Temporal representation of rippled noise in the anteroventral cochlear nucleus of the chinchilla

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This paper describes the temporal responses of anteroventral cochlear nucleus (AVCN) units in the chinchilla to rippled noises. Rippled noise is generated when a wideband noise is delayed and added (cos + noise) or subtracted (cos - noise) to the undelayed noise. Renewal densities were constructed to evaluate synchronous discharges at the delay. In response to rippled noise, AVCN units which show phase locking to best frequency (BF) tones give renewal densities having major peaks at the delay for cos + noise, but nulls at the delay for cos - noise. Most AVCN units which did not show BF phase locking gave renewal densities that did not contain features related to the rippled noise delay; a few of these nonphase-locked units did show peaks in renewal densities for both cos + and cos - noises. Synchrony at the rippled noise delay was also demonstrated with evoked potential recording. Autocorrelation functions of the neurophonic potential showed peaks at the rippled noise delay for both cos + and cos - noises. In addition, peaks could be observed in the autocorrelation functions of neurophonic potentials for rippled noises with delays as short as 1 ms; peaks were never observed in renewal densities of single units for ripple delays as short as 1 ms. The results show that a temporal representation of rippled noise delay does exist in the AVCN and are consistent with current hypotheses regarding functions of AVCN subsystems. The temporal representation of the delay is a presumptive neural code for the pitches of rippled noises.

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INTRODUCTION

Rippled noise has been used as a stimulus in a variety of psychophysical and physiological studies regarding frequency selectivity (Bilsen et al., 1975; Houtgast, 1977; Evans, 1977; Pickles, 1979; Pick, 1980; Narins and Evans, 1980; Dunia and Narins, 1989; Niemiec, 1991) and pitch (Bilsen, 1977; Yost and Hill, 1978, 1979; Yost et al., 1978; Fastl and Stoll, 1979; Yost, 1980, 1982; Buunen, 1980; Warren and Bashford, 1988). Rippled noise is generated when a broadband noise is delayed and added (cos + noise) or subtracted (cos - noise) to the undelayed noise. Thus rippled noise is an example of a stimulus plus its reflection, a situation that occurs in reverberant environments. In these natural settings, reflections that arrive at the listener for delays greater than approximately 25 ms are perceived as echoes, while reflections returning in less than about 25 ms result in a perceived "coloration" of the spectral quality of the stimulus (Berkley, 1987). In the laboratory under ideal conditions, rippled noises produce virtual or repetition pitches for delays between 0.5-20 ms (Yost and Hill, 1978). Given that rippled noises can produce identical pitches to those of other complex stimuli such as tone complexes (Fastl and Stoll, 1979), it is likely that the underlying mechanisms of pitch extraction are similar among complex sounds. Thus any model of pitch must be able to account for the pitches of rippled noises. The perceived pitches of rippled noises are related to the delay, and one model that predicts the pitches of rippled noises is based on the locations of the major peaks in the autocorrelation functions after the stimuli are filtered by a weighted output of the auditory periphery (Yost and Hill, 1979; Yost, 1982). This peripheral weighting model is a psychophysical model, and thus the neural basis for these predicted autocorrelation functions remains to be determined. An understanding of the neural coding of rippled noise is important in order to begin to address this question. As with other complex stimuli, the neural information regarding stimulus features of rippled noise is likely to be encoded in the auditory nerve by average firing rate and the timing of spikes. The putative rate and temporal codes are then processed in the cochlear nucleus where they can be degraded, preserved, or enhanced.

Temporal coding of the delay of rippled noise in the discharge of single auditory units has been previously studied in vertebrates. In this paper, temporal coding of the rippled noise delay refers to a phase-locked or synchronous discharge at the delay. For example, in goldfish saccular nerve fibers, major peaks occur in interval histograms at the delay in response to cos + noise, while nulls are observed in interval histograms in response to cos - noise (Fay et al., 1983). Similar results have been described for spike train autocorrelation functions of cat auditory-nerve fibers generated in response to cos + noise (ten Kate and van Bekkum, 1988). Given that a temporal code for rippled noise exists in the auditory nerve, is this temporal code preserved at the level of the cochlear nucleus? Boerger (1974) shows an example from one unclassified cochlear nucleus unit in the cat where a peak at the delay occurs in the autocorrelation function for cos + noise, and a null occurs for cos - noise, suggesting that a temporal representation of rippled noise may be found...
in the cochlear nucleus. The present study describes the temporal discharge patterns of physiologically characterized units in the chinchilla anteroventral cochlear nucleus (AVCN) in response to cos + and cos − rippled noises having delays known to produce the perception of pitch in humans. The data presented in this paper show that a temporal representation of rippled noise does exist in the discharge of units in the AVCN which can account for some, but not all of the pitches of rippled noises. Before the results of this study are presented, a discussion of the spectral and temporal properties of rippled noise is necessary.

A. Spectral and temporal properties of rippled noise

Figure 1 illustrates the spectral properties of wideband noise and rippled noise. Cos + rippled noise is generated by delaying a wideband noise and adding the delayed version of the noise to the undelayed noise. The resulting stimulus has a power spectrum that varies in a cosinusoidal fashion in which peaks in the spectrum occur at integer multiples of 1/delay. For example, cos + noise with a delay of 5 ms has spectral peaks at integer multiples of 200 Hz (Fig. 1). Cos − rippled noise is generated by inverting the delayed version of the noise before adding it to the undelayed noise (i.e., subtracting the delayed noise from the undelayed noise). For cos − noise, the spectral troughs occur at integer multiples of 1/delay; for a 5-ms delay, the spectral troughs occur at integer multiples of 200 Hz (Fig. 1).

It is most convenient to describe the autocorrelation function when discussing the temporal properties of rippled noise. Figure 1 also shows the autocorrelation functions for wideband noise and rippled noise. The autocorrelation function of the time-domain waveform of wideband noise is flat and shows no correlations at any delay. In contrast to wideband noise, the autocorrelation function of cos + noise shows a single peak (positive correlation) at the delay, while for cos − noise, there is a single null (negative correlation) at the delay. For a 5-ms delay, the autocorrelation function for cos + noise has a peak at 5 ms, while for cos − noise, there is a null at 5 ms (Fig. 1). Rippled noise autocorrelation functions show a single correlation at the delay in contrast to the autocorrelation functions of tone complexes which show multiple, periodic correlations. Thus rippled noise can be described as an aperiodic stimulus having a correlated waveform.

