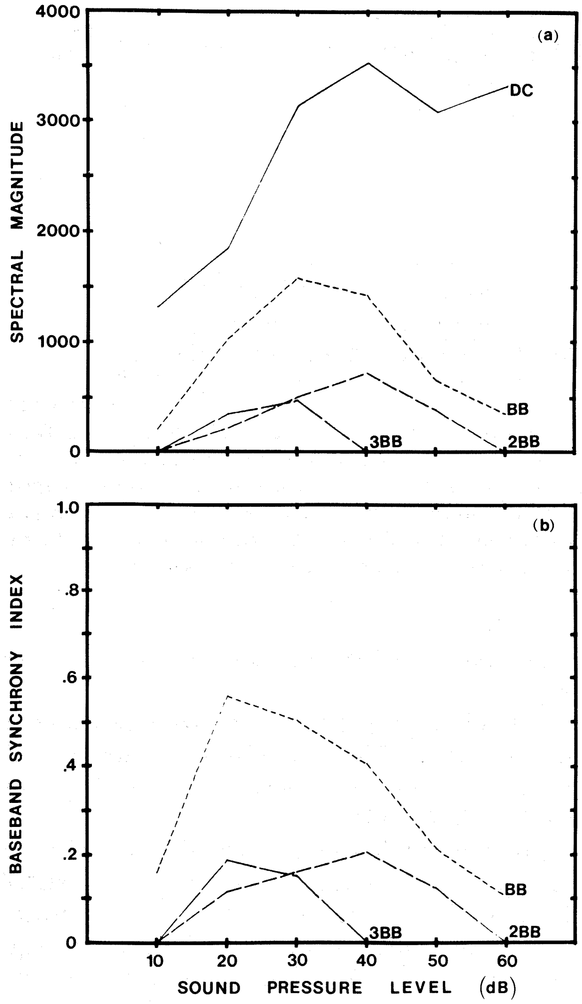

Fig. 11. (a) Spectral magnitudes of the DC and baseband components as a function of stimulus level for a unit with a CF of 5498 Hz. The carrier frequency was 5498 Hz, the modulation frequency was 19.5 Hz, and the modulation index was 20. The curve marked DC in (a) represents the spike rate. The baseband component at the modulation frequency (curve denoted BB in (a)) is clearly strong and dominant. Significant spectral components are also present at the second and third harmonics of the modulation frequency (denoted 2BB and 3BB, respectively). (b) These same data presented in terms of the baseband synchrony indices. The BSI at the modulation frequency reaches a maximum value of 0.56 at 20 dB SPL.

of 0.11 at 60 dB SPL. The higher-order BSIs behave similarly, although they may reach their maxima at somewhat different stimulus levels.

Observation of FM baseband components in the nerve-spike train using an analog low-pass filter

It is well known that the height, width, and shape of the individual spikes that comprise a nerve-spike train are essentially fixed. The information is carried by the temporal pattern of the nerve spikes, i.e., by the rate and times of the spike occurrences. In communications engineering this type of encoding of information is referred to as pulse-frequency modulation (PFM). The simplest demodulation scheme for recovering the information from a PFM-encoded signal is a low-pass filter with a slope of -6 dB/octave (Black, 1953). It should, therefore, be possible to recover the auditory modulation encoded in a train of nerve impulses present on a primary auditory fiber by passing them through a simple RC low-pass filter.

Experimental arrangement

The analog apparatus constructed to carry out this experiment is illustrated in the block diagram of Fig. 12. The FM signal was obtained from a FM signal generator. An oscillator provided the modulating sinewave. The FM signal was amplified and applied to an acoustic transducer with flat frequency response. The FM acoustic wave was delivered to the ear canal of a cat. The modulation was also applied to the horizontal deflection system (x-axis) of an oscilloscope, to provide a time base synchronized with the modulation cycle.

