

Coding of sounds with rapidly varying spectrum in the cochlear nucleus

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The discharge pattern of a single unit in the cochlear nucleus in response to tones and noise bands of which the frequency was modulated trapezoidally over a large frequency range, including the response area of the unit, was studied. The distribution of nerve impulses was found to change in a characteristic way as a function of rate of change in frequency. The probability of firing within a narrow frequency range around the characteristic frequency (CF) of all units studied has a maximal value at a certain (high) rate of change in frequency. At that rate the peaks in the cycle histograms of the responses often became more than ten times higher than at low sweep rates. The effect was seen in the high-intensity range (more than 60 dB) but it was less pronounced near the threshold of the unit. The threshold did not become lowered at any rate of frequency change. A similar pattern was seen in response to bands of noise of which the frequency was varied in the same way as the tone. The magnitude of increase in height of the peaks in the histograms was usually somewhat less for noise than for tones.

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INTRODUCTION

Most electrophysiological studies of coding of sounds in the peripheral auditory system have been performed with pure tones of constant frequency and click sounds. Since both the amplitude and the spectral composition of natural sounds usually vary rapidly, it is important to know how the auditory system processes such signals.

A commonly accepted simplified model of the peripheral auditory system is a bank of filters tuned to different frequencies. The rectified and smoothed output of these filters constitutes the excitation of the individual fibers in the auditory nerve. These fibers terminate complexly on the cells of the cochlear nucleus. The filtering is assumed to be performed by the basilar membrane and the subsequent rectification and smoothing by the sensory receptors (hair cells). The auditory system can thus be assumed to perform a running spectral analysis. The output along the basilar membrane represents the spectral distribution of the incoming sound over a short segment of time. The integration time of such a spectral analyzer is determined by the bandwidth of the individual filter elements and by the smoothing following the rectification. The sum of these two integrations sets a limit for how fast changes in amplitude and in spectral composition the spectral analyser can resolve. In the auditory system the bandwidth of a small segment of the basilar membrane as well as the integration following the rectification is insufficiently known. The basilar membrane may at a first approximation work as a linear system; it may therefore be possible to estimate its vibratory response to complex sounds with time by varying amplitude and spectral composition on the basis on knowledge of its characteristic response to steady pure tones (see, e.g., Glaser and Haven 1972). Knowledge about the further processing of complex sound in the nervous system can only be ascertained through direct experiments in which complex time-varied sounds are used as stimuli. The most suitable of the methods available

at the present time is recording from single nerve cells. Recordings from cells in the cochlear nucleus offer the possibility of studying the neural integration at a peripheral level of the auditory system.

Earlier experiments using tones whose frequency varied linearly more or less rapidly (sweep tones) have shown diverging results. According to Suga (1964, 1965) the threshold response of single units in the cochlear nucleus to such sounds shows little difference compared with the threshold response to tones of constant frequency.

Erulkar *et al.* (1968) studied the responses of cochlear nucleus units to tones whose frequency was modulated with trapezoidal or triangular waveform. Histograms of the distribution of the evoked discharge of the modulation cycle were used to show how the response pattern varied as a function of rate of change in stimulus frequency. The response to tones with rapidly varying frequency, however, could be predicted only in a few units on the basis of the responses to slowly varying tones. Later Fernald (1971) presented a neural model which could mimic the response pattern to such sweep tones. A spatial distribution of synaptic input was assumed to be responsible for the responses to sweep tones.

The range of frequency change used by Erulkar *et al.* (1968) was about $\frac{1}{2}$ of an octave and the maximal rate of change was about 0.5 MHz/sec. Using tones whose frequency varied over a much larger range (ratio of 1:4 or more) Møller (1969, 1971) found a systematic change in response pattern as a function of rate of change in frequency of the stimulus tone. The responses became more localized around the characteristic frequency (CF) of the unit in response to sweep tones at a certain (high) sweep speed compared to that of a tone with slowly varying frequency. In the majority of units the mean firing rate only changed slightly as a function of rate of change in stimulus frequency and the course of the change in the mean firing rate as a function of rate of change in fre-

quency was different from that of the height of the peaks in the histograms.

