Responses of Cochlear Nucleus Units in the Chinchilla to Iterated Rippled Noises: Analysis of Neural Autocorrelograms

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Shofner, William P. Responses of cochlear nucleus units in the chinchilla to iterated rippled noises: analysis of neural autocorrelograms. J. Neurophysiol. 81: 2662–2674, 1999. Temporal encoding of stimulus features related to the pitch of iterated rippled noises was studied for single units in the chinchilla cochlear nucleus. Unlike other periodic complex sounds that produce pitch, iterated rippled noises have neither periodic waveforms nor highly modulated envelopes. Infinitely iterated rippled noise (IIRN) is generated when wideband noise (WBN) is delayed (τ) attenuated, and then added to (+) or subtracted from (−) the undelayed WBN through positive feedback. The pitch of IIRN[+, τ, −1 dB] is at 1/τ, whereas the pitch of IIRN[−, τ, −1 dB] is at 1/2τ. Temporal responses of cochlear nucleus units were measured using neural autocorrelograms. Synchronous responses as shown by peaks in neural autocorrelograms that occur at time lags corresponding to the IIRN τ can be observed for both primarylike and chopper unit types. Comparison of the neural autocorrelograms in response to IIRN[+, τ, −1 dB] and IIRN[−, τ, −1 dB] indicates that the temporal discharge of primarylike units reflects the stimulus waveform fine structure, whereas the temporal discharge patterns of chopper units reflect the stimulus envelope. The pitch of IIRN[±, τ, −1 dB] can be accounted for by the temporal discharge patterns of primarylike units but not by the temporal discharge of chopper units. To quantify the temporal responses, the height of the peak in the neural autocorrelogram at a given time lag was measured as normalized rate. Although it is well documented that chopper units give larger synchronous responses than primarylike units to the fundamental frequency of periodic complex stimuli, the largest normalized rates in response to IIRN[+, τ, −1 dB] were obtained for primarylike units, not chopper units. The results suggest that if temporal encoding is important in pitch processing, then primarylike units are likely to be an important cochlear nucleus subsystem that carries the pitch-related information to higher auditory centers.

INTRODUCTION

A variety of complex sounds produce the perception of pitch in human subjects (Fastl and Stoll 1979), and it is likely that the neural mechanisms underlying the perception of pitch are similar among the various types of complex sounds. Licklider (1951) proposed that the nervous system extracts the pitch of a complex stimulus by performing an autocorrelation analysis of the information encoded in the auditory nerve. Similar conclusions concerning complex pitch and autocorrelation have been made based on computational models of the auditory periphery (Meddis and Hewitt 1991; Meddis and O’Mard 1997). Using a wide variety of periodic complex sounds, Cariani and Delgutte (1996a,b) have shown that autocorrelation analysis of auditory nerve spike trains provides a robust representation of pitch-related information.

Many of the neurophysiological investigations that have studied the temporal representation of fundamental frequency in the auditory nerve and cochlear nucleus have used periodic stimuli having highly modulated stimulus envelopes. These stimuli include sinusoidally amplitude modulated tones (Frisina et al. 1990; Javel 1980; Joris and Yin 1992; Khanna and Teich 1989; Kim et al. 1990; Rhode 1995; Rhode and Greenberg 1994; Zhao and Liang 1995), complex tones (Greenberg and Rhode 1987; Palmer and Winter 1992; Rhode 1994), and synthetic vowels (Keilson et al. 1997; Kim and Leonard 1988; Kim et al. 1986; Palmer 1992; Palmer and Winter 1992; Rhode 1998; Wang and Sachs 1993, 1994). One common observation from several of these studies is that the synchronization to the fundamental frequency measured for chopper and onset units in the cochlear nucleus is larger than that observed for auditory nerve fibers or primarylike units unit types in the cochlear nucleus (Frisina et al. 1990; Keilson et al. 1997; Rhode 1998; Rhode and Greenberg 1994; Wang and Sachs 1994). Although not explicitly stated, the hierarchy of synchrony described in many of the above studies implies that primarylike units may play only a minor role in the temporal encoding of pitch-related information in the cochlear nucleus. One proposed neuronal circuit model of periodicity pitch involves components from onset units, chopper units, and pauser units but does not include any input from primarylike units (Langer 1988). However, the enhanced synchronization of chopper and onset units may only reflect strong temporal responses to highly modulated stimulus envelopes, while having lesser importance for pitch per se.

In contrast to the complex sounds mentioned above, rippled noises generate the perception of pitch, but do not have highly modulated stimulus envelopes. There is a temporal regularity in the waveform of rippled noise, but this regularity is not repeated in a periodic manner. Rippled noise of one iteration is generated when a wideband noise (WBN) is delayed (τ) and the delayed repetition of the WBN is added to the original WBN; this type of rippled noise has been referred to as cosine noise (Bilsen et al. 1975). This delay-and-add network can be repeated N times to generate rippled noises of N iterations (see Yost et al. 1996). Figure 1 shows the circuit used for generating a rippled noise of infinite iterations, i.e., infinitely iterated rippled noise (IIRN). WBN is delayed and attenuated, and the delayed repetition of the WBN is added to the original WBN through positive feedback. This type of rippled noise has a spectrum with sharp peaks at integer multiples of 1/τ (see Fig. 1) and has been referred to as comb-filtered noise (e.g., Raitt-
If the delayed repetition is inverted before it is added (i.e., subtracted), then the spectral valleys occur at integer multiples of $1/\tau$, and the spectral peaks occur at odd integer multiples of $1/2\tau$. For simplicity throughout this paper, IIRN stimuli will be referred to as IIRN[$\pm\tau$, att], where $\pm$ indicates whether the delayed noise was added (+) or subtracted (−), $\tau$ is the delay in milliseconds, and att is the attenuation of the delayed noise in decibels. Thus an IIRN that was generated by adding the delayed noise to the undelayed noise with a $\tau$ of 4 ms and a delayed noise attenuation of $-1$ dB will be referred to as IIRN[++ 4 ms, $-1$ dB].