The correlation that exists in the waveform of rippled noise is also found in the envelope of rippled noise. Figure 2 shows the autocorrelation functions of the waveform fine structures and the envelopes of cos + and cos − rippled noises. In this example, the noise used is 2-kHz, high-pass noise. The envelope was extracted by half-wave rectification of the waveform, followed by low-pass filtering (see Schwartz, 1959). The cutoff frequency of the low-pass filter was 1 kHz. Cos + noise shows a positive correlation at the delay for both the waveform fine structure and the envelope. On the other hand, cos − noise shows a negative correlation in the waveform fine structure, but a positive correlation in the envelope. The oscillations that appear at the beginning of the waveform autocorrelation functions and the sidelobes that occur on either side of the peak/null reflect the 2-kHz, high-pass cutoff frequency of the noise. Likewise, the oscillations in the envelope autocorrelations reflect the 1-kHz, low-pass cutoff frequency. These oscillations and sidelobes are observed whenever rippled noises are bandpass filtered and reflect the bandwidth and center frequency of the filter (see Fig. 6 of Yost et al., 1978).

I. METHODS

Adult chinchillas weighing 450–760 g were anesthetized with intraperitoneal injections of sodium pentobarbital (65 mg/kg). Supplemental injections were given to maintain areflexia. Animals were tracheotomized and placed in a sound-attenuating room (Tracoustics). Body temperature was maintained around 37 °C. The left external meatus was transected, and the animal was placed in a modified Kopf stereotaxic headholder (Model 900). The ipsilateral bulla was exposed and opened. An opening was made in the temporal bone to expose the cerebellum in a similar manner to that described by Frisina et al. (1982).

Tungsten microelectrodes (Microprobe, Inc.) or indium-filled micropipettes (Dowben and Rose, 1953) were advanced through the cerebellum into the cochlear nucleus by a hydraulic microdrive (Kopf 650). Single units were recorded differentially with a second microelectrode placed in the frontal cortex. Differential recording eliminated the EKG.

Stimulus presentation and data acquisition were controlled by a MassComp 5400 computer system. Amplified action potentials were detected with a Schmitt trigger, and the trigger pulses were digitized through one channel of a 12-bit A/D converter (MassComp AD12FA) at a sampling rate of 50 kHz over a 1-s interval beginning at the stimulus onset. The times of occurrence of the trigger pulses relative to stimulus onset were determined on-line with 20-μs resolution and stored for off-line processing. In later experiments, the amplified action potentials were digitized through a second channel of the A/D converter at a sampling rate of 50 kHz and averaged on-line. The waveform of the averaged action potential was stored and used to establish the presence of a prepotential (Pfeiffer, 1966).

Acoustic stimuli were presented to the ipsilateral ear through either a Stax-SR5 earphone or in later experiments a Sennheiser HD 414 SL earphone. The earphone was enclosed in a shielded brass housing, which also held a calibrated probe tube microphone (Brüel and Kjær 4134). Search stimuli were presented as the electrode was advanced and consisted of 100-ms broadband noise or tone bursts at the best frequency (BF) of the background activity. Experimental stimuli were digitally generated by the computer and presented through a 16-bit D/A converter (MassComp DA04H) at a conversion rate of 50 kHz. The primary experimental stimuli consisted of wideband noise and rippled noises having delays ranging from 1–20 ms. This range of delays was chosen, because it corresponds to the range of delays which produce the most salient pitch perceptions in humans (Yost and Hill, 1978). In some cases, responses to low-frequency tones or harmonic tone complexes were evoked to compare to those obtained for rippled noises. In those instances, the period of the tone or tone complex was
FIG. 1. Spectral and temporal properties of wideband noise and rippled noise. Left-hand panels show the power spectra for the first 1.0 kHz of wideband noise and rippled noises with delays of 5 ms. Right-hand panels show the autocorrelation functions of the same wideband and rippled noises.
FIG. 2. Temporal properties of the fine structure and envelope of a 2-kHz high-pass noise and rippled noises generated from the high-pass noise. Left-hand panels show autocorrelation functions of the waveform fine structure. Right-hand panels show autocorrelation functions of the stimulus envelope. The envelope was extracted by half-wave rectification of the waveform followed by low-pass filtering at a cutoff frequency of 1 kHz. The DC component of the envelope was removed before autocorrelation was carried out.
equal to the delay of the rippled noise. The experimental stimuli used were either 400-ms bursts presented once per second or, more typically, 1-s bursts presented once every 2 s. In either case, rise/fall times of the experimental stimuli were 5 ms. The stimulus level was controlled by a programmable attenuator (Coulbourn S85-08).

When a unit was isolated, its BF and threshold were first determined using audiovisual cues. Post-stimulus time (PST) histograms were generated at 20–40 dB above threshold for 25-ms BF tone bursts having 2-ms rise/fall times which were presented once every 250 ms. PST histograms were generated for 250 stimulus presentations. In later experiments, the starting phase of the tone could be presented in a random or asynchronous manner. Interspike interval (ISI) histograms were generated for 100 presentations of a 400-ms BF tone; spikes that occurred during the initial 20 ms of the response were not included in the computation of the ISI histogram. Rate-versus-level functions for BF tones were generated over a 100-dB range in 1-dB steps with one presentation per level. Tone bursts for rate-level functions were 400 ms with 5-ms rise/fall times and were presented once per second. Rate was estimated over the entire 400-ms duration of the stimulus.

The sound level of the rippled noise was set such that typically 5000–10 000 spikes were produced over the 100 presentations of the stimulus. In order to compare the responses of a given unit across experimental stimuli, the sound levels were set such that the same approximate firing rate was evoked in response to the rippled noise stimuli presented. In practice, the sound level rarely had to be adjusted to evoke the same approximate firing rate in response to different rippled noises; however, the sound level of a tone or tone complex did have to be adjusted in order to evoke the same firing rate that was generated in response to rippled noise. Unit responses were studied over as many different rippled noise delays as possible given the limited recording time available. A complete analysis of a unit often took over 1 h; consequently, unit responses were rarely studied at different overall levels.