The present paper is concerned with the neural coding of tones and of bandpass filtered noise the spectrum of which is varied at different rates over a large frequency range. It is based on recordings from single units in the cochlear nucleus of the rat and it represents an extension of the above mentioned studies (Møller 1969, 1971).

I. METHODS

White rats weighing from 250–300 g were used in the experiments. The rats were anesthetized with either urethane (1.5 g/kg b.w.) or Nembutal (35 mg/kg b.w.) injected intraperitoneally. Body temperature was maintained near 37 °C. The trachea was cannulated and a hole was made in the occipital part of the skull. Part of the cerebellum was aspirated to make the cochlear nucleus visible. The outer ear was removed and the head was mounted in a headholder (Møller 1969). Glass micropipettes filled with 3 mol KCl were used for recording unit potentials (tip diameter 1–5 μm and resistance 5–25 M Ω). The electrode was positioned under visual control through a Zeiss Epitokoskop, after which it could be advanced or retracted in steps of 2 μm through remote control by a Stålex micromanipulator.

The sound was generated by a 1-in. B & K condenser microphone (type 4131) connected to the hollow ear bars of the headholder. The sound pressure close to the eardrum (approximately 2 mm from the eardrum) was measured by a probe microphone (B & K type 4134) with a 0.5 mm 2.3 cm long probe. The probe microphone was in turn calibrated by attaching another B & K half-inch microphone (type 4134) to the hollow ear bar in the place of the ear of the rat. The difference (in dB) between the sound pressure measured by these two microphones constitutes the calibration of the probe microphone used in the experiments. The sound source for the calibration was the 4131 microphone connected in the same way as during the experiments.

The frequency characteristics of the entire sound generating system obtained by measuring the sound pressure near the eardrum of a rat in a typical experiment are shown in Fig. 1.

Sweep tones were generated by a Wavetek function generator (type 112) the frequency of which was controlled by a repetitive trapezoidal or triangular wave. The rate of frequency change was controlled by changing the repetition rate of the modulation waveform. Band-pass filtered noise was generated by a heterodyne procedure. Low-pass filtered noise and a sinusoidal carrier were fed into the two inputs of a four quadrant multiplier (Motorola MC 1595 L). The carrier frequency was generated by a Wavetek function generator (type 112) and controlled by a trapezoidal signal in the same way as the sweep tones were produced. The noise was generated by a General Radio noise generator (type 1381.) Low-pass filters with a slope of 42 dB/octave were used, occasionally replaced by less steep filters. Since the noise spectrum does not extend to zero frequency, a

hole appears in the middle of the heterodyned spectrum. In the present set up the noise spectrum extends down to about 2 Hz resulting in a dip about 4 Hz wide in the final spectrum. This dip was regarded as unimportant for the present experiments.

The frequency of both sweep tones and sweep noise was varied symmetrically around the characteristic frequency of the unit.

Repetitive tone bursts were produced by feeding short rectangular waves into the gate control input of the function generator.

During the experiments the discharge pattern was analyzed by an Intertechnique DIDAC 800 Physioscope set to produce cycle histograms. The analyzer was triggered at a certain phase of the modulation wave and it was modified so that each pulse returned the sweep to its initial position immediately before generating a new. This made it possible to use the fraction of the total available analysis channels that precisely covers one full cycle of the modulation. The contents of each channel of the analyzer were punched on paper tape by a Facit type 4070 eight-channel tape punch. The eight most significant bits were punched in binary form and the tapes were later read into an IBM 360/75 computer for processing. This consisted of determining the location and the height of the peaks and computing the total number of nerve impulses in these peaks.

