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Synaptic Events and Discharge Patterns of Cochlear Nucleus Cells. II. Frequency-Modulated Tones

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THE ANALYSIS OF discharge patterns of cells in the auditory pathway to complex acoustic signals such as frequency- (12, 20) or amplitude- (10) modulated tones, noise bursts (4, 7, 8), sustained vowels (11), and animal calls (13) is actively being pursued to define how specific features of these acoustic signals are encoded in auditory units. For instance, there are cells in auditory cortex of cat that discharge to only the ascending or to only the descending portions of a frequency-modulated signal (22). It is not clear whether this type of response specificity can also be detected in cells at the first central station of the auditory pathway, the cochlear nucleus. Suga (14, 15), studying bat cochlear nucleus, found all units to discharge equivalently to the ascending and to the descending portions of a frequency-modulated tone. Watanabe and Ohgushi (21) described similar symmetrical responses in cat cochlear nucleus units to FM sweeps. In contrast, Erulkar et al. (5) found a large number of cells in cat cochlear nucleus to respond in an asymmetrical manner to FM signals.

The present study analyzes the response of eighth nerve fibers and cochlear nucleus cells in the cat to frequency-modulated signals using intracellular recording techniques. The results reveal that there are both symmetrical and complex response patterns in cochlear nucleus cells to frequency-modulated signals that depend on the temporal patterning of excitatory and inhibitory synaptic events. Factors such as the cell's response pattern to brief-duration steady-frequency tone bursts as defined in the companion paper (3) and acoustic parameters such as signal intensity or modulation rate were found to correlate with the FM response types.

METHODS

Surgical preparation

The surgical preparation and experimental methods are described in the companion paper (3).

Stimulus arrangements

The method used to generate pure tones and response-area histograms (tuning curves) which appear in some of the figures in this paper are described in the previous paper (3).

Frequency modulation

Frequency-modulated (FM) tones were produced by modulating a voltage-controlled oscillator (Hewlett-Packard 3300A function generator with a 3305A sweep module) with a triangular voltage. The frequency range of the FM sweep was set to either 0.125-8 or 1.1-25 kHz to encompass the characteristic frequency of the unit. The output of the acoustic transducer ($\frac{1}{2}$ inch Brüel & Kjaer microphone) described in Fig. 1 of the preceding paper (3) was ± 10 dB from 0.4-25 kHz, introducing some amplitude variations in our sweep. Four modulation rates were selected (0.05, 0.5, 5, and 50 sweeps/s (sps)) with the duration of each FM presentation being held constant at 20 s. Thus, at a modulation rate of 0.05 sps, only 1 FM sweep was presented; at 0.5 sps, 10 FM sweeps were presented; at 5 sps, 100 FM sweeps were presented and at 50 sps, 1,000 FM sweeps were presented.

Data acquisition and experimental procedure

See previous paper (3).

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Data analysis

The tape-recorded data were photographed using a Grass (C4) camera to produce film strips for visual examination. Where appropriate the following computer analyses were made using a LINC computer.

1) Peristimulus time histogram of unit discharges (PSTH): the bin width was varied for the different modulation rate so that 185 bins comprised a complete sweep at 0.05, 0.5, and 5 sps. At 50 sps the number of bins was reduced to 150.

2) Average membrane potential: an analysis of membrane slow potentials was obtained by attenuating the spikes using a low-pass filter (Allison filter) with its 3-dB down point set at 75 Hz and averaging the filtered signal. It is important to note that at the slowest modulation rate (0.05 sps) only 1 trial was analyzed (obviously, there could be no averaging), while at 0.5 sps 10 sweeps were averaged, and at 5 sps 100 sweeps were averaged. The averaged membrane potentials for 50 sps has not been included in the figures because in the process of adjusting the number of bins to 150, the tape speed during playback had to be reduced from 15 to 1 7/8 inches/s, rendering the filter ineffective in attenuating the spike discharges.

The LINC computer was programmed to compute the PSTH and the averaged membrane potential determinations simultaneously. Polaroid pictures were taken of each PSTH with its corresponding averaged membrane potential.

3) Symmetry calculation: a comparison of the number of discharges evoked by the ascending and by the descending phases of the FM cycle

has been expressed as the symmetry factor (S). This measure is calculated by taking the absolute difference in unit discharges to the ascending and to the descending parts of the FM cycle and dividing by the sum of the two responses. The sign of S as + or - was discarded as it was not considered relevant for defining the degree of symmetry. Expressed as an equation:

$$S = \frac{\text{no. discharges}^{\text{up}} - \text{no. discharges}^{\text{down}}}{\text{no. discharges}^{\text{up}} + \text{no. discharges}^{\text{down}}}$$

The range of the symmetry factor (S) is 0-1. If the unit is perfectly symmetrical, the value of S is 0 since the number of discharges would be equivalent in the two directions of the FM sweep, rendering the numerator of the equation equal to 0. If the unit were perfectly unidirectional, S would equal 1. The FM response was considered symmetrical if the value of S were 0.2 or less, asymmetrical if the S value were between 0.2 and 0.8, and unidirectional if S were 0.8 or more. Table 1 contains the FM classification and their distinguishing features used in this study.

RESULTS

Eighth nerve fibers

Of the 14 eighth nerve fibers studied, 11 were symmetrical at all intensities and modulation rates while 3 were symmetrical at all intensities and modulation rates except at 50 sps when an asymmetry appeared. Figure 1 shows results from one of the eighth nerve fibers and includes, 1) the PSTH of the unit's response to a tone burst at the characteristic frequency, 2) the tuning curve, and 3) the response to FM

TABLE 1. *Classification of FM response patterns*

FM Class	Abbreviation	Distinguishing Characteristics
Symmetrical	Sym	Response to ascending and descending phases of FM sweep was equal (S factor less than 0.2); response was symmetrical over the four modulation rates and signal intensities tested
Symmetrical, asymmetrical at 50 sps	Sym-A50	Response was symmetrical at all rates tested except at fastest modulation rate of 50 sps
Asymmetrical	Asym	Response to ascending and descending phases of FM sweep was not equal; S factor was greater than 0.2 but less than 0.8 for at least two different modulation rates
Unidirectional	Unidirect	Response was predominantly to one phase of the FM sweep; S factor was greater than 0.8 for at least two modulation rates
Rate-intensity-dependent asymmetry	R-I	Response showed an additional discharge to ascending phase of FM sweep at 5 sps modulation rate and intensities close to threshold; this response was generally associated with buildup units
Rate-dependent inhibition	R-P	Response showed a symmetrical suppression of activity at modulation rates of 5 sps independent of intensity

sps = sweeps per second.

