Physiological Study of Neurons in the Dorsal and Posteroventral Cochlear Nucleus of the Unanesthetized Cat

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SUMMARY AND CONCLUSIONS

1. The responses of neurons in the posteroventral (PVCN) and dorsal (DCN) cochlear nucleus of the unanesthetized cat were determined for both long and short tones. These results were compared with recent studies (13, 14) in the barbiturate-anesthetized cat conducted in the same laboratory using similar stimuli and analysis programs.

2. Every response pattern (poststimulus time histogram to short tones), which has been observed in previous studies using anesthetized animals, was also observed without anesthetic. The converse was also true: no novel response patterns were observed in the unanesthetized cat. This was also true for interval histogram, response area, isorate curve, and frequency sweep data.

3. Some neurons were difficult to classify into existing descriptions of cochlear nucleus response patterns. For example: 1) primary-like, onset, pauser, and buildup response patterns could also show chopper-like properties; 2) onset-inhibitory, pauser, and buildup neurons appeared to form a response continuum rather than exist as separate response categories; and 3) onset neurons with low characteristic frequencies (CFs) often showed sustained and strongly phase-locked responses below ~1,000 Hz. In addition, single neurons often showed more than one response pattern depending on the intensity and frequency of the acoustic stimulus. These ambiguities were also observed under anesthetic (13, 14).

4. Onset neurons within the PVCN appear to be well suited for the encoding of temporal and intensity information. At low stimulus frequencies they often respond to every cycle of a pure tone stimulus and exhibit the highest degree of phase-locking in the cochlear nucleus. The dynamic ranges associated with many onset neurons can exceed 80 dB compared with the 30- to 40-dB dynamic ranges associated with most other cochlear nucleus neurons. Onset neurons show a similar range of activities in the anesthetized cat (13, 14).

5. Neurons in the DCN have response properties that are more complex than those seen in the PVCN. Response patterns can change from sustained excitation to complete inhibition and are more often nonmonotonic near CF. DCN neurons can show well-defined tuning in the frequency domain and may be used to encode spectral information, but appear to be poorly suited for encoding temporal or intensity information as they are weakly phase-locked and have relatively small dynamic ranges. When DCN neurons "chop" they usually do so more slowly than do PVCN neurons. DCN neurons recorded in the anesthetized cat behave similarly (13, 14).

6. The relative frequency of a particular response pattern did vary with anesthetic state. The largest differences were observed for the DCN where onset-inhibitory neurons were nearly five times more common and chopper neurons were about half as frequent without anesthetic. The proportions of other neuron types in the DCN and PVCN differed by smaller margins.

7. Nonmonotonic rate curves were twice as common without anesthetic in the DCN. They were observed for 42% of the DCN neurons studied in the unanesthetized cat compared with 20% for the anesthetized cat.

8. Response properties were characterized parametrically for each response category in both the anesthetized and the unanesthetized cat. Parametric differences depended on the
location of the neuron but there were some general trends. Threshold, spontaneous rate, and the standard deviations of the first-spike latency and the interspike interval tended to have larger values without anesthetic. Differences in these parameters may have resulted from increased noise levels in the unanesthetized preparation. The dynamic range, the maximum discharge rate, the first spike latency, tuning sharpness ($Q_{10}$), the mean interspike interval, and the peak-to-steady-state ratio showed less consistent differences with anesthetic state.

9. These results suggest that it is still useful to study cochlear nucleus responses in the barbiturate-anesthetized cat, but that some caution must be exercised when one evaluates parametric data obtained under anesthetic.

INTRODUCTION

A primary reason for conducting neurophysiological studies in anesthetized animals is to obtain information about brain processes as they operate in normal, awake subjects. To the extent that a neural system responds similarly under anesthetized and awake conditions, anesthetized preparations offer several advantages. Their stability allows detailed analyses of individual neurons that may require recordings of several hours and also facilitates intracellular studies. In the auditory system, anesthetized preparations permit the precise control of sound stimuli and calibration of the acoustic system using probe tubes placed close to the eardrum. These advantages have not been offset by the unnaturalness of the anesthetized preparation because, in general, responses obtained from anesthetized and awake animals have been sufficiently similar to warrant further research under anesthesia, particularly for the sensory nuclei of the brain stem. In this study, single neuron activity was recorded from the cochlear nucleus of the unanesthetized cat to determine the effects of anesthetic state.

Fibers from the auditory nerve enter the cochlear nucleus and then bifurcate into ascending and descending branches; the ascending branch innervates the anteroventral cochlear nucleus (AVCN), whereas the descending branch innervates the posteroverentral cochlear nucleus (PVCN) and the dorsal cochlear nucleus (DCN) (8, 9). Previous studies have examined the response properties of these three subareas of the cochlear nucleus in both anesthetized (4, 5, 10) and unanesthetized (3, 19) animals. To eliminate the effects of anesthetic state, several studies (19, 21) of the DCN have been carried out in paralyzed decerebrate cats. Our approach has been to study PVCN and DCN responses from unanesthetized cats, which have not been decerebrated and to compare the results with a recent series of experiments performed in pentobarbital-anesthetized cats (13, 14).

MATERIAL AND METHODS

Each of eleven docile cats weighting from 2.5 to 3.5 kg with clean external ears and transparent eardrums was given penicillin (1 ml im) and anesthetized with pentobarbital sodium (60 mg/kg) injected intraperitonially. Under sterile operating conditions the dorsal surface of the skull was exposed. A small circle of bone was loosened by drilling in a region above the cochlear nucleus, between the bony ten- torium and the occipital crest, taking care to leave the dura intact. This circle was then filled with bone wax to seal the brain and to secure the loosened section of bone. Four threaded nuts, which were later used to rigidly hold the head during recording, were screwed into the skull at the level of the frontal cortex and sinus. A plastic recording chamber was cemented to the skull directly over the drilled area using dental acrylic anchored to five stainless steel bolts. One bolt was used as an electrical ground. The skin was then sutured in place around the headstage and further secured with cyanoacrylate glue (Krazy Glue). Bacitracin antibacterial ointment was applied topically and within the chamber to prevent infection, and the chamber was covered with a plastic cap. After a recovery period of at least 5 days the animals appeared quite normal, and in the later half of the experiments were then accustomed to the recording apparatus for 2 days before recording began.

At least 1 wk after the headstage and recording chamber had been positioned, the subject was placed in the recording apparatus, its head secured, the chamber opened, and the loosened section of bone and the dura removed. A topical anesthetic, Xylocaine gel, was applied to the area prior to cutting the dura. Most animals showed little reaction to, nor did they vocalize, during this procedure. A small amount of cerebellum overlying the cochlear nucleus was then aspirated. In general there was no reaction to this procedure. A small cylinder of sterile cellulose (film) positioned to retain exposure of the cochlear nucleus by preventing the collapse of the cerebellum. Care was taken to leave the fast folium of the cerebellum overlying the cochlear nucleus
intact, at least for the first two recording days. In some experiments, the recording electrode was passed through this final folium before entering the cochlear nucleus, whereas in others the folium was retracted. In both instances, the placement of the electrodes above the cochlear nucleus was verified visually. After the electrode was in place, the cochlear nucleus was covered with a layer of 3% agar in isotonic saline to reduce brain pulsations. Entry into the cochlear nucleus was signaled by an increase in background activity and the presence of clear responses to auditory stimuli. The fusiform layer of the DCN was associated with a region of greatly increased background activity ~100-400 μm below the dorsal surface of the DCN. The DCN and PVCN were separated by a silent region ~800 to 1,200 μm below the dorsal surface of the DCN in which few cells and little background activity were recorded. This fact along with an abrupt change in the characteristic frequency that is seen upon leaving the DCN and entering the PVCN were used to determine whether a unit was to be considered as being located in DCN or PVCN.

