Dynamic Range of Neural Rate Responses in the Ventral Cochlear Nucleus of Awake Cats

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SUMMARY AND CONCLUSIONS

1. Response thresholds and dynamic range properties of neurons in the ventral cochlear nucleus (VCN) of awake cats were measured by fitting a computational model to rate-level functions for best frequency (BF) tone bursts and for bursts of broad-band noise. Dynamic range measurements were performed in quiet and in the presence of continuous background noise.

2. The sample of neurons obtained in the VCN of awake cats exhibited a variety of peristimulus histograms (PSTHs) and thresholds. All PSTH response types previously described in the VCN of anesthetized cats were found in awake cats. The lowest thresholds for neural responses were observed at sound pressure levels that were equivalent to behavioral thresholds of absolute auditory sensitivity.

3. The response to BF tones or bursts of broad-band noise recorded in quiet backgrounds, the dynamic range properties of most units in the VCN of awake cats were not significantly different from dynamic range properties of auditory nerve fibers (ANFs) in anesthetized cats or VCN units in decerebrate cats. All auditory units showed a larger dynamic range for noise bursts than for tone bursts, but VCN units with primary-like and onset PSTHs showed larger dynamic ranges for responses to noise bursts than that of ANFs and VCN chopper units.

4. When tests were performed in the presence of continuous noise, rate-level functions for BF tone bursts shifted to higher tone levels and showed a more compressed range of driven rates in comparison with data obtained in quiet. Compression of the rate-level function in noise resulted from an increase in driven rate at low tone levels and a decrease in rate at high tone levels. These changes in the rate-level function suggest that noise may reduce the range of BF tone levels that are potentially encoded by a unit's rate responses. By exhibiting larger shifts and less compression in background noise, VCN units in awake cats better preserved the dynamic range of their rate responses to BF tones than ANFs in anesthetized cats or VCN units in decerebrate cats.

5. Rate-level functions were obtained from a small sample of VCN units not only with the cat performing the behavioral task but also with the cat awake and sitting quietly in the testing apparatus. No differences in noise-induced shift or compression were noted between the two testing conditions.

6. The dynamic range adjustments to noise exhibited by VCN units in awake cats are similar to changes in the rate responses of ANFs that are elicited in anesthetized cats by electrical stimulation of the crossed olivocochlear bundle.

INTRODUCTION

Most auditory nerve fibers (ANFs) exhibit a dynamic range of ≤35 dB when stimulated with tones at their best frequency (BF) (Palmer and Evans 1980; Sachs and Abbas 1974; Sachs et al. 1989; Schall and Sachs 1980). By dynamic range, we mean the range of stimulus levels over which a change in level produces a change in a neuron's discharge rate. The dynamic ranges of ANF rate responses are further reduced when tones are embedded in a continuous noise background (Costalupes et al. 1984; Winslow and Sachs 1987). Similar noise-induced reductions of dynamic range are seen in the rate responses of units in the ventral cochlear nucleus (VCN) (Gibson et al. 1985). In contrast to this electrophysiological evidence, human subjects can discriminate small-intensity changes over a 100-dB range of stimulus levels regardless of whether those changes occur in quiet or in background noise (Viemeister 1988).

The considerable dynamic range of human psychophysical performance suggests the existence of mechanisms for expanding the dynamic range of neural responses in quiet and for preserving dynamic range in the presence of background noise. One such mechanism may be provided by the olivocochlear effenter system (Liberman and Brown 1986; Warr 1975; Wiederhold and Kiang 1970). Winslow and Sachs (1987) showed that dynamic range lost in the presence of noise could be partially restored in anesthetized cats by electrical stimulation of the crossed olivocochlear bundle (COCB). Sound-evoked effenter activity may also contribute to the preservation of dynamic range in the absence of electrical stimulation because olivocochlear efferents respond to sound even in anesthetized cats (Liberman 1988). We hypothesized that sound-evoked effenter activity may exert an even greater influence on the dynamic range of auditory neurons in normally functioning cats than that which is produced in anesthetized cats by electrical or acoustic stimulation.

To test this hypothesis, we have developed a procedure for recording single-unit activity in the VCN of awake and behaving cats (May et al. 1991). We have used this procedure to study a number of the electrophysiological response properties of VCN units, including rate-level functions for BF tones in quiet and in the presence of background noise. When data from awake cats are compared with data obtained under similar stimulus conditions from anesthetized or decerebrate cats (Costalupes et al. 1984; Gibson et al. 1985), rate-level functions measured in noise show much less noise-induced dynamic range reduction for VCN units in awake cats than those obtained from anesthetized or decerebrate cats. Comparisons of our results with rate-level functions obtained from anesthetized cats during electrical stimulation of the COCB (Winslow et al. 1987) suggest that sound-
evoked efferent activity may preserve the dynamic range of hearing in noisy environments.