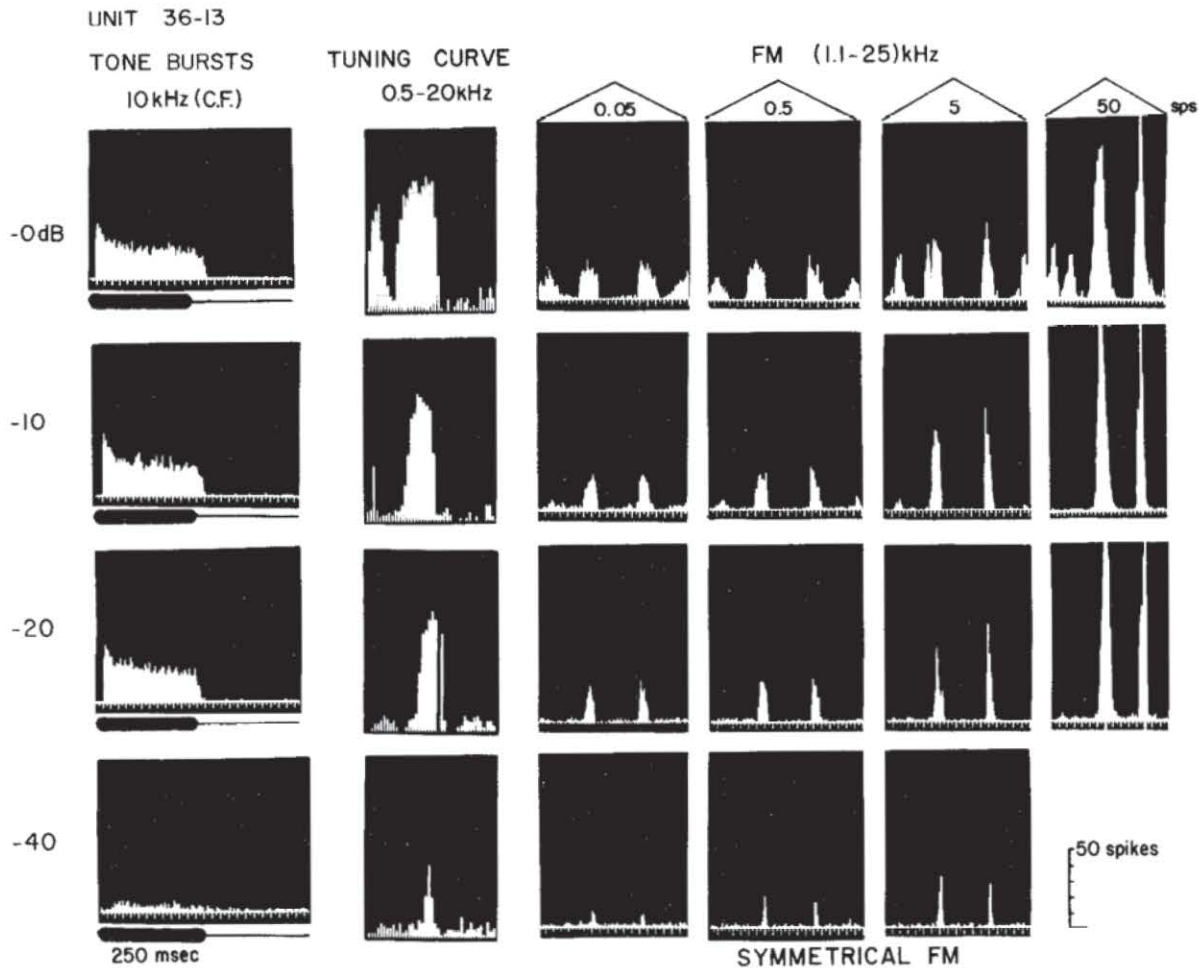


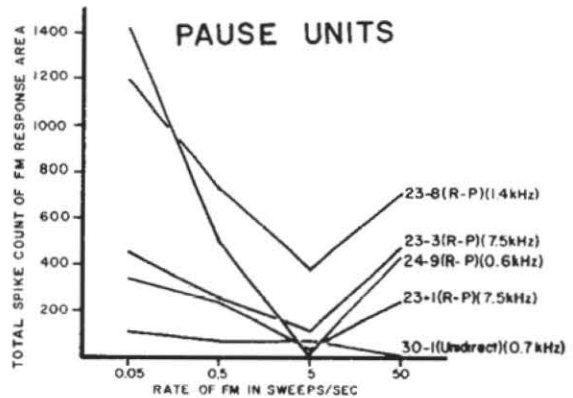
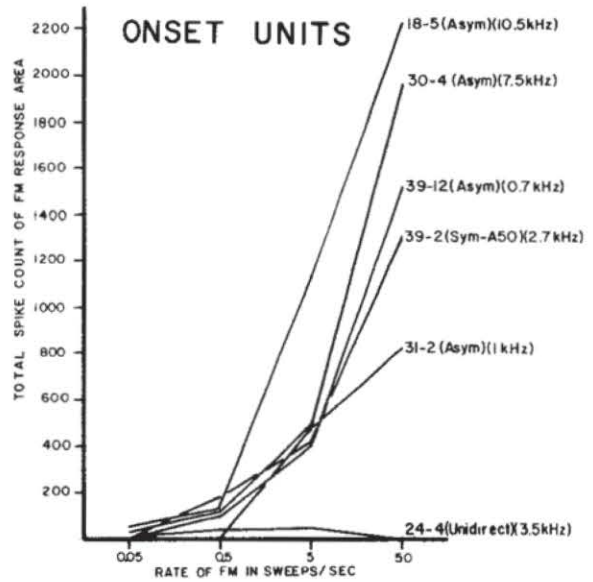
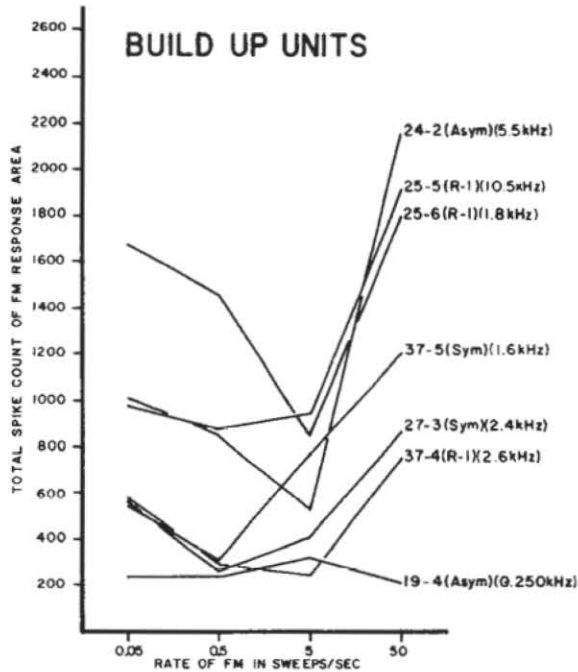
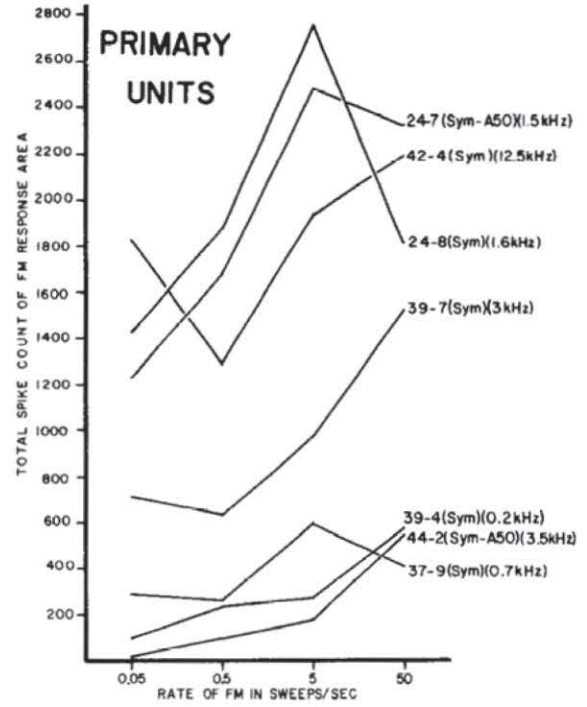
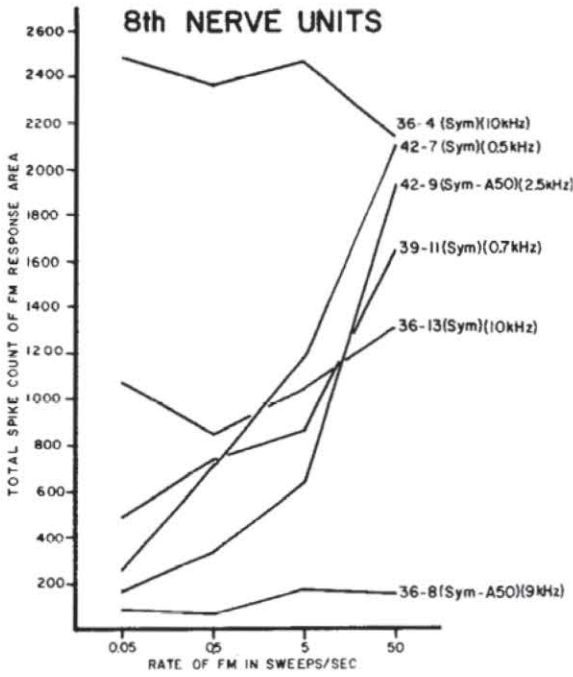
FIG. 1. FM response pattern of an eighth nerve fiber showing symmetrical response. Each FM peristimulus time histogram (PSTH) (right four columns) represents 20 s of continuous modulation. The number of sweeps during the 20-s trial is dependent on the repetition rate (1 sweep at 0.05 sps, 10 sweeps at 0.5 sps, 100 sweeps at 5 sps, and 1,000 sweeps at 50 sps). The range of the FM sweep was 1.1–25 kHz and was in the form of a triangular modulation pattern indicated above each of the histograms. Signal intensity is noted at the left of the figure. The response-area histogram or tuning curve (second column) and the PSTH to a steady-frequency tone burst at the characteristic frequency (first column) is included. This unit has a symmetrical FM response pattern at all rates and intensities tested. The abscissa of the tuning curve is composed of 40 discrete tone frequencies covering the range 0.5–20 kHz in 0.5-kHz steps.

tone sweeps. This unit has symmetrical responses to the frequency-modulated tone at the four sweep rates and intensities tested. At 50 sps the response areas are shifted to the right because the latency of the unit events (2–5 ms) is significant when compared to the duration of the sweep cycle (20 ms).

A regular feature of eighth nerve responses to modulated signals is the increase in number of discharges with modulation rate (Fig. 2). Of 14 eighth nerve fibers studied, 10 had an increase in firing with modulation rate (e.g., units 42-7, 42-9, 39-11, and 36-13), 1 unit had a decrease in firing at faster modulation rates (unit 36-4), and 3 were essentially unaffected by the FM rate (e.g., unit 36-8).