A KCl-filled glass microelectrode was used to pick up the extracellular nerve impulses from a single primary auditory nerve fiber. These nerve impulses were amplified by a negative-capacitance preamplifier and then applied to a level detector for conversion to idealized impulses (fixed voltage and duration) whenever the nerve impulse exceeded a predetermined threshold. The techniques associated with this aspect of the experiment have been described elsewhere (Teich and Khanna, 1985). The carrier frequency of the FM signal was chosen to lie near the CF of the unit.

The idealized spike train was then passed through a low-pass RC filter (represented by the transfer function $|H(\omega)|$) with a cutoff frequency of 2 Hz. The filtered signal was amplified and

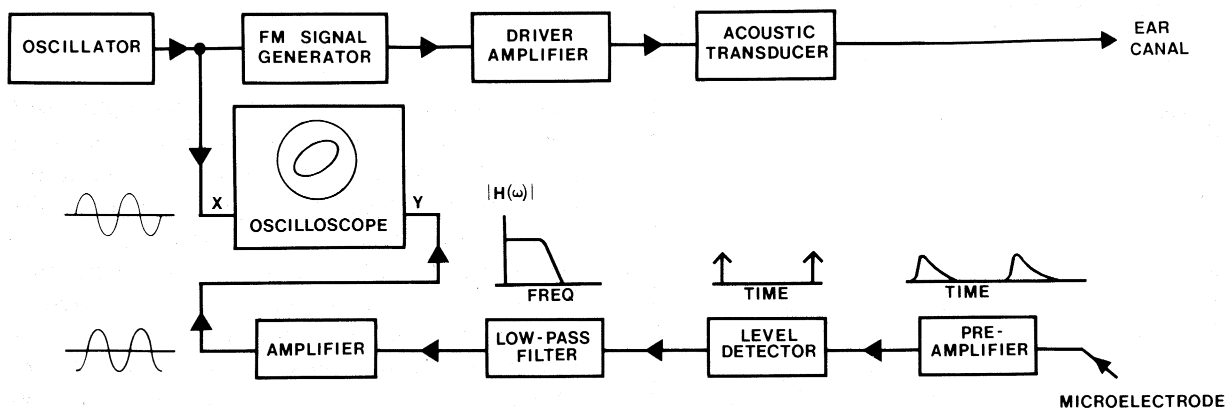

Fig. 12. Block diagram of the analog apparatus used to observe FM baseband components in the nerve-spike train. An oscillator provided the modulation frequency for the FM signal generator. The FM acoustic wave was applied to the ear canal of a cat. The sinewave generated by the oscillator was also applied to the horizontal deflection system (x-axis) of the oscilloscope. The nerve-spike train recorded from a primary auditory fiber, with a microelectrode, was passed through a low-pass filter with a cutoff frequency of 2 Hz. The filtered output was applied to the vertical deflection system (y-axis) of the oscilloscope. Spectral components that bear a fixed phase relationship to the modulation signal or its harmonics produce a Lissajous pattern on the oscilloscope.

applied to the vertical deflection system (y-axis) of the oscilloscope.

Observation of the modulation signal in response to FM signals

An experiment was conducted with an auditory unit with a CF of 4625 Hz. The FM signal SPL was 74 dB and the carrier frequency was below the CF of the unit. The modulation frequency was 5 Hz with a peak deviation of $\Delta f = 200$ Hz ($\beta = 40$).

A continuous Lissajous pattern in the form of an ellipse was seen on the oscilloscope, indicating the presence of the modulation frequency in the nerve-spike train. The size of the ellipse did not change appreciably as the peak deviation was decreased from 200 Hz to 50 Hz, reflecting the fact that the spectral magnitude at the modulation frequency remained roughly at the same level.

For smaller values of the peak deviation, the ellipse was seen only when the carrier frequency was near the CF of the fiber. As the peak deviation and/or the modulation index β were increased, good ellipses were obtained over an expanded range of carrier frequencies. In one set of experiments, the range of carrier frequencies over which good ellipses were observed was expanded from 50 Hz to 600 Hz, as β was increased from 10 to 300.

Dependence of the baseband phase on carrier frequency

Two Lissajous patterns observed in response to an FM signal with a modulation frequency of 5 Hz and a modulation index of 20 are shown in Fig. 13 (CF 6450 Hz).