Temporal discharges of single cochlear nucleus units in response to rippled noises were evaluated using renewal densities. The renewal density has been referred to as the autocorrelation function of the spike train and is constructed by summing the distributions of first-order intervals and all higher-order intervals (Gerstein and Kiang, 1966; Moore et al., 1966; Perkel et al., 1967). Renewal densities were generated in response to 100 presentations of an experimental stimulus. Spikes that occurred during the initial 20 ms of the response to the rippled noise were not included in the computation of the renewal density. Renewal densities shown in this paper are scaled in terms of firing rate as described by Abeles (1982) and include three horizontal lines. The middle horizontal line in the renewal densities shows the expected mean firing rate and is equal to 1/mean ISI. The upper and lower horizontal lines in the renewal densities indicate the theoretical ± 2 standard deviations, respectively, if firing rate is assumed to be an independent Poisson process where the mean equals the variance. In this case, the standard deviation is simply computed as the square root of the mean. The upper and lower horizontal lines are approximately the 95% confidence limits (± 2 s.d.). The three horizontal lines should not be taken to imply any statistical significance, but are used only as a visual guide to evaluate the presence of peaks or nulls in the renewal densities.

Often a low-frequency neurophonic potential could be recorded in many of the experiments that this paper is based on. The neurophonic is thought to represent the ensemble synchronous or phase-locked activity of a local population of neurons (see Snyder and Schreiner, 1984). The presence of the neurophonic often prevented the isolation of spikes with acceptable triggering. In earlier experiments, the neurophonic potential was ignored; however, in later preparations, the neurophonic was studied in response to rippled noise. The neurophonic waveform was amplified 1200× and bandpass filtered from 30 Hz to 10 kHz with a Grass P511 amplifier and subsequently bandpass filtered from 30 Hz to 6 kHz with a Krohn-Hite 3550 filter. The neurophonic waveform was sampled at a rate of 50 kHz through a 12-bit A/D converter (MassComp AD12FA) and averaged in response to 100 repetitions of a 400-ms rippled noise stimulus presented once per second. The rise/fall times of the rippled noise stimuli were 5 ms. In order to evaluate the temporal properties of the neurophonic potential, a 16384 point autocorrelation was carried out on the steady-state region of the waveform between 40–368 ms using Interactive Laboratory System signal processing software (Signal Technology, Inc.).

The location of the recording tracks were verified histologically. Lesions were produced by a constant current source (Stoelting CS-4) for tungsten electrodes or an electrocautery device (Bircher Hyfrecator Model 733) for indium electrodes. The tissue was fixed in 10% formalin and frozen serial sections were stained with cresyl violet.

II. RESULTS

A total of 70 units were isolated from 12 chinchillas; the results in this paper are based on 39 AVCN units which were held sufficiently long enough to study their responses to rippled noise. In addition, the neurophonic was studied in three different electrode tracks from three chinchillas.

A. Neurophonic responses to rippled noise

An example of an averaged neurophonic waveform in response to cos + rippled noise with an 8-ms delay is shown in Fig. 3. The waveform in this example shows a strong onset response (Fig. 3, top panel), while the waveform in the steady-state region has a noiselike appearance (Fig. 3, bottom panel). Because the rippled noise waveform is the same for each stimulus presentation, the response of the recorded neuronal population is similar. Consequently, this synchronous response sums over each of the 100 presentations yielding an average waveform with a noiselike appearance. In this example, the electrical activity was again averaged for 100 presentations of the same cos + noise shown in Fig. 3 following the death of the animal. Note that there is no response resembling the stimulus waveform recorded from the dead animal (inset, Fig. 3) demonstrating that the wave-
FIG. 3. Waveform of an averaged neurophonic in response to cos + noise with a delay of 8 ms at 57 dB SPL. Upper panel shows the initial 100 ms of the neurophonic response illustrating the strong onset response. The dashed lines at ± 40 μV show the range of amplitudes in the lower panel. The lower panel shows the entire duration of the neurophonic waveform. The inset shows the averaged response recorded in the dead animal.

form which was previously recorded is not stimulus artifact, but does reflect neural activity recorded within the cochlear nucleus. Averaged neurophonic waveforms were obtained for wideband noise and for cos + noises having delays of 1, 2, 4, 5, 8 ms and for cos - noises having delays of 4 and 8 ms.

The autocorrelation functions for neurophonics in response to cos + noise with an 8-ms delay are compared to the autocorrelation functions in response to wideband noise in Fig. 4. The autocorrelation functions for the wideband noise condition are not completely flat, but tend to oscillate around zero. These oscillations presumably reflect the filter characteristics of the local neuronal population contributing to the neurophonic in response to wideband stimuli (see Ruggero, 1973). The oscillations in the autocorrelation functions can also be observed for the cos - noise condition, but there is also a large peak in the autocorrelation functions at the 8-ms delay for the cos + noise relative to the wideband noise. Figure 5 shows the autocorrelation functions for neurophonics in response to cos + noise with a 1-ms delay. For this stimulus, a small, but distinct peak can be seen at the 1-ms delay for the cos + noise relative to the wideband noise. Note for the cos + noise conditions that the heights of the peaks at 1 ms are smaller than those for the 8-ms delay relative to the wideband noise at those delays. For cos - noise with 8-ms delay, peaks at the delay were observed in neurophonic autocorrelation functions from all three chinchillas; for the cos + noise with 1-ms delay, peaks in the neurophonic autocorrelation function were observed for two of the three recordings. In the third chinchilla, a peak at 1 ms was not observed in the neurophonic autocorrelation function for 1-ms cos + noise.

A comparison of the autocorrelation functions for cos + and cos - noises having delays at 4 ms are shown in Fig. 6. For both the cos + and cos - noises, there are peaks in the autocorrelation functions with respect to the wideband noise condition at the 4-ms delay. A null at the delay in
the neurophonic autocorrelation functions was not observed for any of the cos–noise conditions studied.