Cochlear nucleus cells

Primarylike cells were similar to eighth nerve fibers in response to FM signals. Of the .25 primarylike units studied, 14 were symmetrical, 9 were symmetrical except at 50 sps, 1 was asymmetrical, and 1 showed rate-intensity dependent asymmetry. Details of the FM response for unit 45-2 is seen in Fig. 3. The response is symmetrical at all the modulation rates and stimulus intensities tested, and the number of discharges increases with increasing modulation rates. The one primarylike cochlear nucleus unit that had an asymmetrical response to the FM tone sweep was distinguished by an extremely rapid rate of adaptation to a steady-



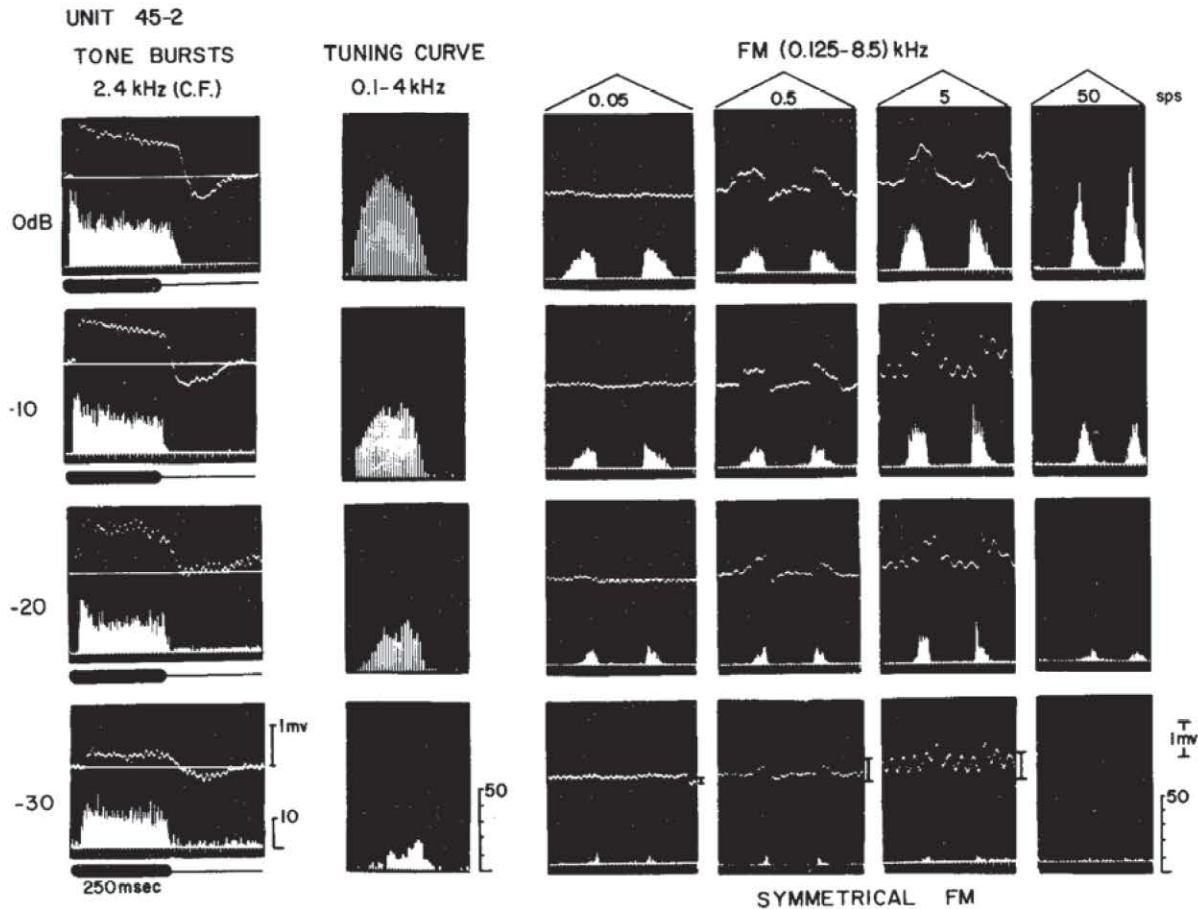


FIG. 3. Detailed FM response pattern of a primarylike cell. The format of the illustration is identical to Fig. 1 except for the addition of the average membrane potentials above the peristimulus time histograms of both FM response and tone-burst stimulation at the characteristic frequency. The unit showed symmetrical FM response pattern at all rates and intensities tested. The periodic fluctuations in the membrane potential at the 5 sps represent 60-Hz interference from line frequency pickup.

state tone compared to the gradual adaptation seen in other primary units.

Primarylike units had an overall increase in firing with increasing modulation rate (Fig. 2). However, in 10 of these 25 units there was an unexpected decrease in firing at just one particular rate (6 units at 0.5 sps—units 42-4 and 39-7 in Fig. 2—and 1 unit at 5 sps). There was one unit whose rate of firing was unaffected by modulation rate.

Synaptic events during FM stimulation corresponded well with the discharge patterns (Fig. 3). The shape of the depolarization shifts, which accompanied spike firings, were remarkably similar to both the ascending and descending phases of the sweep.

Buildup cells had diverse responses to FM

signals. Of the 17 buildup units studied, 2 were symmetrical, 5 were symmetrical except at 50 sps, 4 were asymmetrical, 1 was unidirectional, 4 showed a rate-intensity-dependent asymmetry, and 1 showed a rate-dependent inhibition. An example of a unit that responded in a symmetrical manner is in Fig. 4. This unit also shows so-called "translational" symmetry at 0.05 and 0.5 sps as described by Erulkar et al. (5) in that "the response shows approximately the same time pattern upon entry of the stimulus frequency into the appropriate range whether the stimulus is rising or falling." Inspection of the membrane-potential shifts in Fig. 4 suggests that translational symmetry is due to the hyperpolarization and suppression of firing that commonly follows the termination of

FIG. 2. Responses of eighth nerve fibers, primarylike cells, buildup cells, onset cells, and pause cells as a function of FM sweep rate. The number of spikes occurring in the FM response area (both ascending and descending phases of the sweep) is plotted as a function of FM sweep rate. The unit, its FM response classification, and its characteristic frequency are noted to the right.

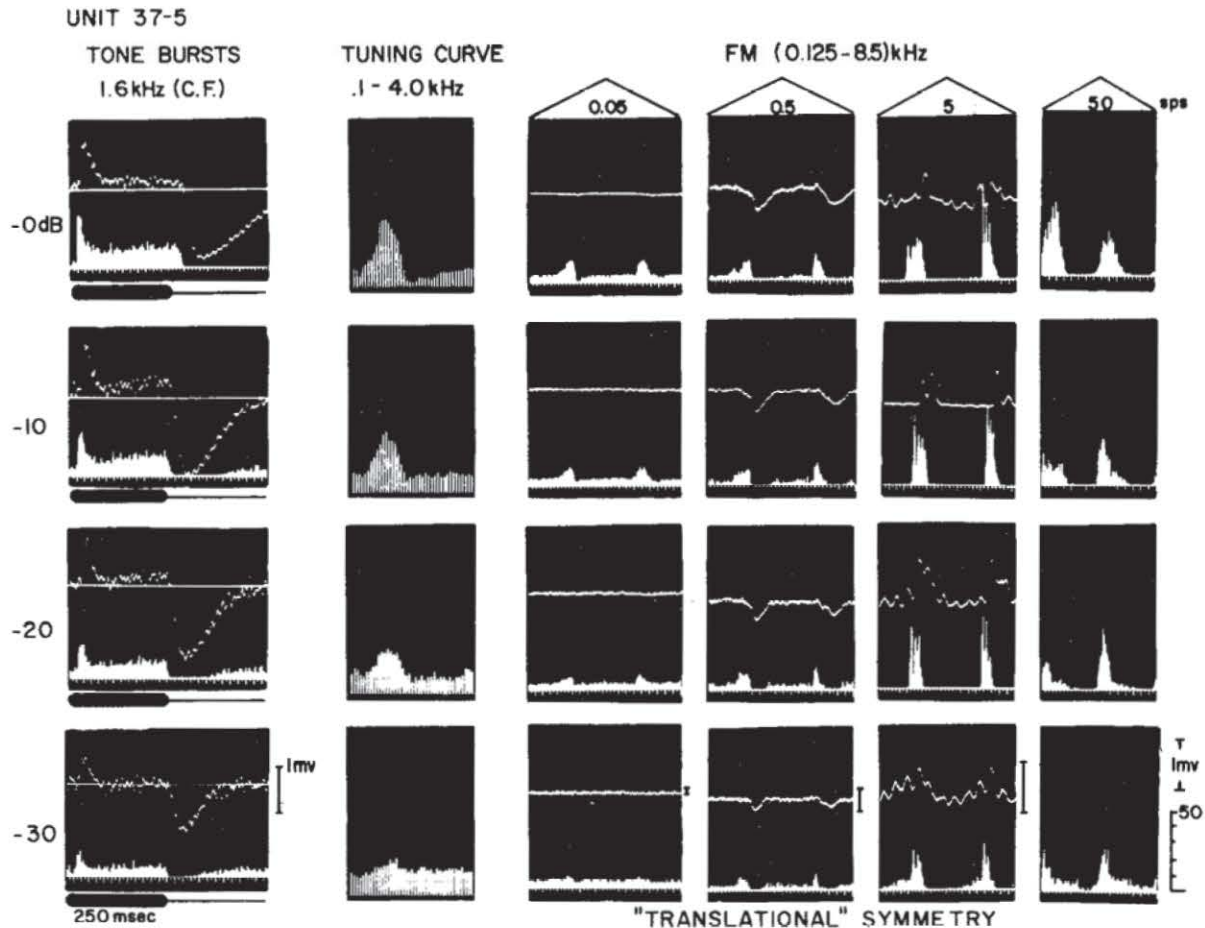


FIG. 4. Detailed Fm response pattern of a buildup cell showing translational symmetry. The format of this figure is identical with Fig. 3. See text for discussion of this unit.