For carrier frequencies below CF, in the range 6.0–6.4 kHz, the inclination of the major axis of the ellipse was roughly $+45°$ from the vertical and the trace moved clockwise, as shown in Fig. 13(a). For carrier frequencies above CF, in the range 6.4–6.9 kHz, on the other hand, the inclination of the major axis of the ellipse was roughly

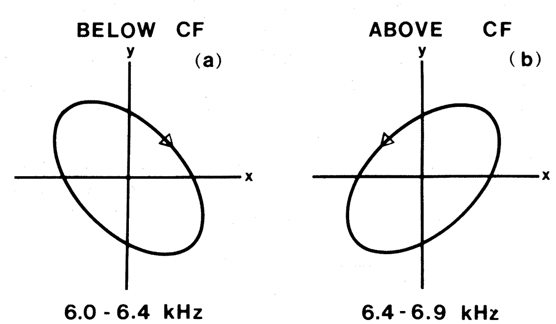

Fig. 13. Lissajous patterns observed for carrier frequencies below CF (a) and above CF (b). The CF was 6450 Hz, the modulation frequency was 5 Hz and the modulation index was 20. The patterns in (a) and (b) show a 180° difference in the phase of the modulation frequency components.

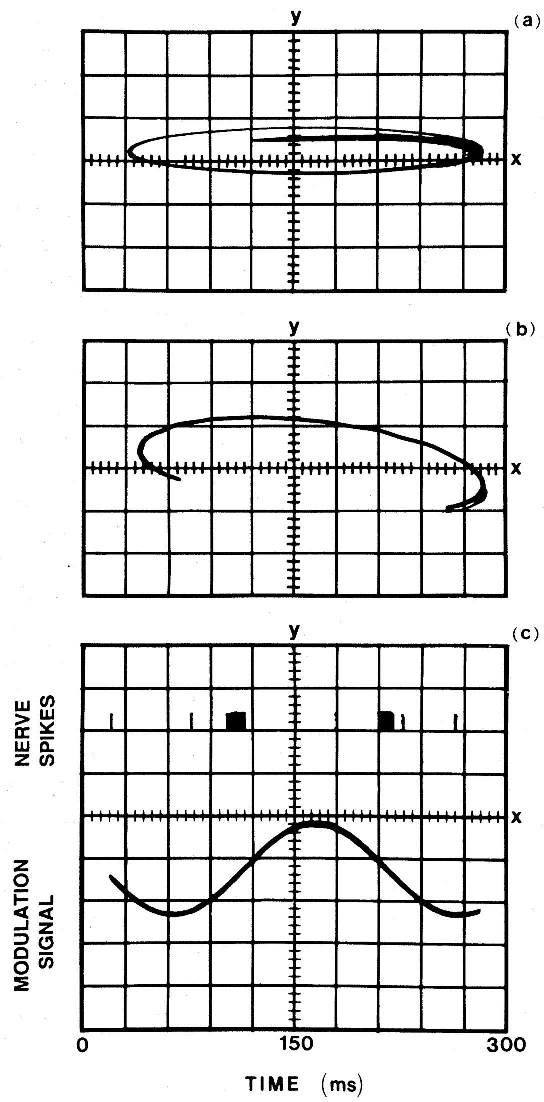

Fig. 14. (a) Lissajous pattern for a nerve fiber with a CF of 5400 Hz. The carrier frequency was at the CF, the signal level was 74 dB SPL, the modulation frequency was 5 Hz, and the modulation index was 20. The jitter in the position of the Lissajous pattern arises from the frequency instability of the FM signal generator. (b) Lissajous pattern for a nerve fiber with a CF of 4800 Hz. The carrier frequency was at the CF, the modulation frequency was 20 Hz, and the modulation index was 25. A partial-ellipse Lissajous pattern indicates a strong baseband signal at the second harmonic of the modulation frequency. (c) Relationship of the nerve-spike occurrence times (upper trace) to the modulation signal phase (lower trace) for a high-frequency nerve fiber (CF 12000 Hz) when stimulated by an FM signal with a carrier frequency at the CF and a modulation frequency of 5 Hz (corresponding to a period of 200 ms). The nerve spikes occur in bursts of relatively brief duration (≈ 14 ms), twice during each cycle of the modulation frequency.