Figure 2 shows examples of the autocorrelation functions of the waveforms for WBN and IIRN. The waveform autocorrelation function of WBN is flat (Fig. 2A), whereas there are positive correlations in the autocorrelation functions of IIRN[++ 4 ms, $-1$ dB] at time lags of 4 ms and integer multiples of 4 ms (Fig. 2B). The perceived pitch of the IIRN[++ 4 ms, $-1$ dB] is at $1/\tau$ or 250 Hz (Fastl 1988; Raatgever and Bilsen 1992; Yost 1996a), and if the pitch strength of a tone complex is 100%, then the estimated pitch strength for the IIRN[++ 4 ms, $-1$ dB] is $50-60\%$ (see Yost 1996b). For IIRN[-- 4 ms, $-1$ dB], there are negative corre-

**FIG. 1.** Circuit diagram for generating rippled noise having an infinite number of iterations. Wideband noise (WBN) is delayed, attenuated, and added to the original undelayed WBN through positive feedback. Inset, left: spectrum of WBN. Inset, right: spectrum of infinitely iterated rippled noise having a delay of 4 ms and a delayed noise attenuation of $-1$ dB.
lations in the waveform autocorrelation function at time lags of 4 ms and at odd multiples of 4 ms but positive correlations at even multiples of 4 ms (Fig. 2C). That is, these negative and positive correlations alternate throughout the waveform autocorrelation function. Perceptually, the perceived pitch of IIRN[−, 4 ms, −1 dB] is at 1/2τ, or 125 Hz, i.e., one octave lower than the pitch of IIRN [+ , 4 ms, −1 dB] (Fastl 1988; Raatgever and Bilsen 1992; Yost 1996a).

Figure 2 also shows examples of the autocorrelation functions for the envelopes obtained from a Hilbert transform of the waveform for WBN and IIRN. The envelope autocorrelation function for WBN is flat (Fig. 2D), whereas there are positive correlations at τ and integer multiples of τ for both IIRN [+ , 4 ms, −1 dB] and IIRN[−, 4 ms, −1 dB] (Fig. 2, E and F). The alternation of negative and positive correlations observed in the waveform autocorrelation function is not observed in the envelope autocorrelation function of IIRN[−, 4 ms, −1 dB].

Recent psychophysical studies have shown that the pitch and pitch strength of iterated rippled noises as well as discrimination data can be accounted for using temporal processing mechanisms (Patterson et al. 1996; Yost 1996a,b, 1997; Yost et al. 1996). We have shown previously that chinchillas can discriminate behaviorally IIRN [+ , τ, att] from WBN and have argued that the underlying neural mechanisms are common between chinchillas and human subjects (Shofner and Yost 1995, 1997). Neurophysiological studies in the auditory nerve and cochlear nucleus using rippled noise of one iteration have shown that a temporal representation related to pitch can be found in the discharge patterns of low-frequency auditory nerve fibers and primarylike units (Shofner 1991; ten Kate and van Bekkum 1988). The present study examined the representation of τ in the temporal discharge patterns of cochlear nucleus units in the chinchilla in response to IIRN stimuli. In this paper, the responses of primarylike and chopper units are compared. If the hierarchy of synchrony previously discussed reflects the relative importance of units in the temporal encoding of pitch-related information, then primarylike units should give the smallest synchronous responses to rippled noise stimuli compared with other unit types.

METHODS

The procedures have been reviewed and approved by the Institutional Animal Care and Use Committee of Loyola University Chicago. Twenty-three adult chinchillas weighing between 500 and 800 g were anesthetized with intraperitoneal injections of pentobarbital sodium (70 mg/kg); supplemental injections were given to maintain areflexia. Body temperature was maintained around 37°C with a DC heating pad. Animals were tracheotomized, and the external auditory canals were exposed and transected. Animals were placed in a modified headholder (Kopf Model 900), and the left bulla was exposed and opened. The cerebellum was exposed by an opening in the temporal bone in a manner similar to that described for gerbils by Frisina et al. (1982). Animals were placed in a double-walled sound-attenuating chamber (Tracoustics) during neurophysiological recording of unit responses.

Indium-filled micropipettes (Dowben and Rose 1953) or tungsten microelectrodes (Microprobe) were used to record single-unit activity. Neural spikes were amplified and filtered using standard electrophysiological procedures. Electrodes were advanced through the cerebellum into the cochlear nucleus using an hydraulic microdrive system (Kopf 650). Using this approach, it was not uncommon to hold an isolated single unit for 1–2 h. However, the use of metal microelectrodes often made the isolation of clear single units difficult, because multiple-unit activity or large neurophonic evoked potentials were recorded frequently. Data regarding spike times were obtained from neural spike trains that clearly were evoked from a single unit and were not obtained by attempting to isolate single unit activity from multiunit clusters of spike trains.