excitatory tonal signals. As can be seen from this unit's PSTH to a steady-frequency tone burst (first column), a very pronounced hyperpolarization occurs after tone offset. Furthermore, the unit's tuning curve shows only an excitatory response area without any tone-evoked inhibition or inhibitory surround, thus making the off-hyperpolarization the prominent inhibitory influence. For a translational unit, hyperpolarization will occur following the FM signal's passage through the excitatory frequency-response area regardless of whether the frequency is ascending or descending. In the proposed scheme of classification of FM response, translational symmetry is not separately classified and these units are considered symmetrical since the number of discharges evoked by the ascending and the descending phases of the frequency sweep were quite similar.

Unit 25-5, in Fig. 5, is an example of a rate-intensity-dependent asymmetry to frequency-modulated signals, that is, an asymmetry developed at particular modulation rates and sig-

nal intensities. This unit has both hyperpolarization at tone offset and hyperpolarization with suppression of activity in response to tones on either side of the excitatory frequency-response area. In response to the FM signal, the unit was symmetrical at the two slowest rates (0.05 and 0.5 sps), but at 5 sps a new area of activity appeared only during the ascent of the sweep at low signal intensities (-20, -40 dB); thus, the designation of asymmetry as rate-intensity dependent. The pattern of response at 50 sps is also asymmetrical. The membrane potential for this unit changes between hyperpolarization and depolarization with a fairly good correspondence to the discharged patterns. It is apparent that the designation of a unit's FM response characteristics as symmetrical or asymmetrical can be markedly affected by slight changes in signal intensity and modulation rate.

The rate of cell discharge as a function of modulation frequency varied for buildup units (Fig. 2). Of the 16 buildup units studied, 8 units showed a decrease in response at 5 sps (e.g., units 37-5 and 27-3); 2 units had an increase in

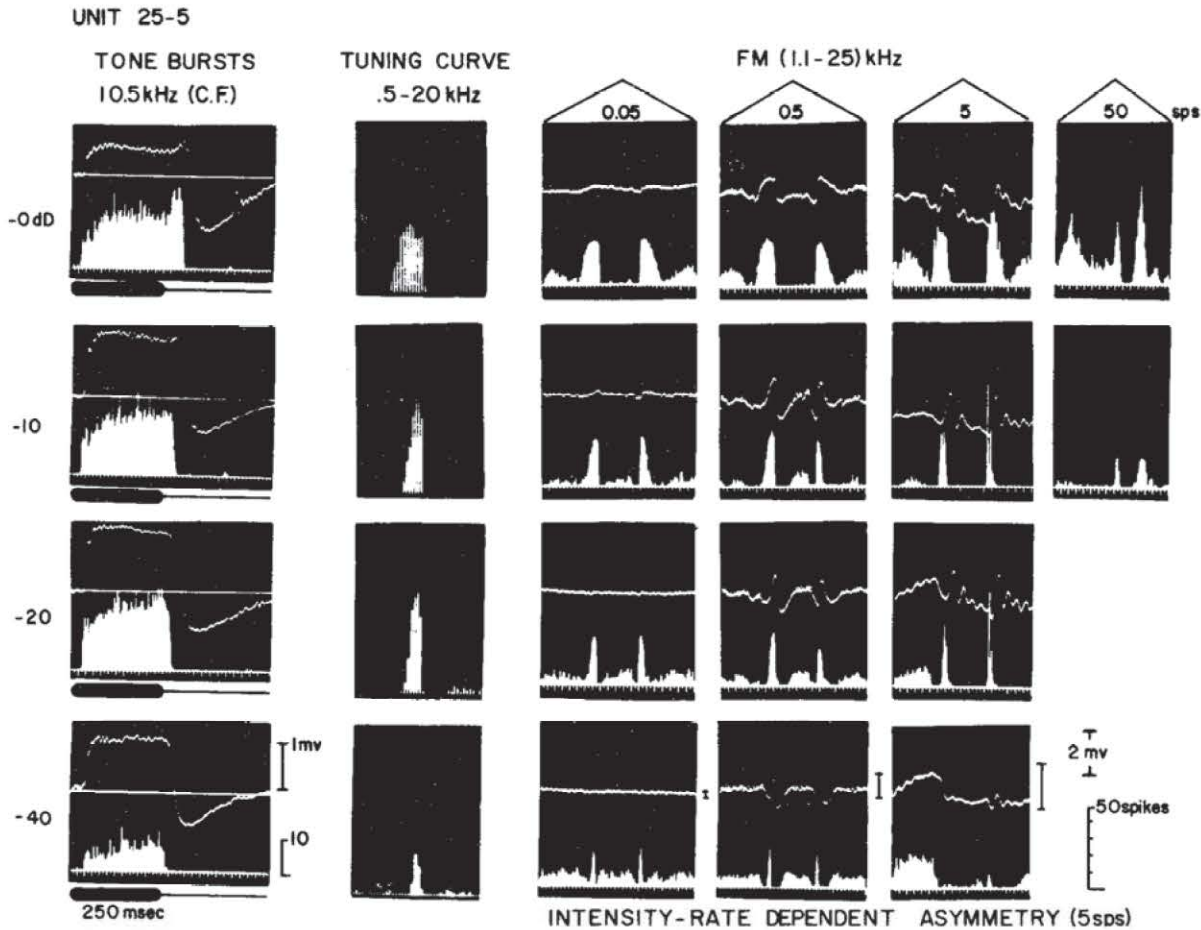


FIG. 5. Detailed FM response pattern of a buildup cell showing rate-intensity-dependent asymmetry at 5 sps when intensity was -20 and -40 dB and at 50 sps at -0 and -20 dB. The format of this figure is identical to Fig. 3. See text for discussion of this unit.

firing rate with increasing rates of modulation, as is typical of primarylike cells; 1 showed a decrease in response rate with increasing modulation rate; and in 1 unit, discharge rate was independent of modulation rate (unit 19-4).

Ten onset units were studied with FM signals and, in general, were asymmetrical (seven units). An example of one cell is seen in Fig. 6. The unit's tuning curve was broad. At slow rates of FM modulation (0.05 (not shown) and 0.5 sps) the unit did not discharge, at 5 sps the unit discharged in an asymmetrical manner in favor of the ascending phase, and at 50 sps the unit discharged to only one direction of the FM sweep. Furthermore, the response to frequency modulation at 50 sps appeared at a lower signal intensity than to the slower modulation rates, whereas for most primarylike and buildup units the threshold at 50 sps was generally 20-30 dB higher than at the other modulation rates. The averaged membrane potential during FM stimulation showed depolarization shifts at a time when spike discharges were absent.

A different unidirectional unit is illustrated in

Fig. 7. This unit responded to frequencies close to 3.5 kHz. The responses to FM tones showed no activity either at the fastest rate (50 sps) or slowest sweep rate (0.05 sps). At 0.5 and 5 sps the response was unidirectional, responding only to the descending phase of the FM signal. However, the membrane potential shows evidence of depolarizing shifts to both phases of the FM signal, but the amplitude of the shift was both larger and more abrupt to the descending than to the ascending phase of the FM sweep.

The plots of discharge frequency as a function of sweep rates (Fig. 2) show that most onset units fire very little or not at all in response to the slowest sweep rates, while the faster rates of modulation evoked considerable activity. The only exception to this statement is unit 24-4 in which there was little activity regardless of the modulation rate.