**B. Single unit responses to rippled noise**

For the purposes of this paper, units fall into two general categories based on whether the patterns of their renewal densities show features related to the delay of rippled noise. Forty-one percent of the units studied (16/39) either show flat renewal densities in response to rippled noise or have features in the renewal densities that are not related to the delay of rippled noise. The BFs of these units ranged from 0.17–14.7 kHz. Based on the PST histograms to short tone bursts and ISI histograms to long tone bursts at BF, these units are classified as irregular choppers, regular choppers, unusual, or primarylike with a notch. Also included in this group are three onset units having BFs from 2.45–3.24 kHz which did not give strong sustained responses to rippled noise. The renewal densities of these onset units in response to rippled noise do not show features related to the delay; however, because of the low firing rates, not enough spikes are generated to construct meaningful renewal densities. The response property common among this group of units is the absence of phase locking to BF tones. Although this category of units does not show features in the renewal densities related to the delay of rippled noise, these units can show phase locking to the periods of low-frequency tones or harmonic tone complexes for periods equal to the rippled noise delays previously tested.

Fifty-nine percent of the units studied (23/39) did have features in the renewal densities in response to rippled noise that are related to the delay, and these units fall into two general groups. One group of units (18/23) have BFs ranging from 0.16–3.1 kHz. These units typically show phase locking in response to BF tones as measured by PST histograms in response to BF tone bursts with synchronous starting phases or as measured by ISI histograms to BF tones.

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**FIG. 5.** Autocorrelation functions of averaged neurophonic potentials in response to wideband noise (WBN, dashed line) and cos+ noise with a 1-ms delay (solid line).

**FIG. 6.** Autocorrelation functions of averaged neurophonic potentials in response to wideband noise (WBN, dashed lines) and cos+ noise (solid line, upper panel) and cos–noise (solid line, lower panel) with delays of 4 ms.
The one exception was a primarylike notch unit having a BF of 3.1 kHz which did not show evidence of phase locking based on the methods used in this paper. For the remainder of this paper, this category of units will be referred to as the phase-locked group. In some cases, primarylike or primarylike with a notch PST histograms could be generated in response to BF tones presented with random starting phases. Four of these units showed a prepotential in the averaged spike waveform. Figure 7 shows an example of a unit with a BF of 1.14 kHz in which features in the renewal densities can be found related to the delay of the cos + rippled noise. The top panels show the PST and ISI histograms in response to BF tones. The PST histogram generated at 40 dB above threshold for BF tones presented with random starting phase shows that this is a primarylike unit; the peaks in the ISI histogram occurring at integer multiples of approximately 0.88 ms indicates that the unit shows phase locking to BF tones. The temporal discharge of the unit in response to wideband noise and cos + rippled noises having delays of 1, 2, 4, 8, and 10 ms are shown in Fig. 7. Note that for the wideband noise condition, there is an oscillation in the renewal density that damps out after three cycles. This oscillation occurs at a period of approximately 1/BF reflecting the filter properties of the unit and is similar to responses of auditory-nerve fibers to wideband noise (Ruggiero, 1973). This oscillation is also observed in the renewal densities for cos + noise with 1- and 2-ms delays; that is, the renewal densities generated in response to cos + noise with 1- and 2-ms delays do not appear to be different from the wideband noise renewal density. This suggests that the temporal discharge patterns of this unit in response to wideband noise, cos + noise with a 1-ms delay and cos + noise with a 2-ms delay are identical. In contrast, the renewal densities in response to cos + noise having delays at 4, 8, and 10 ms show (1) an additional oscillation of 1/BF around the appropriate delay and (2) a peak at the appropriate delay. Thus this unit does encode the delays of 4, 8, and 10 ms of cos + rippled noises in its temporal discharge patterns.

Figure 8 shows examples of rippled noise responses from another unit from the phase-locked group. This unit has a BF of 0.58 kHz, and the BF PST histogram shows a strong phase-locked discharge pattern in response to a BF tone presented with synchronous starting phase. When the starting phase of the BF tone is randomized, the PST histogram shows a primarylike discharge pattern. The inset indicates that a prepotential is present in the action potential waveform. The middle panels show the renewal densities of this unit in response to cos + and cos − rippled noises having delays of 4 ms. There is a clear peak at 4 ms in the renewal density for the cos + noise condition, and a clear null at 4 ms for the cos − noise. An oscillation having a period of approximately 1/BF can be seen around the 4-ms delay in both the renewal densities. The bottom panels in Fig. 8 show the renewal densities computed from the same spike train after the intervals had been randomly shuffled. Because the renewal density is the sum of the first-order and all the higher-order interspike intervals, correlations that exist among higher-order intervals will contribute to the peak or null at the delay. Random shuffling of the intervals should remove any correlations that exist among higher-order intervals, but does not affect the first-order ISI distributions (Moore et al., 1966; Perkel et al., 1967). In the shuffled renewal densities in Fig. 8, there is a slight reduction in the heights of the peak and null, suggesting that correlations among higher-order intervals do not contribute greatly to the response.

The second category of units (5/23) which show features in the renewal densities related to rippled noise delay have BFs ranging from 1.10–5.12 kHz and are classified as chopper and unusual units. In contrast to the phase-locked units, this group of units typically do not show phase-locking to BF tones. The one exception was a unit with a BF of 1.10 kHz that showed a chopper PST histogram in response to short BF tones presented with random starting phases. Although the BF ISI histogram of this unit showed some weak phase locking, its coefficient of variation (CV) was 0.42, which is typical of regular chopper units (Shofner and Dye, 1989). The renewal densities for this nonphase-locked group of units are characterized by peaks at the delay for both cos + and cos − noise and do not show oscillations around the delay as previously described for the phase-locked units. Figure 9 shows an example of a chopper unit with a BF of 5.12 kHz. The CV of the ISI histogram for a BF tone was 0.67 suggesting that this is an irregular chopper (Shofner and Dye, 1989). The renewal densities generated in response to cos + and cos − noises having 8-ms delays are shown; for both the cos + and cos − noises, broad peaks can be observed in the renewal densities around the 8-ms delay. In this example, random shuffling of the ISIs clearly decreases the heights of the peaks, suggesting that for this unit, correlations among higher-order intervals do contribute to the peak. The decrease in the height of the peak shown in Fig. 9 illustrates one of the most drastic reductions observed after random shuffling of the ISIs.