METHODS

In this report, the dynamic range of neural rate responses in the VCN of awake cats is characterized by measures applied to rate-level functions for BF tone bursts and bursts of broad-band noise. The effects of noise on dynamic range were measured by collecting rate-level functions for BF tone bursts in the presence of continuous background noise. Rate-level functions for awake cats were obtained while cats either engaged in a behavioral task or sat passively restrained in the testing apparatus between periods of behavioral testing. The general methods used to measure single-unit responses in behaving cats have been described elsewhere (May et al. 1991). Stimulus paradigms that are used to obtain rate-level functions and peristimulus time histograms (PSTHs) in anesthetized or decerebrate cats have been described in a number of publications from our laboratory (Blackburn and Sachs 1989, Costalupes et al. 1984, Gibson et al. 1985, Winslow and Sachs 1987). These same paradigms were used to obtain data from awake and behaving cats, except that behaving cats elicited stimuli by performing an operant task and those stimuli were delivered to the subject via a free-field acoustic system. The contingencies of behavioral tests are described below.

Animal selection and maintenance

Single-unit responses were recorded from six behaviorally trained cats. The cats were obtained at ~4–6 mo of age from Liberty Labs (Liberty Corners, NJ). On arrival, the cats were given an otoscopic examination to ensure that both ears were free of ear mites and excess cerumen and to confirm that both tympanic membranes were intact and translucent. Each animal participating in the study was maintained in our animal quarters for several months. During that time, subjects were trained to perform a behavioral task, surgically prepared for unit recording, and eventually studied with electrophysiological techniques. After the completion of electrophysiological measures, the subjects received a lethal injection of pentobarbital sodium and were immediately perfused transcardially. Brain tissue containing the experimental cochlear nucleus was examined under a light microscope to verify the location of recording sites. Electrode penetrations were identified by tears in the tissue, electrolytic lesions, and a distinctive pattern of gliosis.

Behavioral training

Behavioral training started immediately on a cat’s arrival in the laboratory and usually took 2 mo to complete. Cats were trained to initiate a trial sequence by depressing a response lever with the right front paw. A trial sequence began with 200-ms bursts of tone or noise repeated at a rate of 1 burst/s. Sound pressure levels of bursts in the sequence varied in random order. After a variable number of these long stimulus bursts, the duration of the stimulus was shortened to 50 ms and the repetition rate of the sequence was increased to 4 bursts/s. The cat obtained a nutrient reward by releasing the lever within 3 s after the change in the temporal pattern of the testing sequence.

Cats quickly learned to discriminate changes in the temporal pattern of the stimuli, and once trained would perform the task reliably during periods of behavioral testing that were interspersed throughout 1- to 2-h recording sessions. Because the discrimination task was based solely on temporal cues, other stimulus features could be freely manipulated in the course of single-unit recording. For example, the frequency of tone bursts could be adjusted to match the BF of any auditory neuron encountered along the electrode penetration, tone bursts or noise bursts could be used as stimuli, and the stimulus could be presented in noise.

Surgical preparation

Details of implantation procedures can be found in May et al. (1991). Cats were chronically implanted with two devices to allow recording of neural responses in the VCN. The first device was a titanium fastener that was attached to the top of the subject’s skull by three titanium screws inserted under the bone and up through the base of the fastener, and by six titanium screws that were inserted through the base of the fastener into the underlying bone. The fastener immobilized the subject’s head during electrophysiological recording and maintained a stable head orientation in our free-field testing apparatus. Once implanted, the fastener appeared as a small rod (12 mm length × 8 mm OD) protruding through the scalp.

The second chronic implant was a recording chamber made of acetal plastic (Dupont Delrin). Like the titanium head restraint device, the dimensions of the recording chamber were kept as small as possible (20 mm length × 10 mm OD) and appeared not to restrict the subject’s behavior outside of the testing environment. The recording chamber was stereotaxically positioned over a 7-mm fenestration in the parietal bone immediately posterior to the tentorium and centered 7 mm lateral to the midsagittal suture. The chamber was aligned 30° off the vertical axis in the parasagittal plane. This orientation allowed the chamber to guide microelectrodes in a ventral and rostral direction through the cerebellum and into the VCN along a path that was approximately parallel to the tentorium. Approximately six titanium screws were inserted into the skull around the perimeter of the chamber; methyl methacrylate dental acrylic was then applied to the screws and the base of the implant to bond the chamber to the surrounding bone.

Single-unit recording

Single-unit recording was performed with the cat suspended in a canvas bag at the center of a wire-mesh cage within a double-walled, sound-attenuating chamber. The cat’s head was immobilized by securing the chronically implanted head-restraint device to a connector on the ceiling of the cage. At the beginning of the recording session, the chamber was flushed with saline and fitted with an electrode holder (David Kopf Instruments). The electrode holder could be manipulated across a two-dimensional coordinate system to access all brain structures beneath the chamber. A platinum-iridium microelectrode, sheathed in a protective stainless steel tube, was inserted into the electrode holder and then manually driven ~1 cm into the cerebellum. A hydraulic micropositioner (David Kopf Instruments) was used to advance the microelectrode for the remainder of the penetration.

As the cat performed the behavioral task, the microelectrode was slowly advanced into the VCN. Noise bursts were used as search stimuli until an auditory unit with well-isolated spike activity was encountered; behavioral testing was then briefly interrupted as the unit’s BF and BF threshold were determined by sweeping the frequency and level of the acoustic stimulus. Next, PSTHs were collected by presenting 50-ms BF tone bursts (1-ms rise and fall time) at a stimulus level 30 dB above the unit’s BF threshold. A single PSTH was computed from the spike trains elicited by 300 repetitions of the short tone bursts. The collection of rate-level functions began immediately after the collection of PSTH data.