Microelectrodes were lowered into the cochlear nucleus using a Trent-Wells hydraulic microdrive. Several types of electrodes were used in an attempt to optimize the recording stability of well-isolated single units. Glass-coated, platinum-iridium electrodes (1-3 MΩ) were generally optimal for the stable recording of well-isolated single-unit activity in all regions of the DCN and PVCN except the fusiform cell layer of the DCN. Well-isolated recordings in the middle of the fusiform cell layer were optimally obtained using micropipettes filled with 3 M KCl (7-15 MΩ). On the few occasions when parylene-coated tungsten electrodes were used, we had little success in isolating unit responses in the fusiform cell layer; this type of electrode may work well in other brain regions where cells are less tightly packed and a smaller number of neurons are responsive to a particular stimulus. The isolation of each unit was assigned a rating of A, B, or C: well-isolated action potentials clearly above background were given an A rating; action potentials closer to background, which required a higher comparator setting and occasionally the loss of a few spikes were given a B rating; rating C was assigned to units that could not be reliably discriminated from the activity of other units. In these experiments only type A records were used for quantitative analyses. Type B records were generally included in more qualitative analyses, which judged the appearance of response patterns, response areas, and frequency sweep responses. Type C records were used to determine whether the equipment was working and to estimate the general response characteristics of a recording site but were not included in the analyses reported in the RESULTS. For comparative purposes, records obtained from anesthetized cats in this laboratory (13, 14) using high-impedance (80-120 MΩ) micropipettes were all type A records.

Auditory stimuli were created digitally and neural spike data were analyzed using the same computerized system (11) used in previous studies of cochlear nucleus activity in this laboratory (12, 15). Auditory stimuli were produced by an encased phone (Mura Stereo Bud). A sound delivery tube attached to the phone was placed near the tragus of the intact pinna. Intensity levels re 0.0002 dyn/cm² were measured at the beginning of each experiment using a calibrated probe tube positioned at the opening of the sound delivery tube.

The data collection protocol was similar to that used in previous experiments (12, 15) to define extracellular responses. After a cell had been isolated, responses to swept-tone stimuli (triangular modulating waveform) were recorded and used to estimate CF. Responses to short tones at CF (25-ms duration, 2-ms rise and fall times, 100-250 repetitions) were then recorded ~20, 50, and 80 dB above the unit’s threshold, and PST histograms of these responses were displayed. A rate curve showing changes in average spike count with 10-dB increases in sound pressure level (SPL) was generated using short tones at CF repeated 10 times at each intensity. On several occasions responses to longer tones at CF (250- to 5,000-ms duration, 2-ms rise and fall times, 10-100 repetitions) were recorded. The unit’s response area was then obtained using short tones. If a unit was still well isolated, response areas were obtained for longer tones, and some of the initial analyses were repeated. In general, it was difficult to hold units in the unanesthetized cat, so that response area data were not as commonly obtained as in the anesthetized preparation. This was partly due to movement on the part of the animal. While the animals were usually quiet and peaceful, there were occasional periods of movement. The cats were not placed in a restraint bag; rather they were enclosed in a box that allowed them to adjust their body position. This resulted in some background noise due to scratching, purring, and occasionally meowing. An intercom was used to monitor these events. Recording was discontinued when excessive movements or loud vocalizations were made. For each subject, recordings were continued for four to five daily sessions each lasting from 3 to 5 h. During a given session, data were obtained from a single electrode penetration, which first passed through the DCN and then into the PVCN.

RESULTS

Categorization of cochlear nucleus neurons by their response patterns at CF

Cochlear nucleus neurons have commonly been categorized by their average responses to
short-duration (25 ms) pure-tone stimuli at their characteristic frequency (CF; the stimulus frequency that elicits responses at the lowest intensity) at intensities 20–40 dB above threshold (4, 5, 10). Such averaged responses are generally displayed as PST (poststimulus time) histograms that show the average firing probability of a neuron after stimulus onset. This type of categorization is clearly problematic if response patterns change with small changes in intensity and frequency. Fortunately, this is not generally the case near CF, although response patterns at the edges of a neuron’s response area can sometimes be quite different from those obtained near CF. A major exception occurs for some of the neurons found in the DCN. At CF, these neurons can show the pauser or buildup pattern at some intensities, but show the chopper pattern at other intensities (5, 13, 14).

Short-tone response patterns obtained from the unanesthetized cat are, in general, very similar to those obtained in the anesthetized cat (1, 4, 5, 10, 13, 14) and will therefore be described using extant labeling schemes (1, 10, 18). These schemes broadly divide response patterns into: primary-like (PL), chopper (C), onset (O), pauser (P), buildup (B), and onset-inhibitory (O&I) categories. In the following sections each of these response categories will be discussed in the context of the present experiments on the unanesthetized cat, and an attempt will be made to relate categorizations based on response pattern with interval histogram, response area, rate curve, and frequency sweep data.

Interval histograms computed from short-tone stimuli can be considerably different than those obtained from long tones (steady-state condition). Nevertheless, they are useful for separating choppers and units that entrain to low-frequency stimuli from those with a pri-
mary-like response. While it would have been desirable to also compare the response of these units with noise stimuli (20) this was not done in the present study because noise responses weren't collected in the anesthetized condition (13, 14).

**Primary-like responses**

In the PVCN and DCN of the unanesthetized cat, strictly primary-like responses were rare and when they did occur were usually associated with the monophasic action potentials that are generally associated with recordings obtained from fibers in extracellular records. In addition, primary-like response latencies to the 25-ms tone pips were similar to those obtained from auditory nerve fibers in anesthetized animals. This suggests that these responses were obtained from auditory nerve fibers and that auditory nerve responses are similar in anesthetized and unanesthetized preparations.

Response patterns from typical auditory nerve fibers in awake cats exhibit the classical primary-like pattern (7). The response pattern shown in Fig. 1A has a sustained response with a slight peak shortly after stimulus onset and a fine structure that indicates that spikes are preferentially locked to a particular phase of the stimulus cycle (phase locking). Phase locking is more obvious with the expanded scale used to display the distribution of interspike intervals (Fig. 1B) in which the peaks are at integer multiples of the stimulus period. The envelope of the interval distribution is highly asymmetric, rising quickly to a maximum and then declining exponentially. The exponential decay of this envelope is expected for a Poisson process (7).