Casual examination of the renewal densities for the present sample of AVCN units suggests that units with low BFs show stronger temporal responses to the rippled noises than do units with higher BFs. In an attempt to quantify this, the strength of synchrony at the delay for cos + and cos − noises with delays between 4–20 ms were measured. A delay of 4 ms was chosen as a lower boundary, since peaks or nulls in the renewal densities for 1- to 2-ms delays were not observed. In addition, because an oscillation of 1/BF at the delay generally was found in the renewal densities of phase-locked units, simply evaluating the height of a peak or null did not fully capture the magnitude of the temporal response. Therefore, the magnitude of the temporal response at the delay was measured from renewal densities as the root-mean-squared deviation in firing rate in a 2-ms window centered at the delay. The root-mean-squared value was then normalized to the mean firing rate and is referred to as Z. Thus Z represents the effective change in firing rate at the delay from the expected mean firing rate. In addition, the CV was computed from empirical spike count distributions generated in response to rippled noises and was expressed in terms of firing rate rather than counts. Expressed in this manner, CV represents the expected change in firing rate from the expected mean firing rate due to variability in discharge alone. Values of Z and CV were computed for all
FIG. 7. Temporal responses of AVCN unit to cos + noise. BF is 1.14 kHz. Upper left-hand panel shows PST histogram in response to BF tones presented with asynchronous starting phases at 40 dB above threshold. Discharge pattern is primarily like. Upper right-hand panel shows ISI histogram generated from BF tones at 30 dB above threshold. Multiple peaks indicate a phase-locked response to the 1.14-kHz tone. Remaining panels show renewal densities generated in response to wideband noise (WBN) and cos + rippled noises having delays of 1, 2, 4, 8, 10 ms. The average firing rates in response to the noises are around 100 spikes/s and are shown by the solid horizontal line; the dashed lines are approximate 95% confidence limits and represent ± 2 standard deviations assuming an independent Poisson process (see discussion in Sec. I). Also note the oscillations that occur in the firing rate having a period of about 1/BF. Bin width for PST histogram is 200 μs; bin width for ISI histogram and renewal densities is 100 μs.
FIG. 8. Temporal responses of AVCN unit to \( \cos^+ \) and \( \cos^- \) noises. BF is 0.58 kHz. Upper left- and right-hand panels show PST histograms in response to BF tones at 30 dB above threshold to synchronous and asynchronous starting phases, respectively. PST histogram to asynchronous starting phases shows a primarylike discharge pattern. Inset in upper left-hand panel shows the presence of a prepotential in the action potential waveform. Middle left-hand panel shows renewal density generated in response to \( \cos^+ \) noise with a delay of 4 ms. Note the peak at the 4-ms delay. Middle right-hand panel shows renewal density generated in response to \( \cos^- \) noise with a delay of 4 ms. Note the presence of a null at the 4-ms delay. Bottom left- and right-hand panels show renewal densities for \( \cos^+ \) and \( \cos^- \) noises, respectively, generated after the first-order ISIs were randomly shuffled. Average firing rates are 46 spikes/s in response to \( \cos^+ \) noise and 45 spikes/s in response to \( \cos^- \) noise. Bin width is 200 \( \mu s \) for PST histogram and 100 \( \mu s \) for renewal densities.
FIG. 9. Temporal responses of AVCN unit to cos + and cos − noises. BF is 5.12 kHz. Upper panel shows PST histogram generated in response to BF tones at 40 dB above threshold. PST histogram shows a chopper discharge pattern. Coefficient of variation of the BF ISI histogram (not shown) is 0.67, suggesting that this is an irregular chopper unit. Middle left-hand panel shows renewal density generated in response to cos + noise having a delay of 8 ms. Note the broad peak around the 8-ms delay in the renewal density. Middle right-hand panel shows the renewal density generated in response to cos − noise having a delay of 8 ms. Again, note the broad peak around the 8-ms delay in the renewal density. Bottom left- and right-hand panels show renewal densities for cos + and cos − noises, respectively, generated after first-order ISIs were randomly shuffled. The average firing rates are 109 spikes/s for the cos + noise and 117 spike/s for the cos − noise. Bin width is 200 μs for PST histogram and 100 μs for renewal densities.
phase-locked and nonphase-locked units which showed features in the renewal densities related to the rippled noise delay. For those units in which temporal discharge patterns were studied in response to both \( \cos^+ \) and \( \cos^- \) noises, a two-tailed \( t \) test was carried out on the distributions of computed \( Z \) values. There was no significant difference between the mean value of \( Z \) computed for \( \cos^+ \) noise and that computed for \( \cos^- \) noise; consequently, \( Z \) values were pooled for \( \cos^+ \) and \( \cos^- \) noise.

Figure 10 shows \( Z \) and \( CV \) as a function of BF for phase-locked units. There is a decrease in \( Z \) as BF increases with the largest \( Z \) values occurring for units having BFs less than approximately 1.5 kHz. In contrast, \( CV \) remains roughly constant across BF at a value around 0.1. The strength of synchrony can be computed as the difference between \( Z \) and \( CV \); the value of \( Z \) minus \( CV \) represents the effective change in firing rate at the delay above that expected due to variability in discharge alone. Figure 11 compares the measured synchrony (\( Z-CV \)) as a function of BF for phase-locked and nonphase-locked units. Synchrony decreases as BF increases with the strongest synchrony values obtained for phase-locked units with BFs less than about 1.5 kHz. No relationship was observed between synchrony and delay for the delay values of 4–20 ms.

Finally, as previously illustrated in Figs. 8 and 9, correlations among higher-order intervals may contribute to the magnitude of the temporal response at the delay in the renewal densities. In an attempt to quantify the amount these correlations may contribute, values of \( Z \) were computed from renewal densities of unshuffled and shuffled spike trains. A two-tailed \( t \)-test was carried out on the difference in \( Z \) following random shuffling for phase-locked and nonphase-locked units. There was no significant difference in the mean change in \( Z \) due to shuffling between phase-locked and nonphase-locked groups suggesting that contributions from correlations among higher-order intervals are the same for both groups of units. Values of \( Z \) obtained before and after interval shuffling are shown in Fig. 12 for all units which show features in the renewal densities related to the rippled noise delay. A linear regression through the origin results in a line with a slope of 0.83. Thus, on average, the value of \( Z \) computed after randomly shuffling of the intervals is 83% of the original value and suggests that correlations among higher-order intervals contribute 17% to the temporal response in the renewal densities at the rippled noise delay.