BF rate-level functions were obtained from a behaving cat by setting the frequency of tone bursts in the temporal discrimination task to the BF of the unit currently under study. The level of 200-ms tones in each testing sequence was varied pseudo-randomly, usually across a 90- or 100-dB range in 1-dB increments.
Rate-level functions were computed from the spike trains elicited by these tones. A maximum of twenty 200-ms tones was presented in each sequence. Consequently, the subject performed the task a minimum of five times to produce a complete rate-level function. After a BF rate-level function was obtained in quiet, rate-level functions were also obtained using bursts of broad-band noise in quiet and BF tone bursts in noise.

A cat participated in recording sessions 2 or 3 times/wk. Usually a recording session involved one electrode penetration, which lasted from 1 to 2 h. Recording sessions were repeated until it became difficult to obtain units in a cat or until 100 units were obtained.

Acoustic calibrations

Stimuli are presented through a free-field acoustic system in our studies of awake cats (May et al. 1991). To control the acoustic characteristics of the sound field, sound-reflecting surfaces in the sound-attenuating chamber were covered with sound-absorbing material (Sonex). Acoustic calibrations were made by placing a 0.5-in. Brüel & Kjær condenser microphone at the location occupied by the cat's head during electrophysiological testing. The frequency response of the acoustic system at this location is shown in Fig. 1.

Stimulus levels for tonal stimuli are expressed in decibels sound pressure level throughout this paper. Noise levels are expressed as decibels spectrum level re 20 \( \mu \text{Pa} \)/\( \text{Hz} \), or in decibels re noise threshold for individual units when the effects of noise are compared across different subject conditions. In the free-field condition, acoustic filtering properties of a cat's head and pinna may result in spectrum levels at the tympanic membrane that differ by \( \pm 50 \) dB from those measured in the free field (Musincant et al. 1990; Rice et al. 1992). Noise levels for all subject groups are specified in decibels relative to the noise threshold of the unit under study to compensate for these differences. This compensation allows meaningful comparisons for data obtained with the closed acoustic system in previous studies of anesthetized and decerebrate cats. However, even with this compensation, off-BF spectral properties of the noise background may differ across subject conditions.

Data analysis

Dynamic range measures of single-unit responses were calculated by fitting a computational model to rate-level functions. The rate-level model used in this analysis was developed by Sachs and Abbas (1976); a more recent version of this model was reported by Sachs et al. (1989). Model fits are computed by minimizing the mean squared error between rate-level functions generated by the model and actual electrophysiological data. Although the Sachs-Abbas model was originally intended for the analysis of electrophysiological data from cat ANFs, parameters of the model can be manipulated to provide good fits to monotonic rate-level functions obtained in the VCN.

The rate-level functions in Fig. 2 illustrate how dynamic range properties of neural rate responses were determined with the Sachs-Abbas model. The electrophysiological data in Fig. 2A are the rate responses of a VCN primary-notch unit to BF tone bursts. The PSTH used to classify this unit is shown in Fig. 3A. The stimulus-driven rates (\( \times \)) shown in Fig. 2 were computed from spike trains recorded during presentations of 200-ms stimuli in the context of the behavioral paradigm. The smoothed curve through the plot of the unit's stimulus-driven rate is the model fit to the data. All dynamic range measures were carried out on the model rate-level function. In this example, the model fit yielded a spontaneous rate (SR) of 8 spikes/s and a saturation rate of 365 spikes/s. The unit's maximum driven rate in quiet (\( QR_{\text{max}} \)) was defined as saturation rate minus SR; therefore, the \( QR_{\text{max}} \) of this unit was 357 spikes/s. The dynamic range of the neural response was defined as

\[
\text{Dynamic range} = L90_\text{Q} - L10_\text{Q}
\]

where \( L90_\text{Q} \) and \( L10_\text{Q} \) are the stimulus levels in quiet that produce discharge rates on the model rate-level function that are 90 and 10% of the unit's \( QR_{\text{max}} \). The \( L90_\text{Q} \) and \( L10_\text{Q} \) of this unit are 37 and 8 dB SPL, respectively. Therefore the dynamic range of the unit is 29 dB according to Eq. 1.

Figure 2B illustrates model data fit to a rate level function for broad-band noise. These data were obtained from the VCN onset unit that produced the PSTH shown in Fig. 3B. All unit types showed a larger dynamic range for noise bursts than for BF tone bursts, but onset units showed the largest dynamic range for noise of all unit types. The onset unit in Fig. 2B shows no indication of saturation at the highest levels of the noise rate-level function, although high levels of noise elicited relatively low driven rates from the unit. In this case, no accurate estimate of dynamic range is possible.

RESULTS

We have studied a total of 211 units in six behaviorally trained cats. These units exhibited no novel PSTH patterns and all of the major PSTH classes previously described in the VCN of anesthetized cats (Blackburn and Sachs 1989; Bourk 1976; Pfeiffer 1966). Representative PSTHs are shown in Fig. 3. Intracellular labeling of physiologically characterized cells indicate that primary-notch (Fig. 3A) and primary-like units (Fig. 3C) are found in the anteroventral cochlear nucleus (Rhode et al. 1983a; Rouiller and Ryugo 1984; Smith and Rhode 1987). Onset units are found in the posteroventral and dorsal cochlear nucleus (Fig. 3B; Rhode et al. 1983b; Rouiller and Ryugo 1984). Chopper units are found throughout the cochlear nucleus (Fig. 3, D and E: Rhode et al. 1983b; Smith and Rhode 1989). Rate-level functions for the units shown in Fig. 3 can be found in Figs. 2, 6A, 7A, and 9.