Other data from these units also show primary-like characteristics. Response patterns for long tones of up to 5 s show a sustained response for the duration of the stimulus. Rate curves at CF increase monotonically over a 20- to 40-dB range and then remain nearly constant at higher levels. Response areas show a monotonic increase in firing rate with increasing intensity over the frequency range of the unit, lack inhibitory sidebands, and, at the most extreme frequencies within the response

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**FIG. 3.** *A and B:* PSTH/IH pair for the short tone at CF (STCF) stimulus condition for a sustained chopper unit (84104-36, CF = 13,000 Hz, TH = 10 dB SPL) in the ventral cochlear nucleus. *C and D:* PSTH/IH pair for the STCF stimulus condition for a wide chopper unit (83178-13, CF = 12,500 Hz, TH = 38 dB SPL) in the dorsal cochlear nucleus.
area, can show transient responses at stimulus onset or offset. Frequency sweep responses are purely excitatory with no indication of inhibitory side bands.

Several neurons resembled primary-like units in having sustained responses but differed from the classical primary-like pattern in important ways. One such unit had a primary-like response pattern (Fig. 1C) and showed a phase-locked response, but the general shape of its interval histogram (Fig. 1D) deviated from the classical primary-like pattern in having a more symmetric appearance. The synchronization coefficient (sync = 0.38), which varies between 0 and 1 (6), was lower than typically found (0.7–0.8) in auditory nerve fibers with CFs near 1 kHz.

Another example of a unit with partial primary-like characteristics is shown in Fig. 2. For short tones at 700 Hz, this unit had a primary-like response pattern (Fig. 2A), phase-locked as well as an auditory nerve fiber (sync = 0.82), and had primary-like interval statistics, although the initial mode is not

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**FIG. 4.** A: response area for the same unit (84104-36) whose short tone at characteristic frequency (STCF) response is illustrated in Fig. 3. A and B. B: response area for the same unit (83178-13) whose STCF response is illustrated in Fig. 3, C and D.
maximal (Fig. 2B). It was not primary-like in having a long response latency (12.2 ms), a buildup pattern at 70 dB SPL (Fig. 2E), and a nonmonotonic rate curve at CF. The response area was typical of many seen in the DCN of unanesthetized cats (Fig. 2G). The maximum rate is achieved by 40 dB SPL but then decreased to nearly zero as the stimulus intensity was increased to 80 dB SPL. With longer tones (250 ms), responses were still generally sustained but there was a reduction in rate at tone onset (Fig. 2C), which becomes more pronounced with increasing intensity (Fig. 2E). Interval distributions obtained from long tones (Fig. 2, D and F) still indicate strong phase-locking but their envelopes are more symmetric than those obtained from primary-like responses. In addition poststimulus activity is present, which lasts for up to 150 ms (Fig. 2, A, C, and E).

**Chopper responses**

The most frequently encountered response pattern in the DCN and the PVCN of the unanesthetized cat is the chopper pattern occurring roughly 50% of the time. Chopper units have response patterns which are multimodal, but, unlike primary-like units, these modes are most apparent immediately after stimulus onset and their spacing is not generally equal to integer multiples of the stimulus period. Chopper interval histograms for both short and long tones have a single, relatively symmetric, narrow mode, which suggests that these neurons fire regularly with a relatively constant interspike interval. The initial peaks in the response result from highly synchronized firing of the cell after stimulus onset. The standard deviation of the interspike interval histogram (SDIH) determines how long modes are clearly visible in the response after

![Graphs showing PSTH, IH, and rate vs. frequency](https://example.com/graph.png)

**Fig. 5.** A and B: PSTH/IH pair for a sustained chopper unit (85006-33, ventral cochlear nucleus) to short tones near CF. C: response area for the same unit (CF = 19,000 Hz, TH = 6 dB SPL).
stimulus onset: the smaller the $\text{SD}_{\text{IH}}$, the longer the period that the modes are visible.

Two chopper units that illustrate the range of synchronization and firing rates of chopper neurons commonly seen in the PVCN and in the DCN are shown in Fig. 3. The response in Fig. 3A is illustrative of a chopper that fires at high rates (300 spikes/s) with a regular interspike interval. The firing regularity of this unit is apparent from the narrowness of its interval histogram, which is unimodal and symmetric (Fig. 3B). This type of unit will be referred to as a sustained chopper ($C_s$). The second unit is categorized as a wide chopper ($C_w$) because it has a wider spacing between the modes of its response pattern (Fig. 3C). This pattern, observed in regularly firing units with low discharge rates (150 spikes/s), which have large interspike intervals (Fig. 3D), is seen more frequently in the DCN.

The response areas of PVCN chopper units usually consisted of a set of monotonically increasing isointensity curves and had inhibitory sidebands when spontaneous activity was present. For instance, the response area corresponding to the narrow chopper in Fig. 3 has isointensity curves that expand as intensity increases and a dynamic range of 30–40 dB (Fig. 4A), which is typical of this response type. The wide chopper unit (Fig. 3C) had a similar CF but differed in having a much lower maximum discharge rate (160 vs. 500 spikes/s) and a higher spontaneous rate (22 vs. 0 spikes/s), which allowed the visualization of an inhibitory sideband at high frequencies (Fig. 4B).

Figure 5 illustrates a variation in the chopper response pattern for a unit with high driven and high spontaneous rates (467 and 20 spikes/s, respectively). Short-tone response patterns show initial modes that are quite narrow and poststimulus activity at higher intensities (Fig. 5A). The response area shows pronounced inhibitory sidebands; high-intensity, high-frequency tones can completely shut off spontaneous activity.

Chopper cells that respond to low frequencies can show phase locking but still “chop” during the 10- to 20-ms period after stimulus onset. The response pattern of one such unit (Fig. 6A) shows two early peaks followed by a

![Figure 6](image-url)
FIG. 7. A, B, and C: PSTHs for the short-tone CF response of a chopper unit (85014-51) in the dorsal cochlear nucleus, which displayed nonmonotonic behavior. D, E, and F: PSTHs for 250-ms tones at 2,000 Hz (100 reps). G: response area for the same unit (CF = 2,300 Hz, TH = 10 dB SPL).
multimodal pattern where the mode spacing is equal to the stimulus period (i.e., phase-locking). The interspike interval distribution associated with this response (Fig. 6B) had a single narrow mode, which was symmetric and quite distinct from interval histograms ob-

![Diagram of PSTH/IH pairs showing response areas and interspike interval distributions.](image)

**FIG. 8.** A: response area for an O unit (83196-10, CF = 3.500 Hz, TH = 18 dB SPL, spontaneous rate = 12.6 spikes/s) in the dorsal cochlear nucleus. B and C: PSTH/IH pair for short tones near CF at 80 dB SPL. D and E: PSTH/IH pair for long tones near CF at 80 dB SPL (50 reps, 350/700 ms). F and G: PSTH/IH pair at 1 kHz where entrainment occurs. See text for details.
tained from primary-like units. In this instance, a low-frequency tone appears to modulate the regular firing rate of this neuron to produce both a chopper pattern and phase-locked behavior. Responses to long tones were more primary-like (Fig. 6 C and D) and exhibited a long-term adaptation constant of ~170 ms.