### III. DISCUSSION

The primary result of the present study is that a temporal representation of the delay of rippled noise does exist at the level of the AVCN. Temporal encoding of the delay in the spike train of single units was evaluated using renewal densities rather than period histograms or ISI histograms. Synchronization as measured from period histograms cannot be used to evaluate the temporal coding of rippled noise, because as previously described, rippled noise is an aperiodic stimulus (see Figs. 1 and 2). The renewal density shows the probability of discharge following an action potential (Moore et al., 1966; Perkel et al., 1967); that is, the renewal density shows the average firing pattern following a spike. The advantage of the renewal density over the ISI histogram is that the representation of the probability of discharge in terms of firing rate in the renewal density allows the mean rate and confidence intervals to be included which makes the presence of peaks or nulls easier to evaluate visually in renewal densities than in ISI histograms. The heights of the peaks or nulls in autocorrelation functions represent the magnitude of the correlation at a particular delay. In the present study, the magnitude of synchrony at the delay was quantified in renewal densities by computing a root-mean-squared deviation in firing rate around the delay. The root-mean-squared deviation in firing rate around the delay is given by:

\[
\text{RMSE} = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} (y_i - \bar{y})^2}
\]

where \( y_i \) is the firing rate at delay \( i \), \( \bar{y} \) is the mean firing rate, and \( n \) is the number of delays.

FIG. 10. Comparison of the values of \( Z \) and values of the coefficient of variation (CV) as a function of BF for phase-locked units measured in response to rippled noises having delays of 4–20 ms. Open squares show data points for \( Z \); closed squares show values for CV. The heavy solid line is a second-order regression through the values of \( Z \): \( y = 0.88x^2 - 0.497x + 0.854; r = 0.774 \). The dashed line is a linear regression through the values of \( CV \): \( y = -0.009x + 0.124; r = 0.155 \).

FIG. 11. Synchrony (defined as \( Z-CV \)) as a function of BF for phase-locked units (open squares) and for nonphase-locked units with peaks at the delay (closed squares). Delay values of the rippled noises are 4–20 ms.
The mean-squared deviation in firing rate was used to measure synchrony, because the temporal response of phase-locked units was characterized by an oscillation at the delay in addition to a peak or null. Measured in this manner, synchrony is the variation in instantaneous firing rate from the mean firing rate at the delay. Random shuffling of the intervals should remove correlations that exist among higher-order intervals, but will not affect the distribution of first-order intervals (Moore et al., 1966; Perkel et al., 1967). Theoretically, random shuffling will allow an estimate of synchrony at the delay encoded in first-order intervals. Random shuffling of ISIs reveals that most (approximately 83%) of the synchrony at the delay is attributed to first-order intervals.

In mammals, not all auditory neurons are capable of encoding the delay of rippled noise in the temporal discharge patterns. Boerger (1974) found 6/49 cochlear nucleus units encoded the rippled noise delay, while ten Kate and van Bekkum (1988) found 20/30 auditory-nerve fibers encoded the delay. In the present study, 23/39 AVCN units were found to be able to encode the delay in their temporal discharge. What is common among these three studies is that the upper limit of BF densities for auditory units which can encode the delay is typically around 3.0-3.5 kHz. This upper limit implies that phase locking to BF tones is an important determinant of the ability of units to encode the delay in their temporal discharge patterns. Although a few nonphase-locked units were found in the present study to be able to encode the delay of rippled noise based on their temporal discharge patterns, the strongest synchrony to the rippled noise delay was obtained for phase-locked units having BFs below about 1.5 kHz. It is interesting to note that in response to BF tones, the strongest synchronization occurs for primarylike units with BFs less than 1.5-2.0 kHz (Blackburn and Sachs, 1989).

Most of the AVCN units recorded in the present study which show features in their renewal densities related to the delay of rippled noise show clear phase locking to BF tones. In addition, prepotentials in the action potential waveform were observed for some units in this group, BF rate-level functions were monotonic, and primarily or primarily with a notch PST histograms were sometimes generated in response to BF tones with random starting phases. These physiological characteristics argue that this group of units largely correspond to bushy cells (Rhode et al., 1983a; Rouiller and Ryugo, 1984; Smith and Rhode, 1987). Bushy cells receive auditory-nerve inputs in the form of large calyx endings directly on the soma (Brawer and Morest, 1975; Cant and Morest, 1979; Tolbert and Morest, 1982; Smith and Rhode, 1987), and depolarization in the calyx endings can be recorded extracellularly as a prepotential (Guinan and Li, 1990). In response to wideband and rippled noises, this group of AVCN units generally shows oscillations having periods of approximately 1/BF which reflect the filter properties of the auditory-nerve fibers in response to broadband noise (Ruggiero, 1973; ten Kate and van Bekkum, 1988). The renewal densities generated in response to rippled noise show peaks at the delay for cos + noise, but show nulls at the delay for cos - noise. Comparison of these renewal densities with stimulus autocorrelation functions (e.g., Fig. 2) suggest that the temporal representation of the rippled noise delay in this group of units reflects the temporal properties of the stimulus fine structure, because a null occurs at the delay for the cos - noise condition. AVCN units having primarylike response characteristics have also been shown to temporally encode the waveform fine structure of two-tone complexes (Greenberg and Rhode, 1987) and the formants of steady-state vowels (Blackburn and Sachs, 1990; Winter and Palmer, 1990a). These findings support the hypothesis that AVCN bushy cells are a subsystem which preserves the fine structure of complex stimuli in the temporal discharge patterns of spike trains (see Young, 1987).