Dynamic range of neural rate responses in the VCN of awake cats was computed from rate-level functions that were obtained while the subject performed the temporal discrimination task or sat quietly in the apparatus. To evaluate the effects of the subject's behavioral state on electrophysiological responses, this paper compares data obtained from VCN units in awake versus behaving cats, as well as data from previous studies of ANFs in anesthetized cats.
FIG. 2. Computing dynamic range from model fits to electrophysiological data. A: rate-level function obtained for best frequency (BF) tones in quiet from a ventral cochlear nucleus (VCN) primary-notch unit (see Fig. 3A). Model data (——) were fit to stimulus-driven rates (×) using the model of Sachs et al. (1989). A dynamic range of 29 dB was calculated from the model fit using Eq. 1. B: rate-level function obtained for noise bursts in quiet from a VCN onset unit (see Fig. 3B). The responses of onset units to noise bursts showed the largest dynamic range in our sample of VCN units in awake cats. This unit did not saturate at the highest noise level tested.

(Costalupes et al. 1984; Winslow and Sachs 1987) and VCN units in decerebrate cats (Gibson et al. 1985).

Neural thresholds

Neural thresholds are shown in Fig. 4 for all of the VCN chopper, primary-like and onset units that we have currently sampled in awake cats. The neural threshold was defined as the BF tone level that elicited a discharge rate 10 spikes/s above spontaneous rate and was calculated from the model fit to the BF rate-level function. The BFIs of units in this sample reflect most of the audible frequency range of the cat. The units that responded best to a particular frequency region represent a range of PSTH response patterns and thresholds. The lowest neural thresholds were found for units with BFs between 7 and 10 kHz. Primary-like and chopper units showed a high degree of threshold variability, whereas data from onset units showed a lesser degree of variability and a tendency to cluster at higher thresholds. High-threshold values for onset units may be an artifact of our fixed 10-spk/s rate increase threshold criterion because onset units have much lower driven rates than primary-like and chopper units. The most sensitive VCN neurons had thresholds that compared reasonably well with behavioral measures of auditory threshold. However, any direct comparison of neural and behavioral thresholds is made difficult by differences in the paradigms used to collect data and in threshold criteria. For this reason, Fig. 4 presents three independent behavioral measures of the absolute threshold (Costalupes 1983; Heffner and Heffner 1985; Neff and Hind 1955).

Dynamic range of VCN units in quiet

The dynamic range of VCN units in a quiet testing environment is summarized in Fig. 5. Figure 5A compares the average dynamic range for all VCN units that we have studied in awake cats with representative data for VCN units in decerebrate cats (Gibson et al. 1985) and ANFs in anesthetized cats (Costalupes et al. 1984). Analysis of variance indicated no statistically significant difference between the three subject-state conditions. All subjects showed a larger dynamic range for noise bursts (mean 41.0 dB) than for tone bursts (mean 32.8 dB). This increase in dynamic range, which is related to a decrease in the slope of the rate-level function for noise relative to the slope of the rate-level function for BF tones [see Fig. 2], is presumably due to the effects of two-tone suppression (Schalk and Sachs 1980).

In Fig. 5B, the dynamic ranges of rate-level functions in quiet are compared for the three principal unit types found in the VCN of awake cats. Units characterized by primary-like, chopper, and onset PSTHs show no statistically significant difference in dynamic range for BF tone bursts. However, onset and primary-like units showed a larger dynamic range than VCN chopper units when rate-level functions were obtained using noise bursts as stimuli (Scheffé's S test; \( P < 0.001 \))\(^1\). Onset units showed the largest dynamic range for noise bursts of all units (52.4 ± 11.6 dB, mean ± SE), but the difference between onset and primary-like units did not attain statistical significance due to the relatively small sample size and high degree of variability for onset data.

Dynamic range of VCN units in noise

A continuous noise background exerts two major effects on the shape of BF rate-level functions. First, relative to the

\(^1\) The relatively conservative Scheffé's (1953) \( S \) procedure was selected for post-hoc comparisons because this analysis is very robust to tests involving unequal sample size.
function obtained in quiet, the function obtained in noise is shifted to higher stimulus levels. Strong evidence suggests that this horizontal shift results from two-tone suppression (Costalupes et al. 1984; Winslow and Sachs 1988). Figure 6 A illustrates a typical horizontal shift using BF rate-level functions in quiet and in 15-dB background noise from the VCN chopper unit shown in Fig. 3 D. The level of background noise is specified in decibels re noise threshold, which was determined for each unit by fitting the computational model to the unit’s noise rate-level function. As arrows in the figure illustrate, the midpoint of the steeply rising portion of the BF rate-level function is shifted to higher tone levels in the presence of noise. The magnitude of the noise-induced shift ($S_{no}$) is determined by Eq. 2

$$S_{no} = L50_{no} - L50_{q}$$

where $L50_{no}$ and $L50_{q}$ are the BF tone levels producing 50\% maximum driven rate in noise and in quiet. According to Eq. 2, a horizontal shift of 19 dB is calculated for the model data in Fig. 6 A.