In the DCN, chopper neurons may exhibit marked inhibitory effects near CF as well as at the edges of their response areas. For example, the response area in Fig. 7G has a CF of ~2,300 Hz but shows a sharp dip in response rate at 2,100 Hz. Response patterns at 2,000 Hz show clear suppression at 20 dB (Fig. 7D); this suppression is also apparent in the later part of the 2,000-Hz response at 60 dB (Fig. 7F). Inhibition is clearly effective in limiting the high-frequency edge of this unit's response area. The high-frequency slope of the response area is greater than 1,000 dB/octave—very high for a neuron with a 2,300 Hz CF.

This unit is also of interest in showing the differential effects inhibition can have on different parts of the response pattern. At CF (2,300 Hz) the onset response is prominent at 40 dB SPL. However, there is a decrease in the prominence of the onset response between 40 and 60 dB SPL (Fig. 7 B and C). There is also an indication of a reduction in discharge rate in the 10- to 20-ms range, which could be indicative of an inhibitory event (also Fig. 7E). Activity during the later half of a 250-ms stimulus is nonmonotonic from 20 to 60 dB (Fig. 7, D, E, and F), whereas the onset response and activity during the first half of the stimulus-on period show a monotonic increase with increasing intensity. This series of response patterns also demonstrates that variations can be observed with changes in intensity or relatively small shifts in frequency away.

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![Diagram](https://i.imgur.com/ABC123.png)

**FIG. 9.** A: response area for an Oc unit (83124-31, CF = 22,000 Hz, TH < 20 dB SPL, spontaneous rate = 0 spikes/s, Q10 = 5.5) in the ventral cochlear nucleus. B and C: PSTH/IH pair for short-tone CF at 50 dB SPL. See text for details.
from CF, although this was not a common occurrence.

Onset responses

Onset responses are distinguished from other response patterns by a prominent peak shortly after stimulus onset. The initial peak rate can exceed 10,000 spikes/s in PST histograms with 100-μs bins and have latencies with standard deviations as small as 20–50 μs. Some onset neurons have extremely large dynamic ranges, which can be as high as 80 dB.

In the ventral cochlear nucleus, onset response patterns have been subdivided into three subcategories (4, 14) based primarily on the responses that follow well-defined onset responses: \( O_1 \) neurons (not observed in this study) show little or no response after a large onset peak; \( O_L \) neurons (Fig. 8B) respond primarily at stimulus onset followed by a sustained response; and \( O_C \) neurons (Fig. 9B) exhibit a weak chopper response after an onset peak. In the DCN, two other unit types have onset components associated with their response patterns: \( O_{IN} \) (Fig. 12, C, D, F, and G) and pauser (Fig. 15, A-C, E, and F) neurons.

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**FIG. 10.** A: response area for a low-frequency unit, which entrains to the stimulus. (85006-39, CF = 500 Hz, TH = 10 dB SPL) located in the ventral cochlear nucleus. B and C: PSTH/IH pair for 25-ms tones at 600 Hz and 60 dB SPL (near CF). D and E: PSTH/IH pair for a long tone (25 reps, 5/6 s) at 500 Hz and 60 dB SPL.
These two response patterns will be discussed in subsequent sections.

We found no clear-cut examples of O1 units in the unanesthetized cat. It should be noted that previous work from this laboratory (14) also found a very small number of O1 units in the anesthetized cat (9 units in 150 animals).

Response data from a typical O1 unit is displayed in Fig. 8. The response area (Fig. 8A) has a CF of 3,500 Hz, a dynamic range at CF of ~30 dB, and monotonically increasing rate-intensity functions at all frequencies. The short-tone response near CF (Fig. 8B) shows a very short pause after an initial peak, whereas the long-tone response (Fig. 8D) shows an initially high firing rate, which adapts after ~100 ms to a steady state. Interval histograms from both long and short tones at CF (Fig. 8, C and E) are similar to those obtained from primary-like units. Another characteristic feature of many O1 response areas is their skewed appearance; the frequency that elicits maximum firing rates is frequently different than CF. Responses at low frequencies (Fig. 8F) often showed strong phase locking with narrow modes spaced at multiples of the stimulus period with interval histograms (Fig. 8G), which were very narrow and nearly unimodal at sufficiently high intensities.

Oc units are responsive to a broad range of frequencies and have the largest dynamic ranges found in the cochlear nucleus. In contrast to the relatively limited (10–40 dB) dynamic ranges associated with most other cochlear nucleus neurons, dynamic ranges for Oc neurons can exceed 80 dB. A response area from one of these units is shown in Fig. 9A. Its isointensity curves form a uniformly increasing set, which show no sign of saturation at the highest intensity studied, 70 dB. Both the onset responses (first 5 ms) and the later response exhibit the wide dynamic range. Short-tone responses at CF (Fig. 9B) have multiple modes at stimulus onset, which characterize these neurons. Interspike interval histograms show a single narrow mode, which reflects the well-timed onset response (Fig. 9C). At higher intensities (not shown) interval histograms look more primary-like (asymmetric with exponential decay) as the proportion of spikes elicited at stimulus onset declines relative to later activity.

FIG. 11. Response area for an Oc (or type 4) unit in dorsal cochlear nucleus. The response data has been smoothed using a 3-point, symmetric filter with equal coefficients (83124-9, CF = 21,000 Hz, TH = 0 dB SPL, spontaneous rate = 22.2 spikes/s).
Units in the PVCN that exhibit the strongest phase-locking response can fire once for each cycle of a pure tone stimulus at frequencies as high as 1,050 Hz (14). A typical example of one such unit from the unanesthetized cat is shown in Fig. 10. This response area is skewed

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**FIG. 12.** Response area for an OIN unit in DCN with 3-point smoothing (83124-10, CF = 20,000 Hz, TH = 6 dB SPL, spontaneous rate = 94.7 spikes/s). B and E: PSTH/IH pair for short-tone characteristic frequency (STCF) at 10 dB SPL. C and D: PSTHs for STCF at 20 and 30 dB SPL. F: PSTH response for long tone (100 reps, 250/500 ms) at CF and 30 dB SPL. G: PSTH response for long tone (50 reps, 1/2 s) above CF at 21,500 Hz and 30 dB SPL.
toward higher frequencies so that the frequency that results in the greatest output is well above CF for intensities >20 dB. Isointensity curves above 40 dB show a nearly linear increase in firing rate with increases in frequency to ~800–1,000 Hz. The slope of this low-frequency increase is ~1 because firing rate is equal to stimulus frequency (one spike per cycle) during the steady state of each response. Although the neuron shown in Fig. 10 showed a sustained response at CF it is included in this section on onset neurons because it resembles Oo neurons in their ability to entrain to low-frequency stimuli. At higher frequencies this neuron showed Oo responses. This suggests that these neurons are more similar to Oo neurons than a classification based on responses at CF would suggest.