The temporal discharge patterns of some units in the present study reflected the temporal properties of the stimulus envelope rather than the waveform fine structure. Most nonprimarylike units, including chopper units, gave renewal densities that were either flat or showed features that were unrelated to the delay of rippled noise. Some, but not all, chopper units showed peaks in the renewal densities that reflected a regularity of discharge (i.e., "chopping") in response to rippled noise. While most chopper units did not encode the delay of rippled noise in their temporal discharge patterns, a few chopper units showed peaks in their renewal densities at the delay for both cos + and cos - rippled noises suggesting that the temporal properties of the stimulus envelope are encoded, because there is a peak at the delay for the cos - noise condition (see Fig. 2). Using tone complexes and AM tones, respectively, Greenberg and Rhode (1987) and Frisina et al. (1990) have also shown that the temporal discharge patterns of chopper units can reflect the stimulus envelope and not the waveform fine structure. Morphologically, chopper units correspond to stellate cells (Rhode et al., 1983a; Rouiller and Ryugo, 1984; Smith and Rhode, 1989), and they received their inputs from auditory-nerve fibers along on the dendrites in the form of small bouton endings (Cant, 1981; Tolbert and Morest, 1982; Smith...
A common method of envelope extraction is half-wave rectification followed by low-pass filtering (e.g., Schwartz, 1959). For chopper units, the stimulus envelope is presumably extracted, because (1) the inputs to the cell are the phase-locked, half-wave rectified representations of the stimulus in auditory-nerve spike trains (2) which are then low-pass filtered by the dendritic trees. Dendritic cylinder models indicate that the cutoff frequency of this low-pass filter decreases as the input becomes farther out on the dendritic trees (Young et al., 1988b). Thus the ability of some chopper units to encode the delay of rippled noise in their temporal discharge patterns may be a reflection of auditory-nerve input which is closer to the soma. AVCN stellate cells (chopper units) may function as a subsystem which extracts and encodes the stimulus envelope in the temporal discharge patterns, at least for low-modulation frequencies.

Synchronization to the delay of rippled noise is also demonstrated in the present study using evoked potential recordings in the AVCN. The autocorrelation functions of neurophonic potentials show peaks at the delay for both cos+ and cos - noise stimuli. Comparison of the neurophonic autocorrelation functions with the stimulus autocorrelation functions (see Fig. 2) suggest that the neurophonic reflects temporal properties of the stimulus envelope rather than the waveform fine structure, because again there is a peak at the delay for the cos - noise condition. This result should not be taken to imply that the neurophonic reflects the ensemble temporal discharge of the chopper units previously discussed. More likely, the neurophonic potential represents the summed response of many phase-locked spike trains (1) that are half-wave rectified versions of the stimulus (2) that are subsequently low-pass filtered by the properties of the recording electrode. Measurement of the transfer functions for the types of microelectrodes used in the present study as well as in other studies reporting neurophonic potentials (e.g., Boudreau, 1965; Starr and Hellerstein, 1971; Sullivan and Konishi, 1986; Blackburn and Sachs, 1990) show that the electrodes can be characterized as low-pass, i.e., the microelectrodes themselves act as low-pass filters.

The finding that the neurophonic reflects the stimulus envelope is also consistent with the conclusion that the scalp-recorded frequency following response (FFR) in humans also reflects temporal properties of the stimulus envelope and not the waveform fine structure (Hall, 1979; Chambers et al., 1986). Because the waveforms of the neurophonic and scalp-recorded FFR are similar, understanding the temporal properties of the neurophonic recorded from animals is an important conceptual bridge between scalp recordings in humans and single unit recordings in animals, particularly since the interpretation of scalp-recorded potentials can be difficult (see Chimento and Schreiner, 1990). The scalp-recorded FFR could be used to establish whether synchrony at the rippled noise delay occurs for human auditory neurons; however, the use of the FFR and neurophonic to study temporal coding of pitch may be limited, since neither of these evoked potentials accurately reflects the ability of auditory neurons to encode the waveform fine structure.

The present results show that a peak at the 1-ms delay can be observed in the autocorrelation functions of the neurophonic in response to rippled noise with a 1-ms delay. However, a peak at 1 ms was not observed in the present study for renewal densities of single units generated for rippled noises with 1-ms delays. Previous studies in the mammalian auditory nerve (ten Kate and van Bekkum, 1988) and cochlear nucleus (Boerger, 1974) also have not reported peaks in the spike train autocorrelation functions at delays as short as 1 ms for single neurons. How can the temporal information be present in a population of neurons if it cannot be found within a single neuron? Young and Sachs (1989) have shown that correlation in neural discharge can be observed from simultaneous recordings of pairs of auditory-nerve fibers in response to broadband noise if the BF of the pair are similar. The correlations between auditory-nerve fiber discharges appear to result from correlated fluctuations in the envelopes at the output of similar cochlear filters. For 1-ms cos+ rippled noise, the autocorrelation function of the output of the cochlear filter will not only reflect the envelope characteristics of that filter, but will also contain the correlations at the 1-ms delay (e.g., Fig. 2). Thus one might expect to observe a peak at 1 ms in the cross-correlation function of a pair of auditory neurons with similar BFs in response to cos+ noise with a delay of 1 ms even if the peak does not exist in the autocorrelation functions of the individual neuronal spike trains. The neurophonic reflects the synchronous activity of a local population of neurons, and it is likely that the BFs of the neurons which comprise the neurophonic potential are similar. Therefore, the peak at 1 ms in the neurophonic autocorrelation functions presumably reflects the correlated discharges across auditory neurons which are being driven by the similar rippled noise envelopes.

The present study examined the coding of rippled noise in terms of a temporal code not unlike the volley principle (Wever, 1949). Delay values that were studied were chosen because they are the delay values which produce the strongest pitch perceptions in humans (Yost and Hill, 1978). While the present study demonstrates that a temporal representation of the delay of rippled noise does exist in the synchronous discharge across neurons in the cochlear nucleus, it does not exclude the possibility that a representation of rippled noise also exists in terms of place codes. A temporal-place representation of the spectrum of rippled noise may exist in the average localized interval rate (ALIR) profile (Sachs and Young, 1980). The ALIR profile has been shown to provide a robust representation of the formant peaks of aperiodic steady-state vowels in the discharge of auditory-nerve fibers (Voigt et al., 1982).