II. RESULTS

A. Frequency-modulated tones

Figure 2 shows typical cycle histograms of the responses of a unit in the cochlear nucleus to stimulation with a tone whose frequency was modulated with a trapezoidal waveform. The histogram in Fig. 2(a) shows the distribution of nerve impulses as a function of frequency of the tone when it was varied slowly. The histogram below Fig. 2(b) represents in a similar way the responses evoked by a tone with rapidly varying frequency. The abscissa represents both frequency and time. In the two graphs the frequency scales are identical but the time scales are different. The peaks to the left represent the responses to rising frequency and those to the right show responses to falling frequency. As can be seen the tone varied in frequency from 5 to 28 kHz

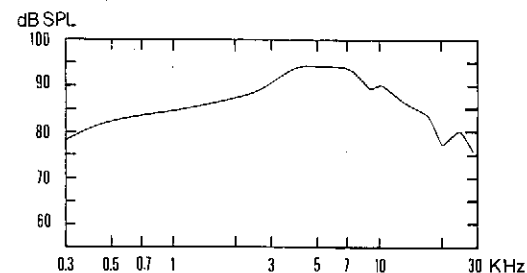


FIG. 1. Sound pressure measured near the eardrum of a rat in a typical experiment to show the characteristics of the sound generating system. Sound pressure level in dB *re* 0.0002 μbar is shown for 1 V rms input to the microphone which is used as sound source (B & K type 4131).

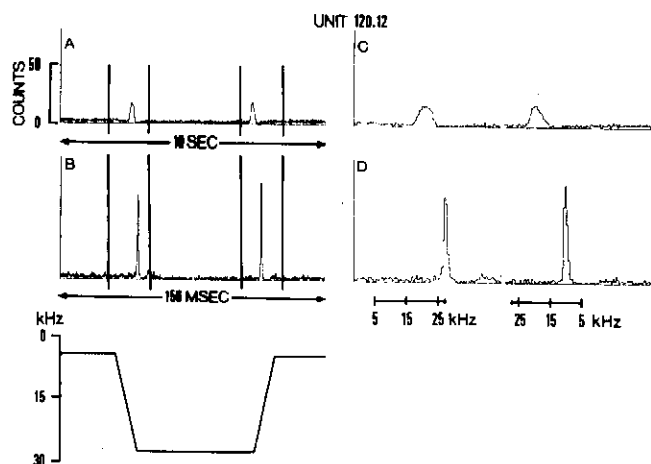


FIG. 2. Cycle histograms showing the distribution of discharges in response to trapezoidal frequency-modulated tones (sweep tones) of different sweep rates. The histograms show the distribution of nerve impulses over the cycle of the modulation. (a) Sweep rate 0.1 Hz (period length of 10 sec); the corresponding rate of change in frequency of the stimulus tone was 35 kHz/sec. (b) Sweep rate 6.4 Hz (period length of 156 msec) corresponding to a rate of change in frequency of 2.25 MHz/sec. (a) and (b) Full sweep; modulation scheme shown below. (c) and (d) The histograms from (a) and (b) on an expanded time scale show the range around the peaks in detail. The parts shown are indicated in (a) and (b) by vertical lines. Each half of the histogram shows 100 bins corresponding to 16% of one full sweep cycle.

during 15% of the total time of one sweep cycle; in other words, the frequency was constant during 85% of the sweep cycle. The parts between the vertical lines of the two histograms in Fig. 2(a) and (b) appear in 2(c) and (d), respectively, on an expanded frequency-time scale to show the peaks in detail.

One sweep occupied totally about 650 channels of the analyzer and each half of the expanded histogram comprised 100 bins. Thus each bin represents a frequency of approximately 460 Hz. Each of the two peaks in the histogram of the responses to the slow frequency change extended over approximately 6500 Hz (14 bins). (The width of the tuning curve of this unit was 3.0 kHz at 10 dB points). At the fast sweep where the frequency was changed at a rate of about 2 MHz/sec the width of the peaks is reduced to about 3250 Hz (7 bins) and the height of the peak has increased about 4.5 times. The frequency range within which a tone evokes discharges is thus significantly decreased with rapid frequency change compared to slow frequency change.