Five pause cells were studied with FM signals. Their response to pure tone bursts are characterized by 1) a long latency (>10 ms) between tone onset and the appearance of unit

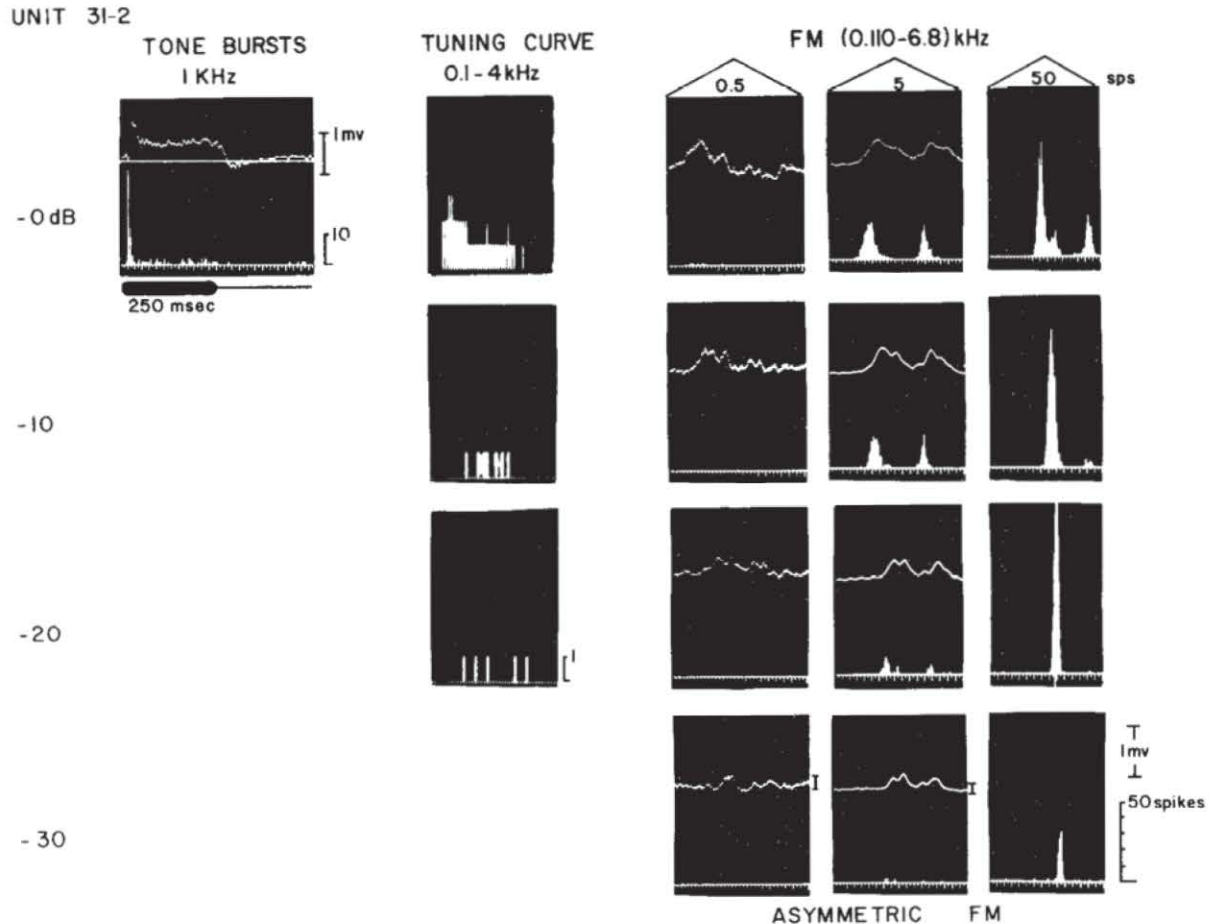


FIG. 6. FM response pattern of an onset cell showing asymmetry at 5 sps and unidirectionality at 50 sps. The format of this figure is identical with Fig. 3. See text for discussion of this unit.

discharges, and 2) the occurrence of prominent inhibitory regions in the tuning curves on either side of the characteristic frequency. The example shown in Fig. 8 shows symmetrical response patterns to FM stimulation at slow modulation rates (0.05 and 0.5 sps), no discharges at 5 sps, and a complex high rate of activity to 50 sps. This response pattern, classified as rate-dependent inhibition, was found particularly in units having a pause response to steady-frequency pure tone bursts. Note that there are depolarizing shifts to both the ascending and descending phases of the sweep at 5 sps even though the unit does not fire.

The rate-dependent inhibition of pause cells is illustrated by plotting the number of discharges evoked by an FM trial as a function of modulation frequency rate (Fig. 2). In most of the pause units the response is maximal at the slowest modulation rate (0.05 sps), declining to a minimum at 5 sps, and then returning again at 50 sps.

There are three inhibitory factors that might contribute to the response characteristics of the

pause units to FM signals: 1) the inhibitory period that occurs at tone onset leading to a delay before activity occurs, 2) hyperpolarization at tone offset leading to suppression of activity for a period after the tone burst, and 3) the inhibition of discharges with membrane hyperpolarization to tones surrounding the characteristic frequency. It may be that modulation at 5 sps is optimal for interaction of these three inhibitory influences to produce maximal suppression of unit activity.

Summary of FM responses

Table 2 contains a summary of the various response categories to FM signals as a function of the unit's response to pure tone signals defined by the shape of the PSTH (3). Eighth nerve fibers and primarylike cochlear nucleus units show, in general, symmetrical responses to FM signals. Buildup units have diverse responses to FM signals but are, in general, asymmetrical or complex in their response to particular modulation rates and/or intensities. Onset units have asymmetrical responses to

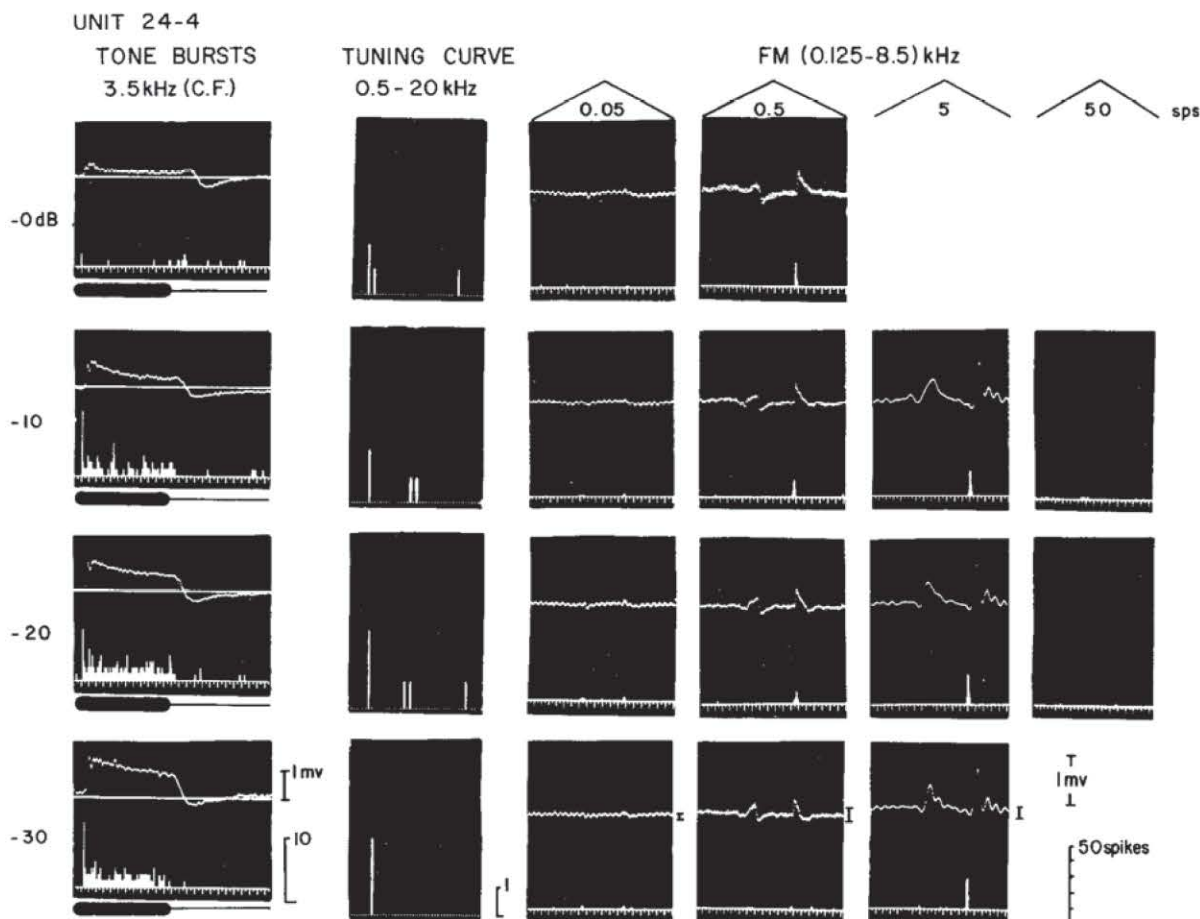


FIG. 7. FM response pattern of a nonmonotonic onset cell showing unidirectional response. The format of this figure is identical to Fig. 3. See text for discussion of this unit.