Data acquisition and stimulus presentation were under the control of either a MassComp computer system or, in later experiments, a Gateway2000 Pentium computer system with Tucker-Davis Technologies (TDT) modules. The sampling and conversion rates were set at 50 kHz for the A/D and D/A devices. The times of occurrences of spikes were determined on-line relative to the onset of the stimulus; the amplified neural spikes were digitized and averaged off-line to examine the averaged spike waveform for the presence of prepotentials (Peiffer 1966). Acoustic stimuli were presented to the left ear through a Sennheiser HD 414 SL earphone that was enclosed in a brass housing; the housing also held a calibration microphone (Bruel and Kjaer 4134). Acoustic search stimuli consisted of 100-ms bursts of either wideband noise or tones at the best frequency (BF) of the background neural activity.

When a unit was isolated, its BF first was determined using audiovisual cues, and data were collected to classify the unit physiologically. Classification of unit types was based on poststimulus time (PST) histograms, interspike interval (ISI) histograms, and regularity analysis (Bourk 1976; Young et al. 1988) as well as the presence or absence of a prepotential. BF tones were generated by the computer and presented through a 16-bit D/A converter (MassComp DA04H or TDT DA3–2 module). Rate-level functions were generated over a 100-dB range in 1-dB steps for either 200- or 400-ms BF tone bursts with rise/fall times of 10 ms presented once per second. One tone burst was presented at each level, and the rate-level function was smoothed using a 5-bin triangular moving window average. Threshold was defined as the level that first evoked an increase in discharge rate by 2 SDs above the estimated spontaneous discharge rate, provided that the next three levels also evoked firing rates >2 SDs above spontaneous rate. PST histograms were typically generated at 20–40 dB above threshold for 250 presentations of a 50-ms BF tone with 2-ms rise/fall times presented once every 250 ms. If the characteristic discharge pattern was obscured in the PST histogram due to strong phase-locking, then additional PST histograms were generated in which each of the 250 presentations of the BF tone had a random starting phase. The use of random starting phases sometimes allowed the characteristic discharge pattern to become apparent.

After the data were collected for unit classification, the responses to WBN and IIRN were studied. A set of WBN and IIRN stimuli were generated using the same equipment and parameter settings that were used previously to measure discrimination thresholds in chinchillas (Shofner and Yost 1995). For WBN and each IIRN, 5 s of the waveform was sampled; the waveform amplitudes were adjusted so that all WBN and IIRN stimuli had equal root-mean-square (rms) amplitudes. The 5-s samples of each noise then were stored on disk as stimulus files. Rate-level functions first were generated over a 100-dB range in 1-dB steps for 500-ms WBN bursts with rise/fall times of 10 ms presented once per second, and threshold was estimated as defined above for BF tone rate-level functions. The responses of the isolated unit then were studied for WBN and IIRN stimuli at a fixed overall level, generally at 20 dB above threshold as determined from the WBN rate-level function. A total of 100 separate samples of WBN or IIRN were presented. Consequently, the waveform of the noise was not the same for each presentation. Each sample had a duration of 500 ms with 10-ms rise/fall times and were presented once every second; these are the same parameters used in the previous behavioral study (Shofner and Yost 1995). Typically, the value of τ was first chosen to be 4 ms, followed by τs of 2 and 8 ms. These values of τ were chosen, because these were the τs at which psychometric functions were obtained for chinchillas (Shofner and Yost 1995). The delayed noise attenuation was fixed at −1 dB; an attenuation of −1 dB generated an
IIRN having the greatest pitch strength without causing the positive feedback circuit (see Fig. 1) to oscillate. The spike trains obtained in response to WBN and IIRN were analyzed as PST histograms, spike count distributions, ISI histograms, and neural autocorrelograms (i.e., all-order ISI histograms). The ordinates of the autocorrelograms are scaled in terms of firing rate as described by Abeles (1982), and each autocorrelogram displays three horizontal reference lines. The middle horizontal line shows the average firing rate obtained from the spike count distributions; the upper and lower horizontal lines show the average rate ±2 SDs. These horizontal lines only serve as visual aids and are not meant to imply statistical significance. For comparison, temporal discharge properties were occasionally obtained in response to harmonic tone complexes consisting of the fundamental frequency and all harmonic frequencies ≤10 kHz. This produced tone complexes having bandwidths similar to the bandwidths of the IIRNs. Tone complexes were synthesized by adding individual components in cosine phase, sine phase, or random phase. The rms amplitude of each tone complex was adjusted to equal the rms amplitudes of the WBN and IIRN stimuli.

RESULTS

Classification of unit types

The responses to IIRN stimuli were studied in a total of 86 single units. A total of 26 units were grouped broadly as primarylike; this sample includes both primarylike (n = 20) and primarylike with notch (n = 6) subcategories of units. Of these units, a total of 10 units were observed to have a prepotential in the averaged spike waveform. A total of 35 units were grouped broadly as chopper units.1 Although a distinction among the various subcategories of chopper units was made, all chopper units were grouped together for the present analysis. A total of nine units were grouped broadly as onset units. Onset units in this sample typically showed some low rate of discharge during the duration of the tone stimulus and showed PST histograms similar in shape to on-A or on-P units described by Bourk (1976). Units were grouped as onset if the firing rate between 20 and 50 ms was <100 spikes (i.e., mean interspike interval was >10 ms) similar to the scheme described by Blackburn and Sachs (1989). An additional nine units having BFs <450 Hz were grouped as phase-locked; these units showed strong BF phase-locking, and a characteristic discharge pattern could not clearly be observed when BF tones were presented with random starting phases. Finally, a total of seven additional units could not be classified easily into any of the preceding groups and are grouped as unusual. Prepotentials were not observed in the spike waveform for any nonprimarylike unit.