$-45°$ from the vertical and the trace moved counterclockwise, as shown in Fig. 13(b).

This behavior reflects the phase of the demodulated baseband signal. It remains unchanged as long as the carrier frequency remains below or above the CF, but changes by 180° as the carrier crosses through CF.

Shape of the Lissajous patterns

The shape of the Lissajous pattern is illustrated in Fig. 14(a). The carrier frequency was at the CF (5400 Hz), at 74 dB SPL, the modulation frequency was 5 Hz, and the modulation index was 20. The jitter in the elliptical shape shows the sensitivity of the auditory system to small variations in the frequency of the source.

In the usual Lissajous pattern, the beginning of the trace for one cycle is connected with the end of the trace for the previous cycle, i.e., the trace is continuous. This was not the case with all of our observations. When the carrier frequency was located at the CF, some of our ellipses displayed a distinct break of slightly less than a half cycle, as shown in Fig. 14(b) (CF 4800 Hz, $f_m = 20$ Hz, $\beta = 25$). This effect will occur if the demodulated output of the nerve-spike train is dominated by the second harmonic of the modulation frequency and if its phase is such that its positive peaks occur at the zero crossings of the modulation signal. These findings are consistent with our observations of the baseband spectral components shown in Fig. 9(c).

Relationship of nerve-spike occurrence times to modulation-signal phase

The relationship of the nerve-spike occurrence times to the modulation signal phase is examined in Fig. 14(c). The carrier frequency of the stimulus was chosen at the CF of the unit (12000 Hz) and the modulation frequency was 5 Hz, corresponding to a period T of 200 ms. The modulation waveform is shown in the lower trace of Fig. 14(c).

The upper trace of Fig. 14(c) shows the nerve-spike occurrences observed at the output of the level detector. The nerve spikes occur in bursts of relatively brief duration (≈ 14 ms), twice during each cycle of the modulation frequency. These bursts occupy less than 7% of the modulation period. The instantaneous frequency of the FM wave sweeps back and forth across the tuning curve of the unit. It intersects the region of strongest response (at the CF of the unit) for a relatively brief period of time, twice per modulation cycle, giving rise to enhanced bursts of activity during those short times. This, in turn, gives rise to a baseband signal with a strong spectral component at the second harmonic of the modulation frequency.

Observation of baseband in response to AM signals

Several analog experiments using AM signals were also carried out with modulation frequencies in the range of 5–20 Hz. Elliptical Lissajous patterns similar to those seen in response to FM signals were observed. This indicates that simple low-pass RC filtering extracts the modulation signal (i.e., the information) from the nerve-spike train for both AM and FM.

Discussion

Clusters of spectral components were present in the nerve-spike train recorded from single primary auditory nerve fibers, when FM signals were applied to the ear. The frequencies of the various components are given by the sequence

$$f_{FM} = jf_c \pm kf_m,\ j = 0,1,2,...;\ k = 0,1,2,.... \qquad (1)$$

The behavior of the spectral components reported in this paper can be understood in terms of a theoretical model that we have developed for the encoding of pure-tone and modulated signals (Teich and Khanna, 1989).

Representation of the carrier and its sidebands in the spectrum of the period histogram

The spectral magnitudes of the components at the carrier frequency and its sidebands depend on where the signal spectrum lies with respect to the tuning curve of the unit. The input FM signal spectrum is represented most faithfully and symmetrically in the nerve-spike train when the carrier frequency is located near the CF of the unit (Fig. 5). When the carrier is below the CF the high-frequency sidebands are emphasized (Figs. 3 and 4), and when the carrier is above the CF the low-frequency sidebands are emphasized (Fig. 6). This is the same general result that is obtained for AM signals (Khanna and Teich, 1989, Figs. 6–8). In general, components located at, or near, the CF of the unit are enhanced whereas those located away from the CF are attenuated.