Mean noise-induced shifts for rate-level functions of VCN units in awake cats are compared with data for ANFs in anesthetized cats and VCN units in decerebrate cats in Fig. 6 B. Means and standard errors reported in this figure and in Fig. 7 reflect the statistics of all data obtained within a 10-dB range of noise levels. The numerical value plotted on the abscissa of the figure refers to the upper limit of that range. Units in awake cats showed an increased shift of ~6 dB relative to units in anesthetized or decerebrate cats. Furthermore, responses to BF tones were not obtained from units in decerebrate and anesthetized cats at the highest levels of background noise shown in Fig. 6 B, because the
discharge rates of those neurons were driven to saturation by responses to the noise alone. Post-hoc comparisons of data from decerebrate and anesthetized cats indicated no difference in the magnitude of noise shifts, but a statistically larger shift was obtained for awake cats relative to both anesthetized cats ($P < 0.0001$) and decerebrate cats ($P < 0.0001$).

Mean noise-induced shifts obtained in awake cats for primary-like and chopper units are presented in Fig. 6C. Primary-like units exhibited larger mean shifts than chopper units in low levels of background noise, but no consistent differences were observed between the two unit types at high noise levels. Consequently, the difference in shift between the two unit types did not attain statistical significance when analysis of variance was performed on data for all noise levels. Data from onset units are not included in this analysis because we have yet to obtain a sufficient sampling of onset responses at different noise levels; however, noise-induced shifts for all of the primary-like, chopper, and onset units in our sample are shown in Fig. 8A. As suggested by the mean data presented in Fig. 6C, the primary-like units in this figure tend to show the largest shift at most noise levels, but there is a high degree of overlap between the distributions of shifts for primary-like and

FIG. 4. Neural thresholds for single-unit responses in the ventral cochlear nucleus (VCN) of awake cats. Symbols indicate the threshold and perstimulus time histogram (PSTH) classification of individual units ($n = 211$); lines indicate psychophysical measures of absolute auditory sensitivity. The most sensitive neural thresholds corresponded well to behavioral thresholds.

FIG. 5. Dynamic range properties of rate-level functions obtained for best frequency (BF) tone bursts and bursts of noise in quiet testing environments. $A$: mean dynamic range measures (mean ± SE) obtained for ventral cochlear nucleus (VCN) units in awake cats ($n = 144$), VCN units of decerebrate cats ($n = 26$), and auditory nerve fibers (ANFs) of anesthetized cats ($n = 69$). No significant difference was observed across the 3 subject conditions. $B$: comparison of dynamic range measures obtained in awake cats for VCN chopper ($n = 47$), primary-like ($n = 84$), and onset units ($n = 13$). Primary-like and onset units exhibited a larger dynamic range than chopper units for rate-level functions that were obtained with noise bursts.
chopper units. The shaded regions in Fig. 8, A and B enclose the range of noise-induced shift and compression exhibited by ANFs in anesthetized cats. These areas were calculated from the data of Costalupes et al. (1984) that is summarized in Figs. 5B and 6B.

The second effect of continuous background noise on the rate responses of an auditory unit is to compress the rate-level function relative to data obtained in quiet. In Fig. 7A, the calculation of noise-induced compression is illustrated for model fits to rate-level functions obtained from the VCN primary-like unit shown in Fig. 3C. Compression of the rate-level function in noise results in part from an in-
increase in activity at subthreshold levels of the BF tone. This activity reflects the unit’s sustained response to the noise background. Compression also results from a decrease in activity at high tone levels, which is presumed to reflect adaptation brought about by the noise response (Costalupes et al. 1984; Smith and Brachman 1980). Compression in noise ($C_{No}$) is calculated from the ratio of the maximum driven rates in noise ($NoR_{Max}$) and quiet ($QR_{Max}$) using Eq. 3

$$C_{No} = 100(1 - NoR_{Max}/QR_{Max})$$  \hspace{1cm} (3)

$NoR_{Max}$ is calculated by subtracting the unit’s noise-driven rate from its saturation rate in noise. The calculation of $QR_{Max}$ was previously described in Fig. 2A. The BF rate-level function in Fig. 7A shows 55% compression in the presence of high-level background noise (50 dB re threshold). In anesthetized cats, most ANFs fail to respond to BF tones at this level of background noise because the fibers are driven to saturation by the noise alone.

Mean noise-induced compression is compared across the three subject conditions in Fig. 7B. At intermediate noise levels, units in awake cats displayed 44% less compression than units in anesthetized cats and 23% less compression than units in decerebrate cats. At the highest noise levels, units in anesthetized and decerebrate cats were completely saturated by the noise response. In essence, units exhibit 100% compression under these conditions. The mean compression for VCN units in awake cats was statistically less than measures obtained in both anesthetized cats ($P < 0.001$) and decerebrate cats ($P < 0.01$). Noise-induced compression in awake cats for chopper and primary-like units is compared in Fig. 7C. Analysis of variance indicated no significant difference in noise compression between chopper and primary-like units. The substantial variability of compression scores for the two unit types is illustrated in Fig. 8B.