Temporal responses to IIRN stimuli

The effect of τ on the temporal discharge pattern of a primarylike unit (Fig. 3) in response to IIRN[τ, +, −1 dB] is illustrated in Fig. 4, A–C. There are peaks in the neural autocorrelograms that occur at time lags of τ and integer multiples of τ for each of the IIRN[τ, +, −1 dB] conditions. In response to IIRN[τ, +, 2 ms, −1 dB], there are peaks in the autocorrelogram at time lags of 2 ms and at integer multiples of 2 ms (Fig. 4A); in response to IIRN[τ, +, 4 ms, −1 dB], there are peaks in the autocorrelogram at time lags of 4 ms and at integer multiples of 4 ms (Fig. 4B); in response to IIRN[τ, +, 8 ms, −1 dB], comparisons subsequently were made using the Tukey’s HSD test. At the α = 0.01 level, there was a significant difference in the means between primarylike versus chopper units and a significant difference in the means between primarylike and on-G units. There was no significant difference in the means between chopper and on-G units. Therefore, it was concluded that the on-G units were not a separate group of units but should be classified as chopper units.
there are peaks in the autocorrelogram at time lags of 8 ms and at integer multiples of 8 ms (Fig. 4C). Note that these peaks are narrow and that there are oscillations in firing rate that occur around $\tau$ and each integer multiple of $\tau$.

Figure 4, D–F, shows the autocorrelograms of the primarylike unit obtained in response to IIRN[$-\tau, \tau, -1$ dB] with delays of 2, 4, and 8 ms. In contrast to the autocorrelograms obtained for IIRN[$+\tau, \tau, -1$ dB], there are nulls in the IIRN[$-\tau, \tau, -1$ dB] autocorrelograms at time lags corresponding to $\tau$ and at odd-integer multiples of $\tau$. For example, when $\tau$ is 4 ms, there is a null in the autocorrelogram at a time lag of 4 ms (Fig. 4E). Note that there is also a pair of positive peaks at time lags of $\pm 3.5$ and $4.5$ ms that flank these nulls. The pair of peaks around the null at $\tau$ reflect the tuning properties of the unit and are not directly related to the pitch of the stimulus. The peaks are further apart for low BF units and are closer together for high BF units. In addition to this pair of peaks, there is also a peak in the autocorrelogram at a time lag of 8 ms (i.e., at $2\tau$). Consequently, there are nulls at time lags of $\tau$ and odd-integer multiples of $\tau$ but peaks at time lags of even-integer multiples of $\tau$. Similar results are observed in the autocorrelograms in response to IIRN[$-\tau, 2$ ms, $-1$ dB] (Fig. 4D) and IIRN[$-\tau, 8$ ms, $-1$ dB] (Fig. 4F). Comparison of these neural autocorrelograms to the stimulus autocorrelograms (Fig. 2) suggests that the temporal discharge properties of the primarylike unit are driven by the waveform fine structure.

The effect of $\tau$ on the temporal discharge pattern of a high BF primarylike unit in response to WBN and IIRN[$-\tau, \tau, -1$ dB] is illustrated in Fig. 5. Note that this unit has a prepotential in its spike waveform (Fig. 5A, inset). Similar to the preceding primarylike unit, the autocorrelograms of this high BF primarylike unit show peaks at $\tau$ and integer multiples of $\tau$ in response to IIRN[$-\tau, \tau, -1$ dB] (Fig. 5C and D). However, in contrast to the previous primarylike unit, the autocorrelograms in response to IIRN[$-\tau, \tau, -1$ dB] also show peaks at integer multiples of $2\tau$ (Fig. 5E and F). That is, nulls at time lags of $\tau$ and odd-integer multiples of $\tau$ are not observed for the high BF primarylike unit. Comparison of these neural autocorrelograms with stimulus autocorrelograms (Fig. 2) suggests that the temporal discharge properties of this primarylike unit are driven by the stimulus envelope.

The effect of $\tau$ on the temporal discharge pattern of a transient-chopper unit (Fig. 6) in response to IIRN[$+\tau, \tau, -1$ dB] is illustrated in Fig. 7, A and B. The temporal discharge pattern of the chopper unit is similar to that described above for the primarylike unit in that there are peaks at $\tau$ and integer multiples of $\tau$ in response to IIRN[$+\tau, \tau, -1$ dB]. When $\tau$ is 4 ms, there are peaks in the autocorrelogram at time lags of 4 ms and at integer multiples of 4 ms (Fig. 7A); when $\tau$ is 8 ms, there are peaks in the autocorrelogram at time lags of 8 ms and at integer multiples of 8 ms (Fig. 7B). The temporal discharge of the chopper unit in response to IIRN[$-\tau, \tau, -1$ dB] is shown in Fig. 7, C and D. The autocorrelograms in response to IIRN[$-\tau, \tau, -1$ dB] are similar to those obtained for IIRN[$+\tau, \tau, -1$ dB] when $\tau$ is 4 and 8 ms. In particular, in response to IIRN[$-\tau, 8$ ms, $-1$ dB], there are no nulls observed at a time lag of 4 ms,
but rather there are peaks at a time lag of 4 ms and integer multiples of 4 ms (Fig. 7C). Similar peaks at time lags of 8 ms and integer multiples of 8 ms also are observed in the autocorrelograms in response to IIRN[−, 8 ms, −1 dB] (Fig. 7D). Example autocorrelograms in response to IIRN[+, 8 ms, +1 dB] and IIRN[−, 8 ms, +1 dB] stimuli obtained from 1 of the 15 units classified as a chopper based on its ISI histogram but having a PST histogram more similar to a primarylike pattern (Fig. 8) are shown in Fig. 9. Again there are peaks in the autocorrelograms at time lags of 8 ms and at integer multiples of 8 ms in response to both IIRN[+, 8 ms, −1 dB] and IIRN[−, 8 ms, −1 dB] (Fig. 9, A and C); there are peaks in the autocorrelogram at time lags of 4 ms and at integer multiples of 4 ms in response to both IIRN[+, 4 ms, −1 dB] and IIRN[−, 4 ms, −1 dB] (Fig. 9, B and D). Comparison of these neural autocorrelograms with stimulus autocorrelograms (Fig. 2) suggests that the temporal discharge properties of the chopper units are driven by the stimulus envelope.