A representation of the spectra of rippled noises could also exist in terms of rate-place profiles. Rate coding of rippled noise has largely been studied using delay histograms (Bilsen et al., 1975; Evans, 1977; Narins and Evans, 1980; Fay et al., 1983; Dunia and Narins, 1989). The results of these studies suggest that the ability of an auditory unit to encode the spectra of rippled noises in terms of average rate occurs at those delays in which a systematic change in the delay results in systematic fluctuations in firing rate. However, the delay values reported in the literature for mammals over which units show the largest systematic fluctuations in firing rate generally occur for delay values outside of the...
range of delays which generate salient pitch perceptions in humans. Nevertheless, comparison of delay histograms between auditory-nerve fibers and cochlear nucleus units in terms of (1) the dynamic range over which rate fluctuations occur (Evans, 1977; Narins and Evans, 1980) and (2) the maximum peak-trough ratio in rate fluctuations (Bilsen et al., 1975) suggest that lateral inhibition in the cochlear nucleus may be important for a representation based on average rate. Yost (1986) has shown that the peak-trough ratios of the spectra of rippled noises that have been passed through a bank of critical-band filters are larger after a lateral inhibitory network is applied to the output of the critical-band filters compared to peak-trough ratios obtained from critical-band filtering alone. Moreover, the frequency region with the largest peak-trough ratio that is observed after application of the lateral inhibitory network occurs around the third to fourth spectral peaks (Yost, 1986), which corresponds to the dominant region of rippled noise pitch (Yost, 1982).

Lateral inhibition (Shofner and Young, 1985; Rhode and Smith, 1986; Winter and Palmer, 1990b), as well as regularity of discharge (Bourk, 1976; Young et al., 1988a; Shofner and Dye, 1989; Blackburn and Sachs, 1989), are physiological properties associated with chopper units, and are properties that may serve to preserve or enhance rate-place representations of stimulus spectra. For example, Blackburn and Sachs (1990) have shown that the formants of steady-state vowels are represented by the rate-place profile of chopper units in AVCN. Thus stellate cells (chopper units) are a possible neural subsystem for preserving or enhancing a representation of rippled noise spectra. Another possible neural subsystem for preserving or enhancing a rate-place representation of rippled noise spectra are the fusiform and giant cells of the dorsal cochlear nucleus (DCN). Fusiform and giant neurons are the principal cells of the DCN (Adams and Warr, 1976; Rhode et al., 1983b; Oliver, 1984; Ryugo and Willard, 1985) and correspond to type IV units in unanesthetized, decerebrate cats (Young, 1980). Units with type IV-like responses properties have also been recorded from the DCN of anesthetized chinchillas (Mast, 1970; Kaltenbach and Saunders, 1987; Caspary et al., 1987). The frequency response maps of type IV units show large inhibitory areas to a wide range of frequencies including BF (Evans and Nelson, 1973; Young and Brownell, 1976; Rhode and Kettner, 1987), yet these units give strong excitatory responses to broadband noise (Young and Brownell, 1976). Moreover, DCN neurons typically show poor phase locking to tones relative to that observed in the AVCN (Lavine, 1971; Goldberg and Brownell, 1973). These characteristics suggest that fusiform and giant cells (type IV units) may be a cochlear nucleus subsystem where a robust rate-place representation of the spectra of rippled noises may be found.

A variety of complex acoustic stimuli can produce the same pitch in human subjects (Fastl and Stoll, 1979), and it is likely that the underlying neural mechanisms of extracting those features important for pitch are similar among these various sounds. Thus it is important to study the responses of single auditory neurons to a variety of different types of complex stimuli which produce pitch and look for commonalities in the physiological responses to these different stimuli. Rippled noises generate virtual or repetition pitch perceptions in humans (Bilsen, 1977; Yost et al., 1978; Warren and Bashford, 1988). For cos + noise, the perceived pitch is at a frequency of 1/delay; for cos — noise, the pitch is more ambiguous at frequencies of 0.9/delay and 1.1/delay (Yost et al., 1978). The pitches of cos + noises with delays greater than 2 ms (i.e., pitches less than 500 Hz) can be predicted from the temporal discharge patterns of AVCN units; a peak occurs in the renewal densities at the appropriate delay value for delays greater than 2 ms. However, the temporal discharge patterns observed in the present study do not predict either the pitches of cos + noises with short delays (2 ms or less; pitches of 500 Hz or higher) or the perceived ambiguous pitches of cos — noises. The peaks that can be observed on either side of the null in renewal densities for cos — noises (e.g., Fig. 8) do not correspond to the ambiguous pitches of 0.9/delay and 1.1/delay reported by humans or by the peripheral weighting model (Yost and Hill, 1979; Yost, 1982); rather these peaks are more of a reflection of the BF of the unit (see Yost et al., 1978; Fay et al., 1983). In a recent model of pitch, Meddis and Hewitt (1991) show that averaging autocorrelation functions across frequency channels for cos — noise will yield weak peaks on either side of the null which correspond closely to the pitches reported by humans (see Fig. 16 of Meddis and Hewitt, 1991). This implies that peaks corresponding to 0.9/delay and 1.1/delay may be observed if renewal densities are summed across units. Thus a temporal code can account for some, but not all of the repetition pitches of rippled noises in humans, and indicates the importance of other possible place codes previously discussed. However, one must be cautious when comparing the results of animal physiology to human psychophysics. Ongoing psychophysical experiments in our laboratory suggest that chinchillas are less sensitive than humans in discriminating rippled noise from broadband noise.

The results of the present study are in agreement with previous studies (Boerger, 1974; ten Kate and van Bekkum, 1988) indicating that the encoding of the rippled noise delay in the temporal discharge patterns of auditory neurons is primarily limited to low BF, phase-locked neurons. On the other hand, units having BFs above 3.0 kHz were found in the present study to be able to phase lock to the periods of low-frequency tones or harmonic tone complexes. Cochlear nucleus units with high BFs and/or nonprimarylike response properties have also been shown to phase lock to the periods of synthetic steady-state vowels (Moore and Cashin, 1976; Kim et al., 1986; Blackburn and Sachs, 1990) and to the modulation frequency of amplitude-modulated tones (Frisina et al., 1990; Kim et al., 1990). If temporal encoding of the delay/period of these complex stimuli is important for pitch, then the greater number of neurons capable of discharging in a synchronous manner to stimuli such as harmonic tone complexes and AM tones may be related to the stronger pitch strengths of these stimuli relative to the pitch strengths of rippled noises (Fastl and Stoll, 1979) for which a more limited number of neurons are capable of discharging synchronously. Rippled noises will be useful stimuli for fu-
ture physiological and psychophysical studies investigating the extraction and processing of those temporal and spectral features of complex sounds which are important for pitch perception as well as for studies of auditory processing in reverberant environments.

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