The effects of noise on rate responses in awake versus behaving cats

Cats often became satiated on liquid cat food and ceased performing the temporal discrimination task before a recording session was completed. When the cat failed to behave, data collection was continued using automated testing procedures for as long as the cat remained awake and quiet in the testing apparatus. Consequently, data for awake cats represent neural rate responses obtained from both awake and awake behaving cats. To test whether such changes in the subject’s behavioral state influenced dynamic range properties of single-unit responses, Fig. 9 compares rate-level functions in quiet and in four levels of background noise for a single VCN chopper unit that was tested using both behavioral and automated paradigms. The PSTH of this unit is shown in Fig. 3E. Data in Fig. 9A were obtained for BF tones presented in the context of the behavioral task; data in Fig. 9B were obtained under similar stimuluses using an automated procedure during an interruption in behavioral testing. No obvious differences were noted for rate-level functions obtained from this unit under the two subject-state conditions.\textsuperscript{2}

Figure 10 extends the comparison made in Fig. 9 to all VCN units studied with both behavioral and automated testing procedures ($n = 25$). The position of each unit in the two scattergrams is determined by the magnitude of

\textsuperscript{2} Low tone levels were not presented in loud background noise to behaving cats because the subject cannot perform the task when the tones are masked by the noise.
shift or compression in behavioral tests versus the magnitude of shift or compression under the same stimulus conditions in automated tests. As previously defined in Eq. 2, calculation of a unit's noise-induced shift is partially based on the BF tone level that drives the unit to 50% of its maximum rate in a noise background (i.e., $L50_{\text{no}}$). Figure 10A compares $L50_{\text{no}}$ values that were obtained for the same unit and noise level using both behavioral and automated testing procedures. The range of shifts shown in the figure was produced by varying the spectrum level of background noise from −15 to 25 dB. In general, units showing the smallest shifts were tested with the lowest level of background noise. Data points falling along the diagonal line in Fig. 10A show no difference in shift magnitude across the two testing conditions. As defined in Eq. 3, calculation of the compressive effects of a noise background was based on...
a unit's maximum driven rate in noise (i.e., \( \text{NoR}_{\text{Max}} \)). Figure 10B compares \( \text{NoR}_{\text{Max}} \) values obtained from VCN units using behavioral versus the automated testing paradigms. Paired \( t \) tests revealed no statistically significant differences in the magnitude of noise-induced shift or compression for units that were studied in both behaving and awake cats.

Data presented in Figs. 9 and 10 suggest that operant behavior is not a crucial determinant of dynamic range for single-unit responses in noisy backgrounds; however, these comparisons do not address questions that relate to the importance of psychophysical training. That is, are neural responses in an awake, untrained cat equivalent to those of a well-trained psychophysical observer? We cannot answer this question at the present time because our current studies of single-unit responses in awake cats involve only behaviorally trained subjects. Untrained cats do not tolerate the long periods of restraint required for single-unit recording.

**DISCUSSION**

Our studies of the cat's auditory nerve and cochlear nucleus suggest that there are a number of electrophysiological measures where no differences are observed between awake, anesthetized, and decerebrate cats. These measures include PSTH response types, tonotopic distribution of BF, and dynamic range properties of single-unit responses to tone and noise bursts in quiet backgrounds. The major exceptions to this similarity involve the effects of background noise on rate responses to BF tones. Units in the VCN of awake cats showed the ability to maintain the rate representation of BF tone level in high levels of background noise, whereas VCN units of decerebrate cats and ANFs of anesthetized cats were driven to saturation at moderate noise levels. 

**Measuring the effects of noise on rate-level functions**

In earlier studies of anesthetized cats and decerebrate cats (Costalupes et al. 1984; Gibson et al. 1985), the effects of noise on rate-level functions were determined by comparing measures of shift and compression for individual units at several levels of background noise. In our studies of awake cats, data were combined across units to determine the mean response of all units tested at a particular noise level. The advantage of the summary statistics shown in Figs. 6 and 7 is that a unit tested at only one level of background noise can be added to the data set. This is an important consideration for studies of awake and behaving cats, where unit isolation is not as stable as it is in anesthetized or decerebrate cats. The disadvantage of combining data in this manner is that summary statistics may obscure how each unit's response to the noise background relates to other physiological characteristics such as PSTH, best frequency, or spontaneous rate. Summary statistics also fail to show how sampling distribution may change with noise level. For example, 29 ANFs contributed to the mean response at the 10-dB noise level in Figs. 6B and 7B, but only 8 units were studied at the 50-dB noise level because all of the other ANFs in the sample were driven to saturation by the noise background. It is misleading to suggest that data from this small sample of units represent typical response properties of anesthetized ANFs. Using summary data to describe the effects of noise on neural rate responses may pose less of a problem for our study of VCN units in awake cats because different VCN unit types do not show statistically significant differences for the noise effects described in Figs. 6C and 7C. In addition, \( \geq 22 \) units contributed to mean values for all but the highest noise level presented in these figures. Only five units contributed to the mean shift and compression values at the intense 70-dB re threshold background noise. However, in contrast to ANFs in anesthetized cats, most VCN units in awake cats were not maximally driven by noise responses at this level. This sample was limited by the fact that no cats were tested at noise spectrum levels \( > 25 \text{ dB} \) to avoid acoustic trauma.

**Models of intensity discrimination**

Viemeister (1983) examined the ability of human subjects to discriminate changes in the intensity of high-frequency noise bursts in the presence of band-stop noise. This experimental design emphasizes the contribution of neural codes for intensity information that are based on rate changes by removing cues borne by temporal features of the neural response as well as minimizing cues borne by a "spread of excitation" to a larger population of neurons as the stimulus grows louder. Viemeister's subjects were able to discriminate 3-dB changes in the intensity of the noise burst over an 80-dB range of sound levels, a result that suggests that intensity discrimination is based solely on BF rate cues.