Short-tone response patterns (Fig. 10B) have very narrow modes of approximately equal height, which are separated by the period of the stimulus. Short-tone interval histograms (Fig. 10C) have a single very narrow mode with a mean equal to the stimulus period. Both histograms indicate a high degree of entrainment to short-tone stimuli and synchronization coefficients are as high as 0.96. Long-tone responses suggest that the firing rate of this neuron adapts over a 500-ms period to a steady state with a lower firing rate. Long-tone interval histograms (Fig. 10E) are more primary-like with several modes at integer multiples of the stimulus period which decline exponentially. This suggests that true stimulus entrainment breaks down for this unit after about 50 ms.

OIN responses
We have called units with an onset response followed by clear suppression of spontaneous activity OIN neurons (16). Units of this type are most commonly found in the DCN and are generally associated with type 4 responses areas (3, 19), which exhibit strong suppression except for low-intensity stimuli near CF. For example, in Fig. 11 only the 0 and 10-dB isointensity curves are above spontaneous levels. The CF of this unit appears to be 21,000

![FIG. 13. PSTHs for two onset-inhibitory units in dorsal cochlear nucleus. A: short-tone characteristic frequency responses of one unit at 80 dB SPL. B: response to long (100 reps, 350/700 ms) tones below CF at 4,000 Hz for the same unit (83178-22, CF = 7,500 Hz, TH = 20 dB SPL, spontaneous rate = 9.7 spikes/s). C and D: long (25 reps, 250/750 ms) tone responses at CF for another unit at 20 and 60 dB SPL (84104-51, CF = 9,000 Hz, TH = 10 dB SPL, SR = 24 spikes/s).]
FIG. 14. Swept-tone response of the onset-inhibitory neuron in Fig. 12 (83124-10) to a linear (triangular) modulating waveform. Only the high-to-low frequency sweep direction is shown. Constant voltage applied to phone, the indicated SPL is at the center frequency. The response to the other direction was similar, though not identical. A, B, and C: sweep period was 3 s for a series of increasing intensities. D: sweep period of 1 s at 20 dB SPL, the same intensity used in B. E: intensity at 60 dB SPL. Sweep rates and SPLs are indicated in each panel.
FIG. 15. A, B, and C: PSTHs for a pauser unit for short-tone characteristic frequency (STCF) conditions at 3 intensities. D: spike rate vs. intensity function at CF with the SPLs used in A, B, C indicated by left, middle, and right arrows, respectively. E: long (25 reps, 250/750 ms)-tone response at a frequency below CF. F: long-tone response at a frequency above CF. G: response area (84097-42, CF = 11,000 Hz, TH = 6 dB SPL, spontaneous rate = 50 spikes/s, dorsal cochlear nucleus).
Hz, although the 0-dB iso-intensity curve shows a peak at 28,000 Hz, which is not present at higher intensities. This region of excitation is flanked on both sides by strong inhibitory regions that become more and more dominant as intensity is increased.

Another example of an ON neuron that was analyzed in more detail is shown in Fig. 12. A narrow excitatory region at CF is most prominent at 10 dB. Inhibition is present above and below CF and is also present at CF for high-intensity stimuli. Rate-intensity curves are nonmonotonic near CF and decline monotonically at other frequencies. Short-tone responses at CF are sustained at 10 dB (Fig. 12B), develop an onset response followed by a short depression in activity at 20 dB (Fig. 12C), and show a maximal onset response and longer-lasting suppression at 30 dB (Fig. 12D).

Interval histograms at low stimulus intensities
have a primary-like appearance (Fig. 12E). Long-tone responses at 30 dB (Fig. 12F) indicate that full suppression lasts ~25 ms followed by a gradual recovery to spontaneous levels; at the end of the stimulus there is a transient depression in activity.

At frequencies away from CF, the majority of OIN neurons show only suppressive responses and have little or no onset peak. Figure 12G shows a response pattern from the above unit for a frequency slightly above CF. Inhibition appears to consist of an initial period of near total suppression followed by a recovery to a sustained level, which lasts for the remainder of the tone; recovery to the spontaneous rate is rapid when the stimulus is turned off. Examples of sustained suppression in which firing is completely eliminated for the duration of long-tone stimuli both below and at CF are shown for two other OIN units in Fig. 13, B and D, respectively. In Fig. 13B recovery of the spontaneous rate is seen to be more gradual than the recovery observed in Fig. 12G.

This unit also provides an example of an OIN neuron that shows a response peak shortly after short-tone stimulus onset, subsequent suppression, and then rebound activity shortly after the stimulus was turned off (Fig. 13A). Rebound activity of this type was not generally found. As for other OIN units, the unit shown in Fig. 13C had a sustained excitatory response at CF for low-intensity stimuli.

Swept tone responses obtained from OIN units usually show only a region of suppression without any excitatory response unless the in-
Intensity is <10–20 dB above the threshold of the unit. For example, the illustrated swept tone responses show excitation at 10 dB SPL (Fig. 14A), a restricted inhibitory zone at 20 dB (Fig. 14B), and a much broader region of suppressed responses at 30 dB (Fig. 14C). This unit’s response is also sensitive to sweep rate. A 20-dB swept tone with a duration of 1 s exhibits sidebands both above and below CF (Fig. 14D); when the sweep duration is increased to 3 s only inhibition at frequencies above CF are seen (Fig. 14B). When the sweep rate was made 10–100 times faster the inhibitory sidebands were missing at these low SPLs. However, if higher SPLs (>40 dB SPL) were used the sweep histogram had minima throughout, regardless of sweep rate suggesting a complex inhibitory input (Fig. 14E).

**Pauser responses**

The pauser response was one of the most frequently encountered in the DCN. Responses obtained from the neuron shown in Fig. 15 resemble responses obtained from most other pauser units with the exception of its offset responses. At CF this cell had a non-monotonic rate-intensity function (Fig. 15D). Response patterns at CF, which correspond to various points along this curve, show sustained responses just above threshold (not shown). At 20 dB (first arrow in Fig. 15D) an onset peak is prominent followed by a slight dip in the sustained component of the response (Fig. 15A). At 40 dB (second arrow) neural activity is completely eliminated for a period of ~10 ms after a pronounced onset response; this period of suppressed activity is followed by a
gradual increase in activity and a sharp offset response (Fig. 15B). At 60 dB (third arrow) the pattern is similar with a longer offset response consisting of two or possibly three modes (Fig. 15C).

The response area of this unit is shown in Fig. 15G. A high spontaneous rate (50 spikes/s) allows the visualization of inhibitory sidebands that limit the excitatory region at CF ($Q_{10} = 11$). Long-tone response patterns from these inhibitory regions show a sustained elimination of neural firing for the duration of the stimulus (Fig. 15E and F). Rate-intensity curves within these sidebands indicate that inhibition is first observed within 10 dB of threshold, becomes maximal at intermediate intensities, and then declines.