The temporal responses to IIRN[+, 4 ms, −1 dB] and to harmonic tone complexes having a fundamental frequency of 250 Hz (i.e., period of 4 ms) for an onset unit are shown in Fig. 10. It can be observed clearly that neither IIRN[+, 4 ms, −1 dB] (Fig. 10A) nor the random phase harmonic tone complex (Fig. 10B) evoked an excitatory response from the unit. In contrast, a large excitatory response can be observed to both the harmonic tone complex added in cosine and sine phase (Fig. 10, C and D). Although 4-ms ISIs were not obtained, the autocorrelograms (Fig. 10, E and F) show that the temporal discharge pattern is related to the periodicity of the tone complex. Figure 11 shows the autocorrelograms of another onset unit in response to WBN, IIRN[+, 4 ms, −1 dB] and harmonic tone complexes. Although this unit gave an excitatory response, the autocorrelograms show no temporal features at a time lag of 4 ms in response to either IIRN[+, 4 ms, −1 dB] (Fig. 11C) or a cosine phase harmonic tone complex with a period of 4 ms (Fig. 11D). In response to a random phase harmonic tone complex with a period of 20 ms, there is a weak peak at a time lag of 20 ms in the autocorrelogram (Fig. 11E). Note the general similarity in the shape among the autocorrelograms for WBN, IIRN[+, 4 ms, −1 dB] and these two harmonic tone complexes. In contrast, the autocorrelogram shows that there is strong phase-locking to the period of 20 ms obtained in response to a cosine phase harmonic tone complex with a period of 20 ms (Fig. 11F). Thus a strong synchronous response from this unit is driven by a stimulus having a highly modulated envelope but a low fundamental frequency.
Quantitative analysis of temporal responses to IIRN\[+, 4 ms, −1 dB\]: peak height

The temporal properties of IIRN stimuli can be quantified by measuring the heights of the peaks at a time lag of \( \tau \) in the stimulus autocorrelation functions. The temporal discharge patterns of units displayed in neural autocorrelograms can be quantified in an analogous manner by estimating the heights of the peaks at a time lag corresponding to \( \tau \). Note that in all of the neural autocorrelograms, the peak heights are expressed in units of firing rate; consequently, the firing rates at a particular time lag in the autocorrelogram will be referred to as instantaneous firing rates. The instantaneous firing rate at \( \tau \) is defined as the maximum firing rate in the autocorrelogram in a 1-ms window centered at a time lag of \( \tau \). To compare across units having different average firing rates, the instantaneous firing rates at a time lag of \( \tau \) were measured in terms of normalized rate at a particular time lag as given by

\[
\text{Normalized Rate} = \frac{R_{\tau} - R_{\text{ave}}}{R_{\text{ave}}} \tag{1}
\]

where \( R_{\tau} \) is the instantaneous firing rate at time lag \( \tau \) and \( R_{\text{ave}} \) is the average firing rate. If the firing rate at \( \tau \) is equal to the average rate, then the normalized rate at \( \tau \) is 0; normalized rate is positive if the firing rate at \( \tau \) is above the average rate and is negative if the firing rate at \( \tau \) is less than the average rate. Normalized rate is −1 when the firing rate at \( \tau \) is 0.

Figure 12 compares the normalized rates at a time lag of 4 ms for WBN and IIRN\[+, 4 ms, −1 dB\] for the primarylike
and chopper units sampled in this study. The normalized rates for WBN also were measured as the maximum firing rate in a 1-ms window centered around the time lag of 4 ms and are shown for comparison. Note that for primarylike units (Fig. 12A) the normalized rates obtained in response to IIRN[+, 4 ms, −1 dB] are generally larger than the normalized rates for WBN, whereas this does not appear to be the case for chopper units (Fig. 12B). Although there is scatter in the data, it can be observed that for the primarylike/phase-locked units, there are no normalized rates measured at a 4-ms lag having negative values for IIRN[+, 4 ms, −1 dB], whereas there are normalized rates having negative values for the chopper units (see Fig. 12B, ▽). In response to IIRN[+, 4 ms, −1 dB], there were 0/51 (0%) negative normalized rates observed for primarylike/phase-locked group (Fig. 12A), there were 14/55 (25.4%) negative normalized rates observed for chopper group (Fig. 12B), there were 7/15 (46.7%) negative normalized rates observed for onset group, and there were 6/10 (60%) negative normalized rates observed for unusual group.