FM signals. Pause units show rate-dependent inhibition characterized by a suppression of activity at 5 sps. Thus, of the 57 cochlear nucleus cells studied, only 16 could be considered to respond symmetrically to FM signals at all intensities and modulation rates tested, and another 16 were symmetrical except at the fastest modulation rates (50 sps). The other 25 cells were asymmetrical, unidirectional, or complex in their response to changes in modulation rate or signal intensity.

Acoustic signal variables affecting FM responses

The main parameters affecting response to frequency-modulated signals are the sweep rate, range of frequency being swept, and intensity. Some general comments can be made about these parameters.

Stimulus intensity influenced responses to FM signals (Fig. 9). In one onset unit (18-5), a change in signal intensity of 20 dB shifted the response from asymmetrical to unidirectional, while in another onset unit (39-12) the same

intensity shift was accompanied by a change from symmetrical to asymmetrical responses. Unit 25-6 is one of the buildup units which showed a rate-intensity-dependent asymmetry that developed when the stimulus intensity was lowered by 20 dB. The appearance of asymmetrical and unidirectional responses to FM signals was most likely to occur with signal intensities close to the unit's threshold.

Modulation rate could also affect the FM-response type. Most of the asymmetries encountered (e.g., rate-intensity-dependent asymmetry of buildup units, rate-dependent inhibition of the pause unit, and the asymmetrical response of the onset units) appeared particularly at modulation rates of 5 sps.

The range of frequencies swept in these experiments was from 0.125 to 8.5 kHz or 1.1 to 25 kHz. We did not investigate the effects of changing the sweep range, and it is possible that this parameter may also strongly influence the FM response types defined in this study. For example, Fig. 10 contains five units that responded more to the ascending than to the descending portion of the sweep; in four of

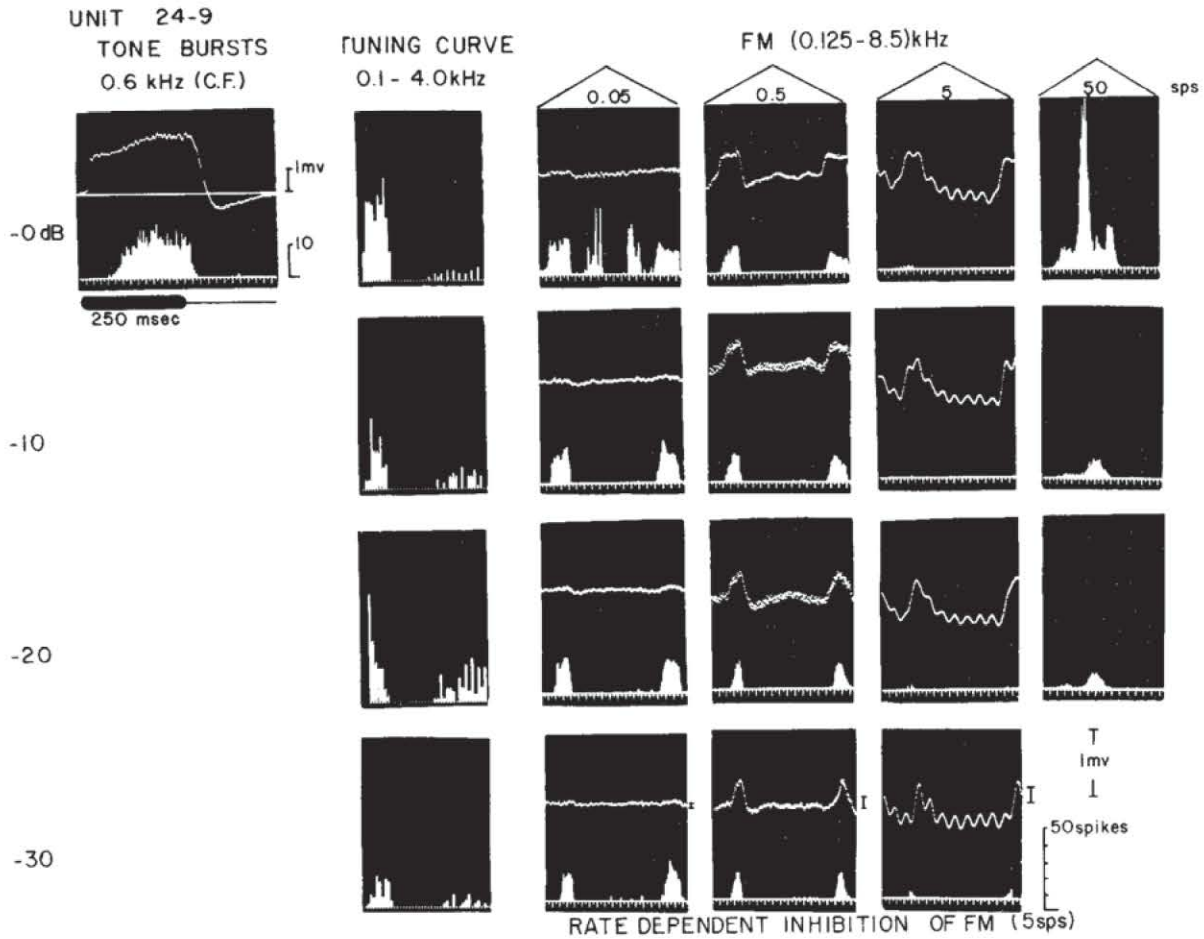


FIG. 8. Detailed FM response pattern of a pause cell showing rate-dependent inhibition of FM at 5 sps. The format of this figure is identical to Fig. 3. See text for discussion of this unit.

these units the difference was sufficient to classify the response as asymmetrical. Note that the discharges in the descending phase though of fewer numbers were tightly clustered to produce a high peak of response as the tone swept down from the inhibitory surround into the characteristic frequency. The membrane potentials also show a sharp depolarization at this junction. It is not unreasonable to expect that

both the number of discharges and their synchrony would be affected by the choice of the sweep range for these units.

Inhibitory influences affecting FM response

Inhibitory influences consist of three major types: 1) the hyperpolarization that occurs after

TABLE 2. Summary of FM responses

FM Classification	Eighth Nerve Fibers	Cochlear Nucleus Cells			
		Primarylike	Buildup	Onset	Pause
Symmetrical	11	14	2		
Sym-A50	3	9	5	2	
Asymmetrical		1	4	7	
Unidirectional			1	1	1
Rate-intensity asym		1	4		
Rate-dependent inhibition			1		4
Total	14	25	17	10	5

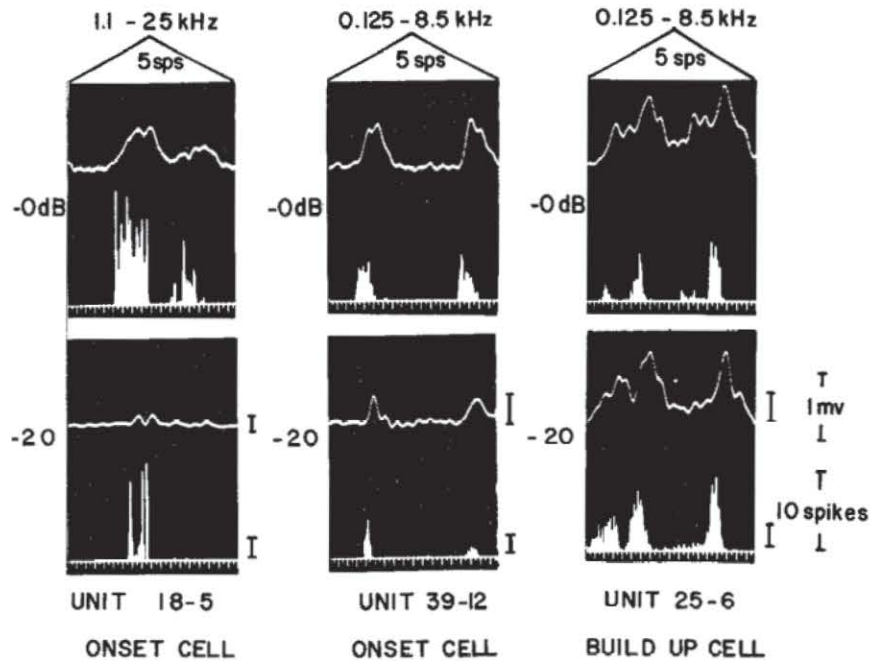


FIG. 9. Signal intensity as a parameter affecting FM response patterns. A drop in 20 dB of intensity affects the FM response patterns significantly for these three units. Unit 18-5 goes from an asymmetric to unidirectional response pattern. Unit 39-12 changes from a symmetrical to asymmetrical response pattern, while unit 25-6 develops rate-intensity-dependent asymmetry.

the signal passes through the excitatory response area similar to the hyperpolarization that occurs at offset of a steady tone burst, 2) the active inhibitory surround on either side of the excitatory frequency-response area which is associated with hyperpolarization, and 3) the inhibition that occurs during brief tone bursts in the excitatory response area that accounts for the various PSTH configurations (buildup, onset, and pause responses).