Some pauser responses have features in common with chopper neurons. For example, the pauser response illustrated in Fig. 16A has a prominent initial peak followed by a pronounced pause in activity; activity levels then resume with a multimodal pattern that is similar to the pattern observed for wide chopper units. The interval distribution associated with this response also resembles that of a chopper neuron with a single nearly symmetric peak (Fig. 16B). The long-tone responses (Fig. 16C) show an onset with a pause, but corresponding interval histograms (Fig. 16D) are less symmetric and suggest that the regular discharge rate is not preserved for long tones. This unit's response area (Fig. 16E) consists of a fairly regular set of monotonically increasing isointensity curves around CF. Inhibitory sidebands are present but are not as effective in limiting the excitatory region around CF as they are in the previous pauser unit (Fig. 15G).

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**FIG. 19.** A and B: PSTH/IH pair for a buildup unit in dorsal cochlear nucleus for short-tone characteristic frequency conditions. Modes in PSTH spaced 2.4 ms (420 Hz) apart. C: response area (84097-20, CF = 7,500 Hz, TH = 10 dB SPL, spontaneous rate = 2.7 spikes/s).
Another variation in the pauser response pattern is illustrated in Fig. 17. This unit had a response area (Fig. 17C) that was highly nonmonotonic near CF and had strong side inhibition. Short-tone responses at CF showed the pauser pattern but with a very weak onset response (Fig. 17A); an onset spike was elicited on less than half the trials. Long-tone responses (Fig. 17B) showed a clear "pause" in activity followed by a gradual buildup in activity with a sharp reduction in activity at stimulus offset. A response from a similar unit is shown in Fig. 17B. Both units suggest that it is sometimes difficult to distinguish pauser units from the buildup units discussed below.

**Buildup responses**

Buildup units are characterized by a gradual increase in activity over a relatively long period of time. For example, the long-tone response shown in Fig. 18A shows a continual buildup in firing rate, which is not complete at the end of the 250-ms stimulus. The corresponding interval histogram (Fig. 18B) is symmetric and quite broad with a mean interspike interval that is high because of the unit's low maximal discharge rate. The isointensity curves in the response area (Fig. 18C) are uniformly monotonically increasing except at CF. This unit had a -15-db threshold and a rate curve that peaked at 0 dB SPL. Another response area collected with short tones (25 ms) was strongly nonmonotonic throughout the response region, presumably due to latency effects.

A variation of the classical buildup response has a chopper pattern superimposed upon a gradual buildup in activity (Fig. 19A). The interval histogram reflects the period of the chopper pattern in its initial symmetric peak, but is unlike most chopper interval histograms in having several modes separated by the chopping period. This neuron appears to fire very regularly at approximately integer multiple of a fixed chopper period, which is considerably longer than the period of the stimulus. This is reminiscent of primary-like firing patterns in that there is a basic firing period which does not always elicit a spike. The response area of this unit is typical of the buildup category. Rate-intensity curves at, above, and below CF are monotonic. Inhibitory side bands are not observed for most buildup-unit response areas because these units generally have little or no spontaneous activity (Fig. 19C).

**Differences between responses in the anesthetized and unanesthetized cat**

To study the effects of anesthetic on PVCN and DCN response properties, comparisons were made between data obtained in this series of experiments in the unanesthetized cat and previous results obtained using barbiturate anesthesia under similar stimulus conditions in the same laboratory (13, 14).

Table 1 shows the relative proportion of the various unit types as characterized by their response patterns and the monotonicity of their rate-intensity curve at CF in both the PVCN and DCN. The most striking differences were observed in the DCN where the number of ON neurons increases from 5% in the anesthetized cat to 23% without anesthetic. Pauser neurons also increased but by a smaller margin, whereas the number of chopper neurons in the DCN decreased without anesthetic. The number of buildup responses remained about the same. Differences were generally smaller in the PVCN, although onset neurons decreased and choppers increased without anesthetic. In the DCN, nonmonotonic rate curves were twice as common without anesthetic. Strongly nonmonotonic responses were never observed in the PVCN.

Table 2 displays mean values and standard deviations in parenthesis for several descriptive

<table>
<thead>
<tr>
<th>Table 1. Response pattern frequency</th>
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<tr>
<td>ON</td>
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<td><strong>NM (DCN)</strong></td>
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Data for anesthetized cats were obtained from a previous study (13, 14). Nos. in parentheses are percentages. Primary-like units are excluded to avoid the problem of mixing data from auditory nerve fibers with other responses in the CN. NM is the percentage of nonmonotonic units found in each study. Categories that are not listed were not observed.
### TABLE 2. Comparison of descriptive parameters between unanesthetized and anesthetized conditions

<table>
<thead>
<tr>
<th>Parameter</th>
<th>PVCN</th>
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<th>DCN</th>
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<td></td>
<td>( C_C )</td>
<td>( O_L )</td>
<td>( C )</td>
<td>( C )</td>
<td>( P )</td>
<td>( B )</td>
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<td>( 23 )</td>
<td>( 22 )</td>
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<td>( \pm 23 )</td>
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<td>( \pm 44 )</td>
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<tr>
<td>( R_{\text{max}}, \text{ spikes/s} )</td>
<td>( 165 )</td>
<td>( 258 )</td>
<td>( 223 )</td>
<td>( 186 )</td>
<td>( 397 )</td>
<td>( 380 )</td>
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<td>( \pm 112 )</td>
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<td>( 1.0 )</td>
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<td>( 3.5 )</td>
<td>( 4.1 )</td>
<td>( 4.6 )</td>
<td>( 2.8 )</td>
<td>( 2.8 )</td>
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<tr>
<td>( \text{SD}_{\text{Hfh}} )</td>
<td>( 3.5 )</td>
<td>( 2.4 )</td>
<td>( 2.5 )</td>
<td>( 2.9 )</td>
<td>( 1.2 )</td>
<td>( 0.9 )</td>
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| \( \text{PTS} \) | \( 14 \) | \( 31 \) | \( 13 \) | \( 19 \) | \( 5.8 \) | \( 5.0 \) | \( \pm 8.4 \) | \( \pm 29 \) | \( \pm 4.6 \) | \( \pm 18 \) | \( \pm 4.9 \) | \( \pm 2.9 \) | \( \pm 2.7 \) | \( \pm 2.7 \) | \( \pm 4.1 \) | \( \pm 4.3 \) | \n
Values are means ± SD. Summary data for the anesthetized cat are from the study of Rhode and Smith (13, 14). PVCN, posteroventral cochlear nucleus; DCN, dorsal cochlear nucleus; OC, neurons that exhibit a weak chopper response after an onset peak; OL, neurons that respond primarily at stimulus onset followed by a sustained response; C, chopper; P, power; B, buildup; TH, threshold; SR, spontaneous rate; \( R_{\text{max}} \), maximum discharge rate in the last 60% of a stimulus across all intensities; DR, dynamic range; \( Q_{10} \), CF/BW where BW = bandwidth at 0 dB about threshold; Lat, first spike latency; \( SD_{\text{Lat}} \), standard deviation of first spike latency; \( \text{Mean}_{\text{Hfh}} \), mean of the interspike interval distribution; \( SD_{\text{Hfh}} \), standard deviation of the interspike interval; PTS, peak-to-steady-state ratio; \( n \), number of units. Onset-inhibitory units are omitted since few of the parameters are meaningful for them, e.g., \( \text{Mean}_{\text{Hfh}} \).
parameters used to characterize cochlear nucleus responses. To control for differences in the number of response types observed in the anesthetized versus the unanesthetized cat (see Table 1) values have been calculated separately for each response type. The most consistent findings were increases in spontaneous rate and threshold in all neuron categories except for choppers in the DCN. The maximum discharge rate decreased significantly for pausers and Ov neurons. The dynamic range was nearly the same except for Ov cells. Latencies were relatively unchanged though the standard deviation of the first spike latency increased in all categories. The apparent increases in tuning sharpness (Q10) for chopper, pauser, and onset neurons may be explained by the Q10 versus CF relation, since CFs were biased toward higher frequencies in the unanesthetized cats to avoid the problem of large field potentials at low frequencies, which were especially prominent when metal microelectrodes were used. Other parameter comparisons suggested little or no difference between anesthetized and unanesthetized conditions for the mean interspike interval, whereas the peak-to-steady-state ratio increased slightly in all but the onset categories.