The normalized rates obtained in response to IIRN[+, 4 ms, −1 dB] for a sample of 15 autocorrelograms from 11/20 primarylike units and 12 autocorrelograms from 5/6 primarylike with notch units were ranked. These primarylike and primarylike with notch units had a similar range of BFs between 0.85 and 5.44 kHz. Based on a Mann-Whitney U test, the normalized rates for the primarylike and primarylike notch units were the same. Therefore the data for primarylike and primarylike with notch units were pooled. Figure 13 shows the average normalized rates obtained for both WBN and IIRN[+, 4 ms, −1 dB] for primarylike and chopper units having BFs between 0.64 and 1.6 kHz (left) and BFs > 1.6 kHz (right). A single-factor ANOVA showed that there was a significant
difference across the eight groups of WBN and IIRN conditions for primarylike and chopper units $[F(7,166) = 15.86; P < 0.0005]$. Onset and unusual units were not included in the analysis because there were relatively few responses in each of the above groups. Paired comparisons were subsequently made using the Tukey’s HSD test and are summarized in Table 1.

For the IIRN[1, 4 ms, 21 dB] conditions, there is a significant difference between the mean of the primarylike and the mean of the chopper units at $a = 0.01$ for units with BFs between 0.64 and 1.6 kHz as well as for units with BFs > 1.6 kHz. Paired comparisons between the responses to WBN and IIRN[1, 4 ms, 21 dB] within a given unit type show that there is a significant difference at $a = 0.01$ between the means for WBN and IIRN[+, 4 ms, −1 dB] for primarylike units with BFs between 0.64 and 1.6 kHz and for primarylike units with BFs > 1.6 kHz.

Quantitative analysis of temporal responses to IIRN[±, τ, −1 dB]: peak location

As previously described, there appears to be a tendency that the autocorrelograms of low BF primarylike units show a peak at a time lag of $τ$ in response to IIRN[+, τ, −1 dB] but show a peak at $2τ$ in response to IIRN[−, τ, −1 dB], whereas the autocorrelograms of chopper units and high BF primarylike units appear to show a peak at a time lag of $τ$ in response to both IIRN[+, τ, −1 dB] and IIRN[−, τ, −1 dB]. To quantify this, it was determined whether the time lag of the first or largest peak in the neural autocorrelogram occurred at $τ$ or $2τ$ for each response to IIRN stimuli, provided that there was a clear temporal response to the IIRN and that data were obtained for both IIRN[1, τ, 21 dB] and IIRN[2, τ, 21 dB] for the same unit.

Figure 14 shows the number of responses occurring at a time lag of either $τ$ or $2τ$ for primarylike and chopper units. For primarylike units, 28/29 (96.6%) of the peaks were at a time lag of $τ$; no peak at $τ$ was observed in this autocorrelogram. In response to IIRN[2, τ, 21 dB], 8/29 (27.6%) of the peaks were located at a time lag of $τ$; the ISI histograms of these primarylike units did not show any evidence of phase-locking to BF tones. In contrast, 20/29 (70%) were observed at $2τ$ in response to IIRN[−, τ, −1 dB]; the ISI histograms of these primarylike units showed phase-locking to BF tones. One response was observed at $4τ$; this was the same unit that showed a peak at $2τ$ for IIRN[+, τ, −1 dB] described above. For chopper units, 12/16 (75%) of the peaks were located at a time lag of $τ$, whereas 4/16 (25%) were located at $2τ$ in response to IIRN[+, τ, −1 dB]. In response to IIRN[−,
11/16 (68.8%) were located at time lags of $\tau$ and 5/16 (31.2%) were at time lags of $2\tau$. To determine whether there was a significant difference in the location of the peaks for primarylike and chopper units, contingency tables were generated and a $\chi^2$ analysis was carried out. The location of the peak in the neural autocorrelogram is not the same in response to IIRN[$+\tau, -1$ dB] and IIRN[$-\tau, -1$ dB] for primarylike units ($\chi^2 = 29.3; P < 0.001$). In contrast, the location of the peak in the autocorrelogram is the same in response to IIRN[$+, \tau, -1$ dB] and IIRN[$-, \tau, -1$ dB] for chopper units ($\chi^2 = 0$; not significant at $\alpha = 0.05$).

**FIG. 11.** Responses of an onset unit having a BF of 1.75 kHz. A: PST histogram obtained in response to BF tone bursts at 20 dB above threshold. B–F: autocorrelograms obtained in response to WBN (B), IIRN[$+, 4$ ms, $-1$ dB] (C), a 40-component random phase harmonic tone complex with a 250-Hz fundamental; i.e., 4-ms period (D), a 200-component random phase harmonic tone complex with a 50-Hz fundamental; i.e., 20-ms period (E), and a 200-component cosine phase harmonic tone complex with a 50-Hz fundamental (F).

**FIG. 12.** Scatter diagrams showing normalized rate as a function of BF obtained in response to IIRN[$+, 4$ ms, $-1$ dB] (∗) and WBN (○) for phase-locked and primarylike units (A) and chopper units (B). Normalized rate was estimated at a time lag of 4 ms.