These features suggest that the spectrum of the input signal is shaped, before nerve-spike generation, by a filter with maximal transmission at the CF of the unit and attenuation both below and above the CF. It is, of course, natural to wonder if this filter shape is the same as, or similar to, the frequency tuning curve (FTC) of the unit. Consider the data illustrated in Fig. 3(a). The spectral components in the applied signal extend from about 400 Hz to 1600 Hz. The CF of the nerve fiber was 2299 Hz and the low-frequency slope of the FTC was −26 dB per octave. The FTC threshold at 996 Hz is roughly about 50 dB SPL, which is close to the applied stimulus level. One might then expect that the spectral components lying below about 996 Hz will fall below the threshold of the unit, and therefore be attenuated in the response spectrum, whereas those above about 996 Hz will be above its threshold and therefore will appear. In the spectrum shown in Fig. 3(b), only the spectral components above the carrier frequency are present. This suggests that the FTC shapes the spectrum seen in the neural response.

Spectral components of the cluster at twice the carrier frequency

The spectral components of the cluster surrounding twice the carrier frequency exhibit the following characteristics: (i) the spacing between the spectral components is exactly at the modulation frequency; (ii) the relative magnitudes of the various spectral components are modified by a filter function in much the same way that the components surrounding the carrier frequency are modified; and (iii) the cluster is broader than that surrounding the carrier frequency (the modulation index β appears larger). The same trend is followed for clusters surrounding higher multiples of the carrier frequency.

The relationship between the spectrum of the clusters is illustrated in Figs. 3(b)–6(b). When the spectral components in the cluster at the carrier frequency lie principally above the carrier frequency, so too do the components in the cluster at twice the carrier frequency (Figs. 3(b) and 4(b)). When the spectral components lie on both sides of the carrier frequency, the components surrounding twice the carrier frequency also lie on both sides of it (Fig. 5(b)). Finally, when the spectral components lie principally below the carrier frequency, those surrounding twice the carrier frequency follow (Fig. 6(b)).

The increase in width of the spectral-component cluster surrounding twice the carrier frequency is evident in Figs. 3(b)–6(b) and in Fig. 7. The AM spectral-component clusters, on the other hand, do not increase in width with increasing harmonic number (see Khanna and Teich, 1989, Figs. 6–8).

Baseband spectral components

The baseband spectral components comprise DC, the modulation frequency, and its harmonics. Since neither the modulation frequency nor its harmonics are present in the FM signal applied to the ear, their presence in the spectrum of the period histogram reveals that the input signal has been demodulated by the inner ear.

FM-to-AM conversion and AM demodulation for an analog FM signal

In one method of FM demodulation, the FM signal is converted to AM by passing it through a device with a transfer function such that the output amplitude varies with input frequency over some range. The resulting amplitude modulation is then recovered by means of a subsequent AM demodulator, as discussed in the previous paper (Khanna and Teich, 1989). From a physiological point of view, a logical candidate for such a transfer function is the filter that gives the FTC its characteristic shape.

Consider a carrier frequency well below the CF of the unit. The FTC filter attenuates instantaneous frequencies below the carrier frequency and enhances instantaneous frequencies above the carrier frequency. A downward frequency sweep of the FM signal thus results in a decreasing amplitude whereas an upward sweep results in an increasing amplitude. This would produce an AM signal that varies at the FM modulation frequency.

Ideal FM-to-AM conversion faithfully reproduces the modulation signal only if the transfer function of the filter varies linearly with frequency. If it does not, then harmonics of the modulation signal are introduced.