Cycle histograms of the responses to sweep tones within a large range of sweep rates of two typical units are shown in Fig. 3. The frequency of the tone varied in the same way as illustrated in Fig. 2 and the histograms have been expanded in the same way as shown in Fig. 2(c) and (d) to show 200 of the total 650 bins of the total sweep cycle. The CF of the two units was 22 and 13.8 kHz, respectively.

The relative heights of the peaks in the cycle histograms of the responses of two units to sweep tones of different

sound intensity are shown in Figs. 4 and 5 as a function of sweep rate. In this as in subsequent graphs the relative height shown is the ratio between the height of the peak at a certain sweep rate and that at a low sweep rate (usually 0.1 Hz). The number of nerve impulses in each of the two peaks of the histograms is also shown as a function of sweep rate. The unit illustrated in Fig. 4 is typical for the group of units where the total number of nerve impulses contained in the peaks is relatively constant independent of the sweep rate. In short, changing the frequency of a tone rapidly mainly induces a redistribution of the nerve impulses, and to a lesser extent an increased firing rate as compared with varying the frequency slowly. The unit illustrated in Fig. 5 belongs to the group whose mean discharge rate increases with increasing rate of change in frequency.

In both units a marked increase is seen in the height of both of the peaks in the histograms within a certain range of rate of frequency change. In the unit in Fig. 4 the total number of nerve impulses is relatively constant up to a sweep rate of about 20 Hz above which it increases with sweep rate. In the unit in Fig. 5 the mean discharge rate increases steadily with sweep rate up to 70 Hz and above 100 Hz it falls. The change in the number of discharges in each peak as a function of rate of change in frequency is usually not correlated

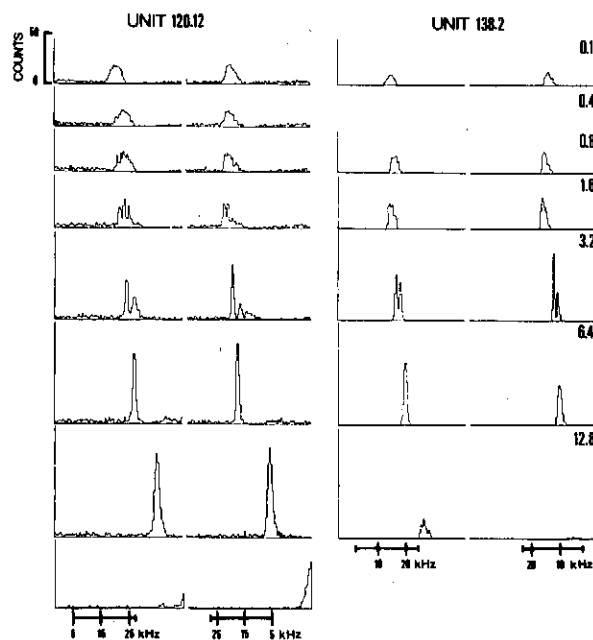


FIG. 3. Histograms of two typical units in response to sweep tones when repetition rates were varied within wide ranges. The time axis of the histograms was expanded in the same way as in Fig. 2(c) and (b) to show only the fraction of the sweep around the two peaks. Each half of the histograms represents 16% of the total sweep. The stimulus intensity was 45 dB SPL (at CF) for the unit illustrated to the left (unit 120.12) corresponding to approximately 25 dB above threshold at CF (22 kHz). The results illustrated to the right (unit 138.2) were obtained with a stimulus sound pressure of 75 dB SPL (at CF) corresponding to about 40 dB above threshold of the unit at CF (13.8 kHz). In both cases one minute of data is represented by each histogram.