**FIG. 13.** Bar graphs showing the average normalized rate of units having BFs between 0.64 and 1.6 kHz (left) and BFs >1.6 kHz (right) for primarylike units (pri), chopper units (chop) in response to IIRN[$+, 4$ ms, $-1$ dB] (●) and WBN (●). Error bars indicate the 95% confidence intervals. Numbers above the bars indicate the number of normalized rates.
correlation functions. Autocorrelograms of some chopper units, as well as nonphase-locked primarylike units show peaks at time lags of \(\tau\) and integer multiples of \(\tau\) in response to both IIRN\([+, \tau, -1 dB]\) and IIRN\([-\tau, \tau, -1 dB]\). That is, the temporal discharge patterns of these units are more similar to the stimulus envelope autocorrelation function than the waveform autocorrelation function.

\(\chi^2\) analysis of the location of the first or largest peak in the autocorrelogram shows that for primarylike units, there is a difference in the responses to IIRN\([+, \tau, -1 dB]\) and IIRN\([-\tau, \tau, -1 dB]\), but the difference does not exist for chopper units. Thus a discrimination between IIRN\([+, \tau, -1 dB]\) and IIRN\([-\tau, \tau, -1 dB]\) can be made based on temporal discharge patterns of primarylike units, whereas a discrimination between IIRN\([+, \tau, -1 dB]\) and IIRN\([-\tau, \tau, -1 dB]\) cannot be made on the basis of the temporal discharge properties of chopper units. Current models that account for the pitch and pitch strength of iterated rippled noises are based on temporal processing of the waveform fine structure (Patterson et al. 1996; Yost 1996a,b, 1997; Yost et al. 1996), and the present study shows that the temporal discharge patterns of primarylike units are driven by the waveform fine structure. More recent psychophysical data argue that the pitch perception of iterated rippled noises cannot be based on stimulus envelope (Yost et al. 1998), and the present results show that the temporal discharge patterns of chopper units are driven by the stimulus envelope of IIRN. This finding is consistent with the idea that chopper units are principal subsystems that encode stimulus envelope in their temporal discharge (see Greenberg and Rhode 1987).

Coloration discrimination

At the present time, it is not known whether chinchillas can discriminate IIRN\([+, \tau, -1 dB]\) from IIRN\([-\tau, \tau, -1 dB]\).

**DISCUSSION**

The responses of primarylike and chopper units in the chinchilla cochlear nucleus were measured to the same IIRN stimuli that have been studied previously in psychophysical experiments using chinchillas (Shofner and Yost 1995) and human listeners (Fastl 1988; Raatgever and Bilsen 1992). Temporal responses of single units were studied using autocorrelograms or all-order ISI histograms. Neural autocorrelograms show the probability of discharge after a given spike; that is, they show the average firing pattern of a unit after a spike. Autocorrelation analysis provides a robust representation of the pitch related information encoded in the spike trains of auditory nerve fibers (Cariani and Delgutte 1996a,b; Palmer 1992). The present results show that a temporal representation of \(\tau\) can be obtained in neural autocorrelograms in response to IIRN\([\pm, \tau, -1 dB]\) from both primarylike and chopper units. To gain some insight into the relative importance of primarylike and chopper units, it is informative to make comparisons between the neurophysiological data and behavioral results with respect to IIRN pitch and coloration discrimination.

**IIRN pitch**

The perceived pitch of IIRN\([+, 4 ms, -1 dB]\) corresponds to \(1/\tau\) or 250 Hz, whereas the pitch of IIRN\([-4 ms, -1 dB]\) corresponds to \(1/2\tau\) or 125 Hz (Fastl 1988; Raatgever and Bilsen 1992). In other words, human listeners can discriminate IIRN\([+, 4 ms, -1 dB]\) from IIRN\([-4 ms, -1 dB]\) based on pitch. Autocorrelograms of some primarylike units show peaks at time lags of \(\tau\) and integer multiples of \(\tau\) in the neural autocorrelograms in response to IIRN\([+, \tau, -1 dB]\), but nulls at times lags of \(\tau\) followed by a peak at \(2\tau\) in the autocorrelograms in response to IIRN\([-\tau, \tau, -1 dB]\). These primarylike units typically show phase-locking to BF tones. Thus the temporal discharge patterns of this phase-locked group of primarylike units are similar to the stimulus waveform auto-

### Table 1. Summary of the paired comparisons based on Tukey’s HSD test

<table>
<thead>
<tr>
<th>Unit Type, BF, Stimulus Condition</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primarylike, 0.64–1.6 kHz, WBN</td>
<td>Not significant</td>
</tr>
<tr>
<td>vs. Chopper, 0.64–1.6 kHz, WBN</td>
<td>Not significant</td>
</tr>
<tr>
<td>Primarylike, &gt;1.6 kHz, WBN vs.</td>
<td>Not significant</td>
</tr>
<tr>
<td>Chopper, &gt;1.6 kHz, IIRN</td>
<td>Not significant</td>
</tr>
<tr>
<td>Primarylike, 0.64–1.6 kHz, IIRN vs. Chopper, &gt;1.6 kHz, IIRN</td>
<td>Not significant</td>
</tr>
<tr>
<td>Primarylike, 0.64–1.6 kHz, WBN vs.</td>
<td>Not significant</td>
</tr>
<tr>
<td>Chopper, 0.64–1.6 kHz, IIRN vs.</td>
<td>Not significant</td>
</tr>
<tr>
<td>Chopper, &gt;1.6 kHz, IIRN</td>
<td>Not significant</td>
</tr>
<tr>
<td>Primarylike, 0.64–1.6 kHz, IIRN vs. Chopper, &gt;1.6 kHz, WBN</td>
<td>Not significant</td>
</tr>
<tr>
<td>Primarylike, 0.64–1.6 kHz, WBN vs.</td>
<td>Not significant</td>
</tr>
<tr>
<td>Chopper, 0.64–1.6 kHz, IIRN vs.</td>
<td>Not significant</td>
</tr>
<tr>
<td>Chopper, &gt;1.6 kHz, IIRN</td>
<td>Not significant</td>
</tr>
</tbody>
</table>

The particular paired comparison is indicated in bold italics. WBN, wide-band noise; IIRN, infinitely iterated rippled noise.