The hyperpolarization at tone offset seen in buildup unit 37-5 (Fig. 4) was shown to be re-

sponsible for the so-called translational symmetry of Erulkar et al. (5).

A translational configuration in FM response was seen in 21 units (9 primarylike, 10 buildup, and 2 pause) when the modulation rates were 0.5 and 5 sps and the signal intensities were 10 to 20 dB above the unit's threshold. Though hyperpolarization at tone offset was seen in all four types of units as classified by their post-stimulus time histograms, translational symmetry was observed in only three of these four types. None of the onset units showed transla-

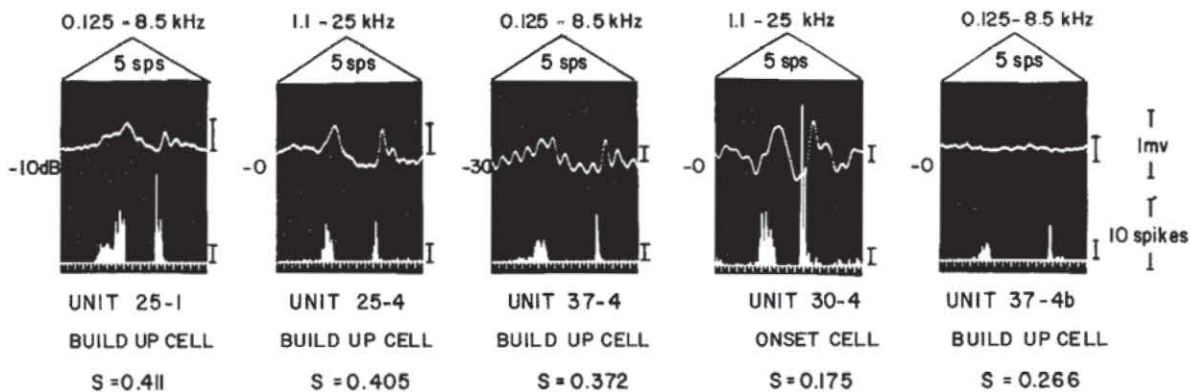


FIG. 10. Units which show a more restricted response to the descending phase of the FM sweep. S at the bottom of each photograph is the value of the symmetry factor (see METHODS). Four units show an asymmetric response (S greater than 0.2), with the response greater to the ascending phase of the FM sweep. One unit (30-4) shows approximately equal responses to the two phases, but like the other units, it shows a greater peak of response over a narrower frequency range to the descending phase of the FM sweep. See text for further discussion.

tional configuration even though hyperpolarization at tone offset was qualitatively similar to the other three types of units studied.

There can be interactions between two types of inhibition in certain cells presented with a frequency-modulated signal at least 30 dB above the unit's threshold. For instance, with an ascending-frequency signal the low-frequency portion of the inhibitory surround is first encountered, followed by the excitatory-response area, with its accompanying off-hyperpolarization superimposed on the hyperpolarization of the subsequent higher frequency inhibitory surround. A reverse pattern of events will occur during the descending portion of the FM sweep. Thus there is a combination of two inhibitory processes in the response when the inhibitory surround and off-hyperpolarization occur together, leading to an intense and long-lasting membrane hyperpolarization (Fig. 11, upper traces). When the stimulus intensity is lowered, the hyperpolarization due to the inhibitory surround is diminished, whereas the hyperpolarization at tone offset persists, resulting in the occurrence of a translational configuration (Fig. 11, lower traces).

DISCUSSION

In this study of cat cochlear nucleus cells a variety of responses to FM signals were seen.

These were, 1) symmetrical at all modulation rates and intensities; 2) symmetrical except at the fastest modulation rates tested (50 sps); 3) asymmetrical at all modulation rates and intensities; 4) asymmetrical at only one particular modulation rate or signal intensity; 5) unidirectional; and 6) marked suppression of activity at one modulation rate, usually 5 sps, called "rate-dependent inhibition." Only 16 of the 57 cells studied responded in a symmetrical manner to the FM signals. These results are not in agreement with some previous workers who have indicated that cochlear nucleus units respond to FM signals in only a symmetrical manner (15, 16, 21). However, more recent studies by Erulkar et al. (5), Evans and Nelson (6), and Møller (9, 10) suggest that there are units in cochlear nucleus with asymmetrical responses that may depend, in part, on the rate of frequency modulation.

In our study there was a correlation between the particular FM response pattern and the cell type as defined by the discharge pattern evoked by a pure tone burst (i.e., primarylike, buildup, onset, and pause-type units, (3)). Thus, responses of eighth nerve fibers to FM signals were symmetrical except for three units (20% of the sample) which showed asymmetry at 50 sps, the fastest rate. Responses of primarylike cochlear nucleus units to FM signals were also

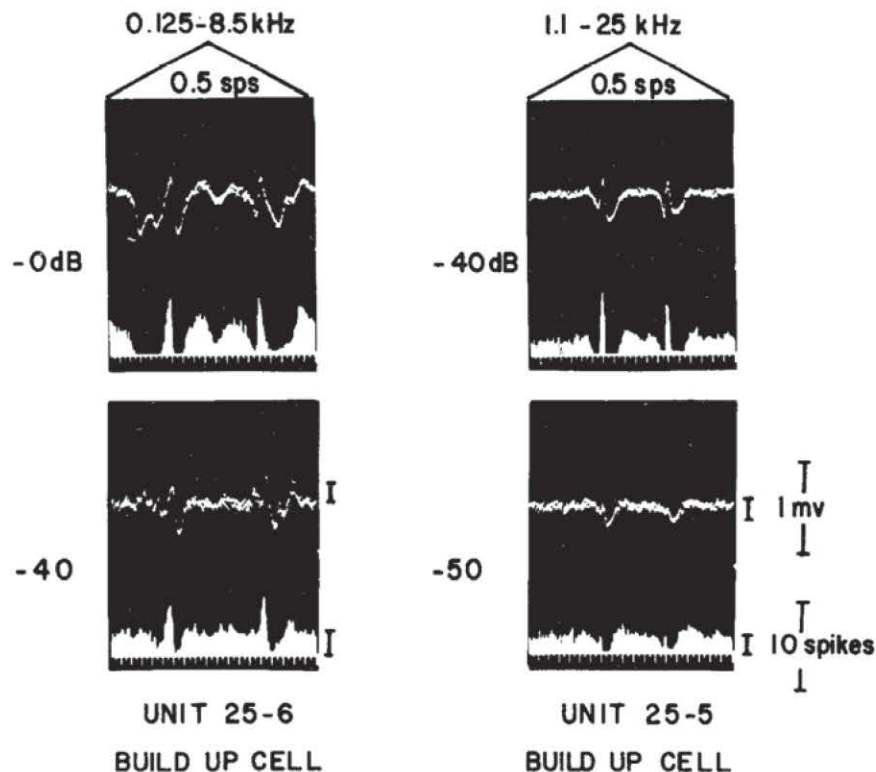


FIG. 11. Relative contributions of the inhibitory surround (tone-evoked membrane hyperpolarizations) and the off-hyperpolarization (membrane hyperpolarization which occurs at the end of tonal excitation of the unit) to the FM response pattern. See text for discussion of the units.

symmetrical, similar to that observed in eighth nerve fibers. However, the other three classes of cochlear nucleus cells consisting of buildup, onset, and pause units responded in an asymmetrical or other complex manner to FM signals. Buildup units were diverse in their FM response type. Onset units were generally asymmetrical in their response to FM signals. Of 10 onset units studied, 7 were asymmetrical, 1 was unidirectional, and 2 were symmetrical except at 50 sps. Pause units showed a characteristic inhibition or minimal response at 5 sps. At slower rates of modulation (0.05–0.5 sps) the units showed a symmetrical response. If activity occurred at 5 sps, the rate at which inhibition was maximal, it too was symmetrical.