Because the slope of a filter such as the FTC varies with frequency, the harmonic content of the baseband signal (and the demodulation sensitivity) will be expected to change as the applied carrier frequency moves along the tuning curve. This is observed experimentally. When the carrier is well below the CF (Fig. 3(b)), the slope of the tuning curve changes rapidly with frequency and a large number of modulation harmonics are observed. When the carrier is in a more linear region of the tuning curve, but still below the CF (Fig. 4(b)), the fundamental modulation frequency dominates and a smaller number of harmonics are observed. When the carrier is at the CF, the second harmonic of the modulation frequency dominates because the filter function attenuates the signal when its frequency goes both below and above the carrier frequency. An FM signal with a carrier frequency located at the peak of such a filter produces an envelope that varies at twice the modulation frequency. The resulting spectrum should therefore exhibit a large second harmonic of the modulation frequency, relative to the fundamental. This is consistent with the observed spectrum (Fig. 5(b)). Finally, when the carrier frequency is above the CF, FM-to-AM conversion takes place on the high-frequency slope of the FTC, and the magnitude of the modulation fundamental should again increase with respect to its second harmonic. This is observed experimentally (Fig. 6(b)).

Phase shift of the baseband signal

If the filter slope is involved in FM-to-AM conversion, the instantaneous frequency of the signal should see a positive filter slope when it lies below the CF, and a negative filter slope when it lies above the CF. A 180° phase difference is indeed seen in the baseband signal when the carrier frequency moves from below to above the CF (Fig. 13). The phase remained the same as long as the carrier frequency was below CF; it shifted by

180° when the carrier frequency was increased above CF. These observations suggest that the filter underlying the FTC converts the FM signal into an AM signal which, in turn, is demodulated by the nonlinearities in the cochlear transduction mechanism.

Characteristics of the baseband components and their significance

Strong baseband components have been observed in the response of all of the low-, medium-, and high-CF auditory nerve fibers we have examined. These components remain strong for carrier frequencies below, at, and above the CF, over a wide range of modulation frequencies and modulation indices (see Figs. 3–14). They are present at essentially all signal levels observed, from −10 dB:re FTC to 90 dB SPL.

Baseband components typically increase in magnitude with increasing signal level, up to the point where the rate function saturates. Further increases of stimulus level then result in a gradual decrease of their magnitudes (see Fig. 11). The magnitudes of these components generally increase with increasing modulation index and/or modulation frequency (see Fig. 10 and Table I).

The baseband components remained strong up to the highest frequencies examined, even though the carrier and sideband magnitudes became negligibly small (as a result of loss of phase locking). The baseband signal at the modulation frequency is therefore seen to provide an important means of carrying information in high-CF fibers, as well as in low- and medium-CF fibers. A similar observation has already been made with respect to the case of AM (Khanna and Teich, 1989).

The importance of the baseband components in carrying FM information is further illustrated by several general observations: (i) Baseband components appear at signal levels close to the neural threshold; (ii) their magnitudes can be appreciable over a broad range of stimulus levels; and (iii) their magnitudes increase with increasing modulation index and modulation frequency. These observations suggest the presence of an efficient FM demodulation process in the inner ear. The presence of these robust low-frequency components suggests that they may provide important cues in the speech-recognition process.

We provide a plausible rationale for the significance of the baseband components. Communication sounds consist of acoustical carrier waves that are amplitude- and frequency modulated by low-frequency information-carrying waves. These modulated sounds are demodulated by the peripheral auditory system whereby the information carried by the low-frequency components is recovered. The modulation information is encoded in the firing patterns of the afferent nerve fibers in such a way that these components can be recovered by passing the nerve-spike train through a low-pass filter. Such a filter is present in the nerve-cell membrane at each synaptic junction. A nerve-spike train arriving at a synapse would be filtered and the low-frequency baseband (modulation) component would appear in the post-synaptic potential as an analog waveform. Similar baseband components would be produced by the nerve-spike trains arriving at each of the other synapses. These analog waves would be integrated in the cell. The integration would be strong because the low-frequency baseband components would be nearly in phase. These integrated waveforms should be observable with a microelectrode placed intracellularly in the neuron. The integrated signal would then trigger a new output nerve-spike train.

Information transmission in the auditory nervous system would appear to consist of two basic elements: communication based on digital nerve-spike trains between neurons and analysis/synthesis of information based on nonlinear analog processing within neurons.

AM and FM signals provide a key to the understanding of information transmission in the nervous system.

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