Models of intensity discrimination that rely on the average rate responses of ANFs have suggested that the dynamic range of auditory behavior may result from mechanisms that integrate rate information carried by more than one neuron. For example, VCN chopper units may enhance the neural encoding of synthetic speech sounds by selectively listening to low-threshold, high-SR auditory nerve fibers at low sound levels and to high-threshold, low-SR fibers at high sound levels (Blackburn and Sachs 1990; Wang and Sachs 1991). Even if inputs from different classes of ANFs are summed in the cochlear nucleus according to rules that optimize intensity discrimination, models based solely on BF responses fail to achieve the dynamic range of human psychophysical performance (Delgutte 1987; Viemeister 1988; Winslow and Sachs 1988). One of the questions that motivated our present study was whether or not the dynamic range properties of units in awake cats might be greater than those in anesthetized cats and therefore provide the dynamic range needed to make models of intensity discrimination more predictive of psychophysical performance. Data shown in Fig. 5 offer a negative answer to this question but still may have some bearing on an interpretation of intensity discrimination in notched noise. Although we do not know to what extent spread of excitation may occur in the band-reject noise testing condition, we do know that rate-level functions for BF tones are not fully compressed by background noise in anesthetized cats (Costalupes et al. 1984; Winslow et al. 1987), and there is even less compression in awake cats (May and Sachs 1992). Therefore it is likely that units with BFs in the pass band of the masking noise are capable of contributing to the discrimination of tones at the center of the rejection band.
The role of efferent feedback in the auditory processing of signals in noise

Our experiments with awake cats were designed to test the general hypothesis that efferent feedback can modulate the response of auditory units to acoustic signals in noise. In part, this hypothesis was founded on the previous behavioral research of Dewson (1968), who showed that speech discrimination in noise is adversely affected by COCB lesions. In a related electrophysiological study, Winslow and Sachs (1987) demonstrated that electrical stimulation of the olivocochlear efferent system can enhance the rate responses of ANFs to tones in noise. Figure 11 illustrates the effects of COCB stimulation on the rate-level functions of an ANF in an anesthetized cat. The solid line in Fig. 11A indicates the unit's rate responses to a 100-dB range of BF tone levels in a quiet background; dashed lines in both panels of Fig. 11 show the unit's BF rate-level function in the presence of background noise. Model fits to these data indicate that the rate-level function obtained in noise is shifted 12 dB and compressed 49% relative to data obtained in quiet. The solid line in Fig. 11B indicates the unit's rate responses to the same sequence of BF tone levels in the same level of background noise, but during electrical stimulation of the COCB. With efferent stimulation, the rate-level function in noise is shifted 17 dB and compressed 21% relative to data obtained in quiet. The increased shift and decreased compression that result from COCB stimulation are reminiscent of differences in dynamic range adjustments to background noise that were observed when the responses of VCN units in awake cats were compared with those of ANFs in anesthetized cats in Figs. 6B and 7B.

Figure 12 provides a more quantitative comparison of the effects of noise on the rate responses of VCN units in awake cats and ANFs in anesthetized cats during electrical stimulation of the COCB. In Fig. 12A, symbols indicate noise-induced shifts exhibited by the small sample of ANF rate-level functions shown in Winslow and Sachs (1987).

The methods used by Winslow and Sachs to estimate the magnitude of noise-induced shifts and compression were based on least-squares error analyses of normalized rate-level functions, and not a computational model. These methods are described by Costalupes et al. (1984). Each symbol compares the noise-induced shift obtained when an individual ANF was tested in the same level of background noise with and without COCB stimulation. The range of shifts shown in the figure was produced by performing comparisons for different ANFs at different levels of background noise. All fibers showed a slightly larger noise-induced shift with COCB stimulation. Our single-unit recording techniques do not allow us to compare rate responses from the same neuron with the cat awake and with the cat anesthetized. Instead, the solid line in Fig. 12A approximates this comparison by plotting the mean shift in background noise for VCN units in awake cats versus the mean shift exhibited by ANFs in anesthetized cats at the same noise level. This comparison is made at five levels of background noise (10–50 dB re threshold) using data from Fig. 6B. Relative to ANFs in anesthetized cats, VCN units in awake cats showed larger shifts at each noise level. In addition, the shifts exhibited by VCN units in awake cats were similar in magnitude to those observed for ANFs in anesthetized cats during COCB stimulation.

In Fig. 12B, symbols plot the magnitude of noise compression for ANFs in anesthetized cats with and without COCB stimulation. The solid line in this figure plots mean compression data shown in Fig. 7B for VCN units in awake cats versus ANFs in anesthetized cats. VCN units in awake cats show less noise compression than ANFs in anesthetized cats without COCB stimulation but similar compression values to those of anesthetized cats with stimulation. The similarity of noise-induced shifts and compression seen in awake cats and anesthetized cats during efferent stimulation suggest that dynamic range adjustments in the VCN are strongly influenced by olivocochlear efferents.