A notable difference existed between choppers in the PVCN and DCN in the unanesthetized condition. PVCN choppers had double the threshold, triple the spontaneous rate, and a greater maximum discharge rate than those in the DCN. On the average, PVCN choppers also had shorter first-spike latencies. Differences between choppers in the DCN and PVCN were less striking under anesthetic.

**DISCUSSION**

*Effects of anesthetic on cochlear nucleus responses*

Our analyses suggest that all the major response patterns that have been observed in the anesthetized cat are also present in the unanesthetized cat, and vice versa. Primary-like, chopper, onset, buildup, and onset-inhibitory (OIN) histogram patterns are present in both preparations. Response area patterns are also similar, as are correspondences between the appearance of a unit's response area and its response pattern at CF. Monotonic and nonmonotonic rate curves are observed both with and without anesthesia, and frequency sweep responses and interval histogram patterns are similar for the two conditions.

The range and types of response patterns observed in the anesthetized and unanesthetized cat appeared to be similar, but there were differences in the relative proportion of units with a particular response pattern at CF. The most striking differences were in the DCN: chopper neurons in the DCN were half as common and OIN neurons were almost five times more prevalent without anesthesia. Other neuron types showed smaller differences, although the proportion of buildup units was nearly equal in the two preparations.

No marked differences in unit behavior were noted as a function of the day of the recording. Nor was any marked change in unit behavior noted while the animal was moving, purring, meowing, sleeping, or awake. Nevertheless we have the impression that the isointensity curves were noisier than those found in the anesthetized animal, a result which could be due to the above mentioned phenomena.

While the relative number of units in each response category appears to be related to anesthetic state, the possibility exists that these differences may have resulted in part from variations in sampling. For example, it is well known that units with specific response patterns are localized within particular subareas of the cochlear nucleus. If these subregions were not sampled uniformly in the two sets of experiments, one could explain some of the differences observed. Relative differences may also have resulted from differences in recording conditions. Under anesthesia it is possible to record unit activity with high-impedance (100 MΩ) glass micropipettes both intra- and extracellularly; without anesthesia lower-impedance (3–10 MΩ) metal and glass electrodes are required for stable extracellular recording. Since it is generally more difficult to record well-isolated unit activity with low-impedance electrodes, a relatively smaller number of well-isolated units may have been studied in the tightly packed fusiform cell layer of the DCN for the unanesthetized cat.

One way of reducing biases that result from an uneven sampling of the various unit types is to use analyses which quantitatively compare response parameters for units from a single response category. When analyses were performed individually for chopper, pauser,
buildup, and onset units the most striking effects of anesthetic state were: 1) a higher spontaneous firing rate for all four categories, 2) a larger standard deviation in the first-spike latency for all categories, and 3) 10-dB higher thresholds for pauser and buildup units in the unanesthetized cat. Some of these differences may be due to the fact that the animals can move about within their boxes, purr, and meow. Since the sound is being delivered quasi-free field, these background sounds may be affecting the population statistics. Other parametric comparisons suggested more varied effects of anesthetic state.

Although these parametric analyses control for the type of unit being studied there may still be some inherent problems. For instance, it is more difficult to study low-frequency responses in unanesthetized cats because low-frequency stimuli are frequently accompanied by synchronous potentials, which tend to obscure unit records. These synchronous responses are probably the result of the lower-impedance electrodes required for stable recording in the unanesthetized cat. This bias reduces the number of low-frequency units that can be studied in the unanesthetized cat and may explain some of the parametric differences observed for the two preparations. For example, differences in Q₁₀ values between anesthetized and unanesthetized cats probably result from this bias.

Responses from the auditory nerve of the unanesthetized cat

Responses obtained from monophasic records showed primary-like response patterns to short and long tones, response latencies nearly identical to those of auditory nerve fibers, had interval statistics which were polymodal, and had regular response areas which always showed monotonic increases in firing rate with increases in stimulus intensity at a given CF and did not have inhibitory sidebands. Thus it would appear that the response properties of auditory nerve fibers are similar for the anesthetized and unanesthetized conditions.

Comparisons with other work in unanesthetized cats

Despite the methodological biases inherent in making comparisons between anesthetized and unanesthetized animals, our results suggest that cochlear nucleus response properties are influenced by anesthetic state. Our results are in general agreement with previous studies using unanesthetized cats that were also decerebrated (3, 16, 19) but the effects due to anesthetic, which we observed in the unanesthetized nondecerebrate cat, were less dramatic than the effects observed in these earlier studies. This disparity may result from differences in experimental design and differences between the decerebrate and nondecerebrate preparations.

Evans and Nelson (3) found that the proportion of units they classified as type 4 or 5 increased from 8% under anesthetic to 70% in the unanesthetized cat, an approximately ninefold increase. Young and Brownell (19) didn't find any type 4 units in the DCN of the anesthetized cat, though a systematic study was not made, but commonly studied type 4 units in the decerebrate cat. The only comparable change observed in the present study was a fivefold increase in the percentage of type 4 or 5 units in the decerebrate cat. The only comparable change observed in the present study was a fivefold increase in the percentage of OIN cells from 5% under anesthetic to 23% without anesthetic; this increase was smaller than that observed by Evans and Nelson (3) and comprised a relatively small fraction of the total DCN population. Other response categories were much less influenced by anesthetic state.

When we reclassified our DCN units using Evans and Nelson's scheme (3) we obtained a similar result. While the proportion of type 4 units was greater in the unanesthetized compared with the anesthetized DCN, this increase was much smaller than that reported by Evans and Nelson; 19% of all DCN units were type 4 under anesthetic compared with 42% without anesthetic. We have not included type 5 units in this analysis because we encountered very few type 5 units in either preparation. This finding, which is in agreement with Young and Brownell (19), may have resulted from the relatively large frequency and intensity increments used in the study of Evans and Nelson (3). The only difference between type 4 and type 5 units is the presence of a small excitatory region near threshold in type 4 units. This region can easily be missed in response area data with large steps in intensity or frequency. Shofner and Young (17) report 27% of the units in DCN of Type IV (OIN or On-Off) responses. These authors (17) use a modification of Evans and Nelson's categories, which includes the response to noise.
Along similar lines, Evans and Nelson (3) suggest that strong nonmonotonic rate-intensity curves and predominately inhibitory response areas are found almost exclusively in unanesthetized animals. We found inhibition to be more common in unanesthetized animals but also commonly observed inhibitory influences under anesthetic. Quantitively, 42% of the DCN units we studied had nonmonotonic rate-intensity curves without anesthetic compared with 20% under pentobarbitol.