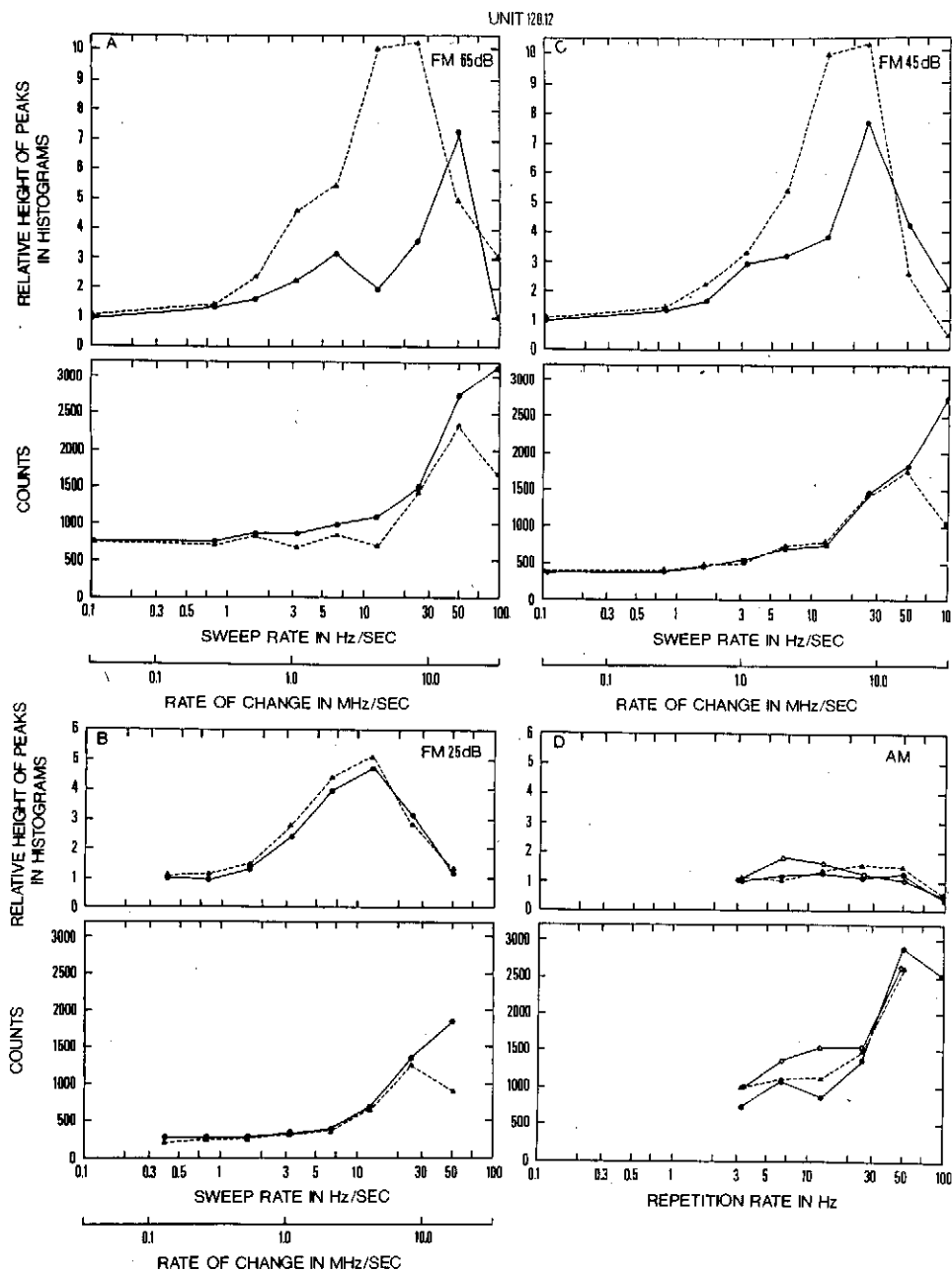


FIG. 4. (a-c) Relative height of the peaks in the cycle histograms of the responses to trapezoidal frequency-modulated tones (upper graphs) and number of spikes contained in each peak (lower graphs). Response to rising frequency sweep is indicated by solid lines and to falling frequency by dashed lines. The different graphs represent different sound-pressure levels, shown by legend numbers on each graph in dB above threshold at CF. The frequency of the stimulus tones varied during 15% of the total sweep cycle according to the same scheme as shown in Fig. 2 (b) and (c). (d) Relative height of the peaks in the cycle histograms of the responses of the same unit to amplitude modulated tones at CF together with the total number of spikes in each peak shown in the same way as for sweep tones. Open circles: 65 dB above threshold of the unit; triangles: 45 dB and closed circles: 25 dB. The CF of the unit was 22 kHz; its threshold at CF was approximately 20 dB SPL. This unit had a moderate degree of spontaneous activity. Total time of stimulation at each sweep rate was one minute.

with the variations in the height of the peaks in the histograms.