Efferent influences on the rate responses of VCN units

FIG. 11. The effects of crossed olivocochlear bundle (COCB) stimulation on noise-induced changes in the rate responses of an auditory nerve fiber (ANF) in an anesthetized cat [Winslow et al. 1987: unit 1.06, 01/31/84, best frequency (BF) 10.8 kHz]. A: BF rate-level functions obtained in quiet and in noise (0.0 dB SPL / Hz). The rate-level function obtained in noise exhibited a 12-dB shift and 49% compression relative to the function obtained in quiet. B: BF rate-level function in noise with and without electrical stimulation of the COCB. Efferent stimulation increased the magnitude of the noise-induced shift to 17 dB and decreased the magnitude of noise compression to 21%.
were determined in our study by comparing data obtained in awake cats with archival data obtained in anesthetized and decerebrate cats. Although the same stimulus parameters were used across all three subject conditions, stimuli were presented to awake cats using a free-field acoustic system and to anesthetized and decerebrate cats using a closed system (Sokolich 1977). An important difference between these paradigms is that the closed system stimulated only the ipsilateral ear of our anesthetized and decerebrate control groups, whereas the free-field system delivered stimuli to both ears of our awake cats. Binaural stimulation not only recruits contralaterally responsive olivocochlear efferent neurons (Liberman and Brown 1986), it also facilitates the responses of ipsilateral efferent neurons (Liberman 1988). Both of these binaural effects are important concerns in the interpretation of our own results because such increases in the level of efferent activity may enhance the auditory processing of tones in noise for our binaurally tested behavioral subjects but not for our monaurally tested control groups. Liberman and colleagues have recently shown that the addition of contralateral noise to the testing paradigm does improve the rate representation of ANFs for tones embedded in a noise background (Kawase and Liberman 1992). The most effective method for demonstrating this phenomenon is to present tones in low levels of background noise to the ipsilateral ear and relatively loud noise levels to the contralateral ear.

Figure 13 summarizes our own study of the effects of monaural versus binaural acoustic stimulation on the rate responses of ANFs in anesthetized cats. Our binaural paradigm differed from that of Kawase and Liberman in that our objective was not to maximize efferent effects by unequal stimulation of the two ears but rather to test anesthetized cats under closed binaural conditions that modeled the free-field tests experienced by our awake cats. This objective was achieved by presenting the same tone levels and background noise to both ears. The results of one of these tests are illustrated by data shown in Fig. 13A. The leftmost rate-level function was obtained in quiet; the two remaining functions were shifted to higher tone levels by the addition of continuous background noise (14-dB re noise threshold). One of these rate-level functions was obtained using monaural stimulation; the other was obtained with binaural stimulation. Binaural versus monaural testing produced no major changes in the degree of noise-induced shift or compression that was exhibited by this ANF.

The results of our monaural versus binaural tests in two untrained, anesthetized cats are summarized in Fig. 13B and C. In Fig. 13B, each data point represents the noise-induced shift for an individual ANF under monaural versus binaural conditions. For these data, the magnitude of the shift is indicated by the BF tone level that drives the unit to 50% of its maximum driven rate in the presence of background noise (i.e., \( L_{50_{\text{No}}} \)). The range of shifts shown in the figure was produced by testing at noise spectrum levels that varied from as low as -20 dB to as high as 20 dB. The difference between monaural and binaural \( L_{50_{\text{No}}} \) values was not statistically significant in paired \( t \) tests. Figure 13C summarizes measures of noise compression for the same sample of ANFs. For the comparison of binaural versus monaural compression effects, the magnitude of compression was indicated by a unit’s maximum driven rate in noise (i.e., \( NoR_{\text{Max}} \)). \( NoR_{\text{Max}} \) values obtained with monaural and binaural tests also failed to differ in a statistically significant manner. On the basis of these measures, it is unlikely that binaural stimulation made a substantial contribution to the enhanced dynamic range properties of auditory neurons in awake cats.
One important question is left unanswered by our study of neural responses in the VCN of awake cats: can the functional significance of efferent activity be derived by comparing single-unit data obtained in awake and behaving cats with data obtained in anesthetized or decerebrate cats? Single-unit responses in awake cats can provide an accurate assessment of normal efferent function, but do neural responses in anesthetized cats reflect minimal efferent influences or merely the failure to achieve optimal performance? Lesioning paradigms offer a more direct test of the role of efferent feedback in auditory processing, but these paradigms do not lend themselves very well to conventional electrophysiological studies, which usually test subjects for short periods of time under the influence of anesthesia (Liberman 1990). Long-term recording in behaviorally trained cats, on the other hand, can provide a useful technique for evaluating neural responses in awake animals before and after a lesion is placed in the nervous system. In particular, these techniques can be extended to studies of the effects of COCB lesions on the neural encoding of complex acoustic stimuli such as human speech. As Dewson’s (1968) behavioral study has already shown for speech discrimination, neural rate responses in the VCN of awake cats predict that olivocochlear efferents play a critical role in the neural representation of complex sounds in noisy environments.

We thank our colleagues J. Costalupes, D. Gibson, and R. Winslow for the use of data from their studies of noise effects on auditory responses in anesthetized and decerebrate cats. E. Young provided invaluable assistance in the conceptual and technical design of these experiments. C. Aleszczyk and D. Miller contributed greatly to surgical procedures, behavioral training, and data analyses.

Original research was supported by National Institutes of Health Grants NS-08333, DC-00023, and DC-00109.


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