Symmetrical responses to FM-modulated tones were found in 11 of the 14 eighth nerve fibers and in 14 of the 25 primary-type cochlear nucleus cells and represent a faithful reproduction of the time-frequency pattern of the acoustic signal. Thus, equivalent discharges were elicited to FM signals regardless of the direction of the FM sweep. Certain temporal features of the FM signal, however, could affect the response symmetry of these units. First, with modulation rates of 50 sps, 3 of the 14 eighth nerve fibers and 9 of the 25 primarylike cochlear nucleus cells developed asymmetrical patterns, responding more to one direction of the FM sweep. Apparently at these sweep rates the unit's firing pattern is influenced by factors other than the signal's time-frequency pattern. Second, the number of discharges evoked by the FM signal could be modified by sweep rate. Most typically, there was an increase in the number of discharges evoked as the modulation rate increased. There are probably two factors that account for this increase in discharge frequency with modulation rate. First, at slow rates of modulation the unit might be expected to show some adaptation in firing as it does to a pure tone burst. Probably a more important explanation for the increased firing at faster rates is that since the duration of each FM trial was kept constant at 20 s, the characteristic frequency was crossed more often as modulation rate increased. For instance, the characteristic frequency was crossed 2 times at 0.05 sps (once on the up sweep and the second time on the descent), 20 times at 0.5 sps, 200 times at 5 sps, and 2,000 times at 50 sps. Since the firing of an eighth nerve fiber is maximum at the onset of the signal, it follows that unit activity will increase as a function of the number of times the characteristic frequency is crossed. Møller (9, 10), studying rat cochlear nucleus, found that discharges became more restricted to the unit's characteristic frequency as the sweep rate increased, but the average discharge

frequency (spikes per second) appeared to be independent of modulation rate, in contradistinction to the present study. Møller (9) postulates that the pattern of this restricted response at certain sweep rates is mainly the result of interaction of excitatory and inhibitory factors.

Asymmetrical responses to FM signals were found in 11 of 57 cochlear nucleus cells, principally those having buildup and onset response patterns. All were characterized by a greater number of discharges evoked to the ascending than to the descending sweep. The finding of asymmetrical responses to a wide range of modulation rates (0.5–50 sps) suggests the presence of mechanisms that can influence cochlear nucleus units for a considerable time. Active inhibitory processes must play an important role in the generation of the asymmetrical responses. All of the cells with asymmetrical responses showed either a suppression of spontaneous activity to tones on either side of the characteristic frequency and/or a hyperpolarizing membrane response to these tonal signals. The inhibition was more pronounced to tones of a higher than lower frequency relative to the characteristic frequency. Thus, a FM signal will be more likely to evoke discharges as the signal ascends through the characteristic frequency than in the reverse direction since in the latter mode inhibition would be greater, and thus more effectively limit the number of discharges.

Three units which responded predominantly to only one direction of the FM sweep, i.e., unidirectional responders, were found in the study. One unit was of the buildup type, one was onset, and one was a pause unit. The decision to classify this kind of unit as distinct from asymmetrical is arbitrary but is made because previous workers stressed that unidirectional FM responders are restricted to higher levels of the auditory pathways and are not found in cochlear nucleus (21). The present results indicate quite clearly that a small but significant portion of the cochlear nucleus cells studied do indeed respond to one direction of the FM sweep.

The significance of temporal features of the acoustic signal was evident in buildup units in which responses to FM sweeps at slow modulation rates (0.05 and 0.5 sps) were symmetrical, whereas at 5 sps, responses were either asymmetrical or an additional response area would appear to the ascending phase of the sweep (i.e., rate-intensity-dependent asymmetry). The dependence on sweep rate for the demonstration of these asymmetries may reflect interaction of the three inhibitory features of these units: 1) the suppression of activity which de-

velops after the onset of unit firing in response to steady-frequency tone burst. 2) the tone-evoked hyperpolarization which occurs on either side of the response area in some units, and 3) the hyperpolarization at tone offset. Nelson et al. (12), in their FM study of inferior colliculus, found that inhibitory components of the response to frequency-modulated signal were emphasized at high rates of modulation. It may be that at slow rates of frequency change each inhibitory component acts independently and does not temporally interact with other inhibitory components. For example, in unit 25-5 (Fig. 5) the inhibitory surround can be clearly seen on either side of the frequency response area at 0.5 sps; whereas at 5 sps, the inhibitory surround cannot be distinguished.

Sensitivity to temporal features was also evident in pause units in which responses to FM signals were virtually abolished at sweep rates of 5 sps. These units have a latency of at least 10 ms before responding to steady tones at their characteristic frequency. In contrast, the ability of tones in the inhibitory surround to suppress spontaneous activity requires only 5 ms (3). Thus, as the tone ascends in frequency the unit has insufficient time to respond to the excitatory-response area before the signal achieves the region of high-frequency inhibitory surround with its short-latency effects.

Finally, onset units were characterized by a dramatic increase in response at fast modulation rates. There are two possible explanations for this. Most obvious is that the onset units only give a burst of spikes to the onset of the tonal stimulus or to a signal moving rapidly across the response area. Since there was an equal time spent for each FM trial, for each successive increase in modulation rate there is an increase in the number of sweeps, and hence an increase in the number of times the response area is crossed. The response, however, at 0.5 sps (10 sweeps in 20 s) was often as small as that at 0.05 sps (1 sweep in 20 s), suggesting that onset units may require a minimum rate of frequency change (df/dt) to evoke responses. Suga (20) has shown for phasic onset units of inferior colliculus that the rate of frequency change is indeed an important factor for excitation. For one of his onset unit a response occurred when the frequency swept one octave (35–70 kHz) in 4–6 ms, but the same unit gave no response if the same frequency change occurred over 15 ms.

Responses to FM Signals

The cochlear nucleus is the first central station in the auditory pathway and represents the first synaptic interruption in the flow of nerve impulses in the auditory pathway. From the re-

sponse to steady-state tone bursts it has been shown that there are at least four response classes (primarylike, buildup, pause, and onset) in cochlear nucleus compared with the one primary response found in eighth nerve (3). Furthermore, in the study presented in this paper there are several kinds of FM responses in cochlear nucleus cells compared to eighth nerve. It is clear, however, from other studies of auditory nuclei (14–19, 21, 22) that the "higher" centers (inferior colliculus, medial geniculate, and auditory cortex) give responses to FM signals that are yet more complex than those found in cochlear nucleus. For example, Whitfield and Evans (22) described for the cat auditory cortex a class of units which responded to one frequency range on the ascending sweep and to another but quite separate frequency range on the descending sweep. Furthermore, there are units in auditory cortex which respond to FM signals but not to tone bursts (2, 21, 22). Suga (20) found that 3% of neurons in bat inferior colliculus respond only to FM sounds. In bat auditory cortex (18) 14% of the cells were FM specialized (i.e., they did not respond to either pure tone or noise bursts). Similar FM-sensitive neurons have been recorded in inferior colliculi of birds (1).

Suga (20) has shown in the bat that each unit in the cochlear nucleus will respond to all three basic acoustical signals (tone burst, FM signals, and noise bursts). In higher centers, such as medial geniculate or auditory cortex, there are units which specialize in detecting only one of these three types of signals. His studies show an increase in specificity of responding as one ascends the auditory pathway.

Our results are in keeping with Suga's view with the exception that responses to acoustic signals may also be extremely complex at the level of the first central synapse in the auditory pathway, i.e., the cochlear nucleus. Our study has defined that there are cells in cochlear nucleus that respond to specific features of the acoustic signal (direction of a FM sweep, rate of modulation, etc.). The significance of such complex responses to time-varying acoustic signals suggests that the process of signal feature extraction already has begun at the first central auditory site, the cochlear nucleus. It may be that the auditory system is arranged so that the extent of such specific signal responsiveness in a population of cells increases as one ascends the pathway from eighth nerve to auditory cortex.

SUMMARY

Responses of 99 cochlear nucleus cells and 24 cochlear nerve fibers were studied with FM

signals; 14 cochlear nerve fibers and 57 cochlear nucleus cells were studied at four rates of modulation and several signal intensities.

Classification of FM response patterns as symmetrical, asymmetrical, or unidirectional was based on the calculation of a symmetry factor (S), which compared the number of discharges evoked by the ascending and by the descending phases of the FM sweep. Certain FM response patterns could not adequately be described by the symmetry factor alone and variables of modulation rate and signal intensity had significant influence.

A correspondence was found between the four response classes evoked by a steady-frequency tone burst (primarylike, buildup, onset, and pause) and the FM response pattern.

Cochlear nerve fibers showed symmetrical response patterns to FM stimulation.

Primarylike units were similar to eighth nerve fibers and generally showed symmetrical FM responses. Occasional eighth nerve fibers and primarylike cells developed asymmetry at the fastest rate of modulation (50 sps).

Buildup units showed a variety of response patterns to FM signals.

Onset units generally showed asymmetrical

response patterns with the greater response occurring to the ascending than to the descending phase of the FM sweep.

Pause units showed a characteristic inhibition of activity at 5 sps (rate-dependent inhibition).

Of the 57 cochlear nuclear cells studied in response to FM signals, 16 were symmetrical, another 16 were symmetrical except at the fastest modulation rate, 12 were asymmetrical, 3 were unidirectional, and 10 showed complex responses to certain signal rates or intensities.

It is clear that the cat cochlear with its complex cytoarchitecture is involved in the recoding of acoustic information. Some units in cochlear nucleus demonstrate differential responses to the direction and to the rate of frequency movement. Other cochlear nucleus cells respond as eighth nerve fibers and may serve as simple "relays" in transmitting information from the cochlea to higher auditory centers.

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