At the present time, it is not known whether chinchillas can discriminate IIRN\([+, \tau, -1 dB]\) from IIRN\([-\tau, \tau, -1 dB]\).

*FIG. 14.* Bar graphs showing the number of occurrences that the peak in the neural autocorrelograms occurred at a time lag of \(\tau\) or \(2\tau\) for primarylike and phase-locked units (A) and chopper units (B). Responses to IIRN\([+, \tau, -1 dB]\) are shown by ■; responses to IIRN\([-\tau, \tau, -1 dB]\) are shown by □.
Behavioral studies using chinchillas (Shofner and Yost 1995, 1997) have been based on coloration discrimination paradigms (see Bilsen and Ritsma 1970). In the coloration discrimination experiment, the listener discriminates IIRN from WBN, and chinchillas can easily discriminate $\text{IIRN}[+, 4 \text{ ms}, -1 \text{ dB}]$ from WBN (Shofner and Yost 1995, 1997). In the present study, the magnitudes of the temporal responses were compared between $\text{IIRN}[+, 4 \text{ ms}, -1 \text{ dB}]$ and WBN. The response to WBN provides insights into the temporal response to a noise that does not generate a pitch and then can be compared with the temporal response to a noise that does generate a relatively salient pitch. For human listeners, the pitch strength of $\text{IIRN}[+, 4 \text{ ms}, -1 \text{ dB}]$ is $\sim 50\% - 60\%$ of the pitch strength of a harmonic tone complex (see Yost 1996b).

The magnitude of the neural response was estimated as the normalized rate at $\tau$ milliseconds from the neural autocorrelograms. The peak at $\tau$ is generally the largest $\tau$-related peak in the autocorrelogram. Yost (1996b) has shown that the pitch strength of $\text{IIRN}[+, \tau, \text{att}]$ can be accounted for using a model based on the height of the first peak in the autocorrelation function. The average normalized rate at a time lag of 4 ms in response to $\text{IIRN}[+, 4 \text{ ms}, -1 \text{ dB}]$ is larger for the sample of primarylike units than that of the chopper units, whereas the average normalized rate at a time lag of 4 ms is the same for primarylike and chopper units in response to WBN. Moreover, the average normalized rates at 4 ms are larger for primarylike units in response to $\text{IIRN}[+, 4 \text{ ms}, -1 \text{ dB}]$ than in response to WBN, whereas the average normalized rates at 4 ms for chopper units in response to $\text{IIRN}[+, 4 \text{ ms}, -1 \text{ dB}]$ are not different from those obtained in response to WBN. However, for some units the largest peak in the neural autocorrelogram is observed at a time lag of $2\tau$ rather than at $\tau$ (e.g., see Fig. 9, B and D). Peaks at $2\tau$ also should convey information about pitch strength. A single-factor ANOVA and subsequent paired comparisons based on either the normalized rates at $2\tau$ or an average of the normalized rates at $\tau$ and $2\tau$ also showed that the responses of primarylike units are larger than chopper units. Moreover including the data at $2\tau$ does not make the difference between IIRN and WBN statistically significant for chopper units. Thus the largest $\tau$-related temporal responses for IIRN are those associated with primarylike units not chopper units. Chopper units do show an enhancement of synchronization compared with primarylike units in response to the fundamental frequency of SAM tones, complex tones and synthetic vowels (Frisina et al. 1990; Keilson et al. 1997; Rhode 1998; Rhode and Greenberg 1994; Wang and Sachs 1994). Although the periodic stimuli that have been used in the preceding studies do generate the perception of pitch in human listeners, these stimuli also possess highly modulated stimulus envelopes. The enhanced synchronization to the fundamental frequency observed for chopper units in response to periodic complex sounds having highly modulated envelopes is not found for their temporal responses to IIRN stimuli.

Conclusion

The results of the present study show that primarylike units give larger temporal responses than chopper units to IIRN, and the temporal responses of primarylike units can account for the differences in pitch between $\text{IIRN}[+, \tau, -1 \text{ dB}]$ and $\text{IIRN}[-, \tau, -1 \text{ dB}]$, whereas those of chopper units cannot. However, it cannot yet be concluded that primarylike units are the principal cochlear nucleus subsystem that encodes the pitch related information in their temporal discharge. The present study did not sample onset-type-I (on-I) and onset-chopper units, which have been suggested to be important cochlear nucleus subsystems that encode pitch-related information in their temporal discharge patterns (Greenberg and Rhode 1987; Kim and Leonard 1988; Kim et al. 1986). Recent studies have shown that on-I units may not give strong temporal responses to IIRN stimuli. Nevertheless, the results of the present study suggest that the contribution of primarylike units in the temporal encoding of pitch-related information is not insignificant. Although primarylike units may not be the principal subsystem, they are likely to be an important cochlear nucleus subsystem underlying the perception of pitch.

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