The increase in height of the peaks is most pronounced at sound intensities well above the threshold. In many units falling stimulus frequency results in a somewhat greater increase in peak height than rising frequency (cf., Fig. 4). Well above threshold the maximal peak height also occurs at a lower rate of change in frequency for falling frequency compared with rising frequency.

In order to study whether the sharpening of the histogram in response to sweep tones was a result of the tones staying within the response areas of the unit for a shorter time as the sweep rate was increased, the responses to tones of constant frequency (equal to the CF of the unit) and variable duration were studied. These amplitude modulated tones were presented in a similar way as the sweep tones and the ratio between tone and

silence was kept constant as the repetition rate was increased.

An analogous type of sharpening of the response pattern could, however, not be achieved by such amplitude modulated tone. In some units the histograms of the responses to such sounds did not show any appreciable change in height with changing duration of the sound (cf., Fig. 4). In other units there was an increase in height as repetition rate was increased but it was never as pronounced as that achieved in response to sweep tones (cf., Fig. 5).

Since the rate of frequency change is varied by varying the repetition rate, the effect studied might be a result of the change in repetition rate rather than of a change in sweep rate. In order to rule out such a possibility the slope of the trapezoidal waveform and thus the rate of frequencies was varied in a series of experi-

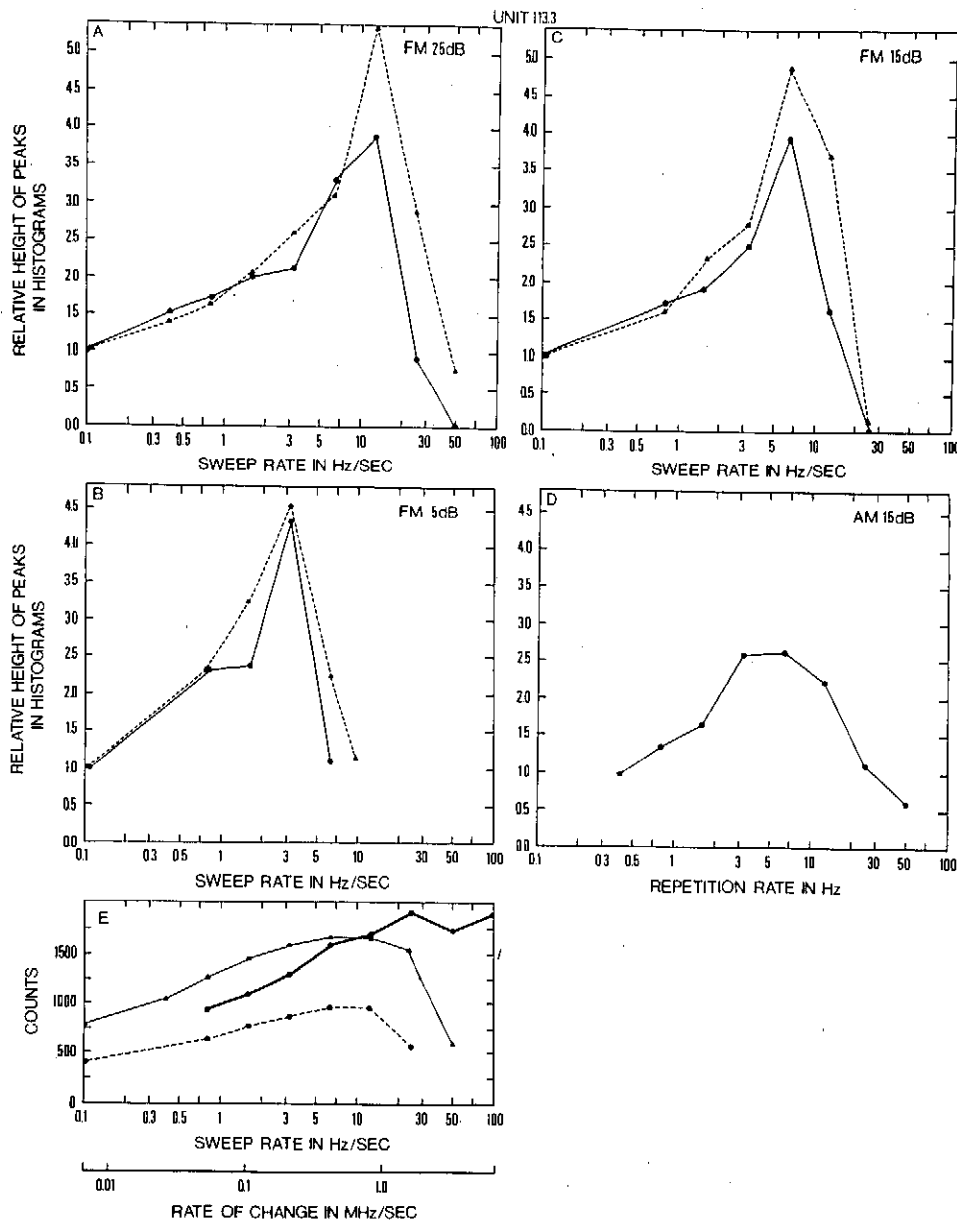


FIG. 5. (a-c) Relative height of the peaks in the histograms of the responses to trapezoidal frequency modulated tones of a unit whose discharge rate increased as a function of sweep rate, shown in a similar way as in Fig. 4. The sound level in dB above threshold at CF is shown by legend numbers in each graph. (d) The relative height of the peaks in the histograms of the responses to amplitude modulated tones. (e) Total number of discharges in each peak as a function of sweep rate. Continuous thin lines represent sweep tones 25 dB above threshold, dashed line 15 dB above threshold, heavy line, amplitude modulated tones 15 dB above threshold. Data were collected during one minute at each sweep rate and the frequency of the sweep tones varied during 60% of the total sweep time. The CF of the unit was 15.0 kHz and its threshold was approximately 35 dB SPL.