The DCN units that we studied had response areas which were relatively simple. We never observed clear multiple excitatory regions in a single cell, although Young and Brownell (19) describe several units in the DCN that have multiple excitatory regions. This disparity may result from differences in the way the two studies analyzed unit responses. To create response area data, we used 25-ms tones presented every 105 ms. When type 4 units were encountered, we also tried to obtain response area data using longer tones but were not always successful (although when we were successful we never saw multiple excitatory regions). In contrast, Young and Brownell (19) obtained response area data using 200-ms tones repeated every 1,000 ms. It is conceivable that multiple excitatory regions are more apparent using longer stimuli.

Their analysis also differs from ours in plotting the ratio between the perstimulus rate and the intertrial spontaneous rate (spike rate during the last half of the interstimulus interval) instead of the per-stimulus firing rate itself. Excitatory regions are defined as areas in which this ratio exceeded 1.2 and inhibitory regions as those with ratios smaller than 0.8. If the spontaneous firing rate of a neuron is constant during the data collection period and is unaffected by the effects of the previous stimulus, these two analyses should yield identical results. If not, normalizing the spike rate by the interstimulus spontaneous rate controls for fluctuations in the spontaneous rate during data collection and may therefore be a more sensitive indicator of the immediate effects of inhibition. On the other hand, this approach may create problems if the spontaneous rate between stimuli is affected by the cell's previous response to a stimulus.

Initial studies (19) suggested that the chopper response was either absent or greatly reduced in the DCN of unanesthetized decerebrate cats. In the present set of experiments, we found large numbers of chopper responses in the DCN of unanesthetized and anesthetized cats. This result agrees with other studies (17, 22), which also suggest that chopper responses are common throughout the PVCN and DCN of the unanesthetized cochlear nucleus. As Young and Brownell (19) point out in their initial study of the DCN, this discrepancy probably results from a stimulus paradigm that was not ideal for the demonstration of chopper responses. In particular, only long-tone responses were studied and the bin width used to create PST histograms may have been too large to view the chopper pattern. Recent experiments by Shofner and Young (17) included PST response patterns. They found 33% of the units in DCN to be choppers, which compares very nicely with the 30% we found.

Responses in the DCN

It was often difficult to distinguish pauser, buildup, and OIN neurons on the basis of their response patterns at CF, particularly when short-tone stimuli were used. For example, pauser and OIN neurons both have an onset response followed by a sharp decline in activity. The length of this period of reduced activity could vary dramatically so that pauser units with a long pause period may be mistaken for an OIN neuron unless very long stimuli are used. Similarly, buildup units resemble pauser units except for the absence of an onset response. These similarities between pauser, buildup, and OIN units suggest that it may be more appropriate to think of their responses as forming a continuum in which the time course of the inhibitory influences that shape poststimulus firing rates is varied. This suggestion is also supported by individual units which show pauser, buildup, and OIN unless very long stimuli are used. Similarly, buildup units resemble response patterns at different points of their responses areas.

Chopper responses were frequently observed in the DCN but differed somewhat from those studied in the PVCN in having wider modes. They have thus been termed wide choppers in contrast to the narrow choppers seen in the PVCN. Wide choppers had response areas, which showed varying degrees of side inhibition depending on the amount of spontaneous activity present. We observed a larger number of monotonic rate-intensity
curves at CF for the chopper population than for pauser and buildup neurons, although some nonmonotonicity was occasionally observed.

Several of the pauser and buildup neurons studied in the DCN had chopper-like properties in that a multiple peak pattern was superposed upon a pauser or buildup pattern. In fact, it was sometimes difficult to classify these neurons. These buildup and pauser units also resembled chopper units in their tendency to be monotonic at CF.

Inhibitory influences were more common in the DCN than in the PVCN. This is particularly true for the unanesthetized animal where 42% of the neurons in the DCN show nonmonotonicities at CF. As a result, many DCN neurons have restricted response areas in the frequency dimension and may therefore act as spectral filters. This is particularly true for those pauser, buildup, and O_{IN} neurons, which only respond to a narrow range of frequencies and over a 10–20 dB range of intensity near threshold. These neurons correspond to the type 4 neurons of Evans and Nelson (3). In general, DCN neurons have dynamic ranges that rarely exceed 30 dB and are very poorly phase locked. This suggests that they encode information in the intensity and temporal domains more poorly than the neurons in the PVCN.

The role of the cochlear nucleus in encoding acoustic information

In both anesthetized and unanesthetized animals, different neurons in the cochlear nucleus appear to encode different features of an acoustic stimulus. For example, the onset neurons in the PVCN appear to be ideal for encoding intensity and timing information. They have large dynamic ranges, precisely timed onset responses, and show the strongest phase locking in the cochlear nucleus. They appear to accomplish this by summing inputs over a wide frequency range and are therefore broadly tuned (14). In contrast, the strong inhibitory sidebands observed for the pauser and O_{IN} units of the DCN result in highly tuned response areas. The most striking example is seen in the type 4 response area, which shows little or no excitatory response except to low-intensity stimuli near CF. Compared with PVCN neurons, neurons in the DCN have relatively small dynamic ranges, show little or no phase locking, and exhibit relatively wide chopper patterns, which suggests that they are poor encoders of timing or intensity information. The primary-like responses recorded in the AVCN are particularly good encoders of temporal, intensity, or spectral information and have relatively simple response areas. These neurons probably relay information to cells in the superior olive, which receive acoustic input from both ears, and which may encode information related to the position of a sound source in space.

Anesthetic state does not appear to reduce the range of cochlear nucleus responses which are observed, but it does appear to influence them. In the DCN, the elimination of anesthetic can increase spontaneous activity, the magnitude of inhibition, and nonmonotonicities at CF. Overall, this results in better tuning in the frequency and the intensity domains and more complex response patterns in general. If these influences are present and modifiable in the behaving animal, they could be used to selectively filter acoustic inputs. On the other hand, if these processes are only seen under anesthetic, then some caution should be exercised when evaluating information obtained from anesthetized animals. This is particularly true for quantitative parametric data about cochlear nucleus response properties.

The neural mechanisms that cause changes in cochlear nucleus response properties when anesthetic is present are not known. They could result from a local influence within the cochlear nucleus, from influences originating in brain regions, which provide input to the cochlear nucleus, or both. For example, more than one neural process may produce inhibition in a single cochlear nucleus neuron. Caspary et al. (2) find that a glycine blocker will “convert” a nonmonotonic rate-intensity curve at CF to a monotonic one but does not affect the inhibitory sidebands. This suggests that some DCN neurons are influenced by more than a single inhibitory input.

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