ments. The results showed that the change in height of the peaks in the histograms was related to the rate of change in frequency of the stimulus tone and not to the repetition rate of the modulation provided that the frequency of the tone was varied over a large frequency range and that the stimulus only resided within the response area of the unit for a small fraction of the total modulation cycle. Figure 6 shows typical examples of findings from such experiments. The relative height of the histogram is plotted as a function of rate of change in frequency. The individual curves represent trapezoidal modulation with different slope. Figure 6 (a) and (c) show the results obtained for increasing frequency and 6(b) and (d) show the response to decreasing frequency sweeps. The dashed and solid lines in Fig. 6(a) and (b) represent responses to sweep tones in which the frequency varied during 60% and 15% of the modulation cycle, respectively. In Fig. 6(c) and (d) the dashed and solid lines represent responses to tones in which the frequency varied during 15% and 7.5% of the cycle, respectively.

It is seen that the curves are similar when plotted on a scale showing rate of frequency change. On the basis thereof, it is concluded that the response pattern is a function of rate of change in frequency of the stimulus tone and not a function of the repetition rate of modulation.

The rate of change in frequency of which the maxima in peak height of the histograms occurred varied from 0.3 to 25 MHz/sec.

The maximum usually occurred at a lower rate of frequency change for units with low CF than for units with high CF. There was, however, a considerable spread in values and many units with high CF had the maximal response height at a low rate of frequency change.

The response patterns shown in Figs. 2-6 are typical for most units encountered in the cochlear nucleus which had CF between 1.5 and 35 kHz, the latter frequency

