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Wiener Kernels of Chinchilla Auditory-Nerve Fibers: Verification Using Responses to Tones, Clicks, and Noise and Comparison With Basilar-Membrane Vibrations

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Abstract

Responses to tones, clicks, and noise were recorded from chinchilla auditory-nerve fibers (ANFs). The responses to noise were analyzed by computing the zeroth-, first-, and second-order Wiener kernels (h_0 , h_1 , and h_2). The h_1 s correctly predicted the frequency tuning and phases of responses to tones of ANFs with low characteristic frequency (CF). The h_2 s correctly predicted the frequency tuning and phases of responses to tones of all ANFs, regardless of CF. Also regardless of CF, the kernels jointly predicted about 77% of the features of ANF responses to “frozen” samples of noise. Near-CF group delays of kernels and signal-front delays of responses to intense rarefaction clicks exceeded by 1 ms the corresponding basilar-membrane delays at both apical and basal sites of the chinchilla cochlea. This result, confirming that synaptic and neural processes amount to 1 ms regardless of CF, permitted drawing a map of basilar-membrane delay as a function of position for the entire length of the chinchilla cochlea, a first for amniotic species.

INTRODUCTION

The relationship between basilar-membrane (BM) vibrations and the discharges of auditory-nerve fibers (ANFs) has been most systematically explored in chinchilla, especially at the cochlear site with characteristic frequency (CF) of 9–10 kHz. For this site, BM and ANF responses to similar stimuli are available from healthy cochleae in different groups of animals (Robles et al. 1986; Ruggero and Rich 1983, 1987; Ruggero et al. 1990, 1996b) and, exceptionally, also for the same cochleae of 2 individuals (Narayan et al. 1998). These data sets have permitted investigators to draw a number of conclusions regarding the transformations that acoustic signals undergo between mechanical vibrations and the generation of spike trains in the auditory nerve (Ruggero et al. 2000). However, a crucial gap remains in our knowledge of basal regions of the chinchilla cochlea: the phases of responses at CF of high-CF ANFs are not known at all because of the weakness of phase locking at high frequencies (Johnson 1980; Palmer and Russell 1986). Now we bridge that gap, taking

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advantage of the ability of 2nd-order Wiener kernel analysis to extract timing information even in the absence of phase locking.

The present study complements a companion paper (Recio-Spinoso et al. 2005), which described 1st- and 2nd-order Wiener kernels computed from the responses to white Gaussian noise of chinchilla ANFs. Here we validate Wiener analysis by comparing responses to tones, clicks, and noise with predictions based on the Wiener kernels. First we show that the responses to tones and the Wiener kernels of responses to noise have similar frequency tuning, regardless of ANF CF. Second, we exploit the residual phase locking in responses to tones of high-CF ANFs to show a satisfactory match between the timing of responses to tones and noise, again regardless of CF. Third, we show that ANF responses to “frozen” noise are well predicted by the zeroth-, 1st-, and 2nd-order Wiener kernels (h_0 , h_1 , and h_2), jointly. Finally, we use near-CF group delays from Wiener kernels and signal-front delays from responses to intense rarefaction clicks to estimate the synaptic and neural delays interposed between spike generation and mechanical vibrations of the chinchilla cochlea and to construct maps of BM delay as a function of distance throughout the length of the chinchilla cochlea, a first for amniotic species.

METHODS

Animal preparation and physiological recordings

Most of the techniques used here for animal preparation were published previously (Ruggero and Rich 1983,1987). Adult chinchillas were anesthetized with an initial injection of ketamine (100 mg/kg, subcutaneous) and with sodium pentobarbital (65 mg/kg, intraperitoneal), supplemented with additional doses of pentobarbital to maintain a complete absence of limb-withdrawal reflexes. Rectal temperature of the animals was maintained near 38°C using an electric heating pad. Tracheotomy and tracheal intubation allowed for forced respiration, which was used only as necessitated by apnea or labored breathing. The pinna was resected and part of the bony external ear canal was chipped away to permit visualization of the umbo of the tympanic membrane and insertion of the earphone-coupling speculum. After opening the bulla widely, the tendon of the tensor tympani muscle was severed and the stapedius was detached from its bony anchoring to prevent reflex muscle contraction at high stimulus levels. A silver-ball electrode was placed on the round window to record compound action potentials.

The auditory nerve was approached superiorly after craniotomy and aspiration of part of the cerebellum. Capillary-glass microelectrodes (filled with 3 M NaCl or KCl solutions, impedance 20–70 M Ω) were positioned under visual control through an operation microscope and were advanced into the nerve by means of a remotely controlled hydraulic positioner.

Stimulus generation and protocols

Frequency–threshold tuning curves (FTCs) were obtained for responses to tone pips using an automated procedure (Lieberman 1978;Ruggero and Rich 1983). CFs and CF thresholds were determined by fitting a standard function to the FTC tips (Recio-Spinoso et al. 2005). Electrical tones were produced with a Tucker Davis WG1 or a custom-built digital waveform generator under computer control (Ruggero and Rich 1983) and transduced into an acoustic waveform by a Beyer DT-48 earphone. The amplitude and phase of the waveform were specified according to a calibration table generated in situ at the beginning of the experiment.

Gaussian white noise was produced using an analog device (General Radio 1381), a Tucker Davis WG1, or, exceptionally (when 2nd-order kernels were not computed), by sampling from a read-only memory containing 8,192 16-bit words. In all cases, the bandwidth of the noise

stimulus was reduced to 15 kHz by analog filtering. The levels of the noise stimuli were usually selected so that they elicited rate responses slightly higher than spontaneous activity. Noise levels at CF are expressed as spectrum level (in dB SPL/Hz) or total pressure (in dB SPL) in an equivalent rectangular bandwidth computed individually for each ANF [see METHODS and Fig. 16 of companion paper (Recio-Spinoso et al. 2005) for details].

Noise stimuli were delivered either continuously (duration range: 40 s to 18 min; duration average: 3.75 min) or in multiple presentations of the same waveform (frozen noise; duration: 20, 40, or 100 ms, with duty cycle 1:2, presented with level identical to that of the continuous noise). During continuous tone or noise stimulation, both the stimulus and the evoked spike signals were recorded on a stereo digital audiotape recorder (Sony DTC-690: 16-bit resolution, sampling rate 44.1 or 48 kHz) for later analysis. The stimulus waveform was digitized with 16-bit resolution (TDT AD1) and stored in the computer, which also stored the neural responses as a series of spike times (measured at their initial edge with a TDT ET1) with 1- μ s resolution. The frozen noise samples were captured by digitization from the analog noise source and were later presented by a 16-bit D/A converter (TDT DA3-2).

Analysis of responses to noise

The 3 Wiener kernels of lowest order— h_0 , h_1 , and h_2 —were computed from the spike times and the digitized noise stimulus (sampling period: 22.68 or 20.83 μ s). h_0 is the average response rate. h_1 and h_2 , respectively, were derived from the 1st- and 2nd-order cross-correlations between the spike train and the noise stimulus [Eqs. 7 and 11 of the companion paper (Recio-Spinoso et al. 2005); see also Marmarelis and Marmarelis 1978; Schetzen 1989]. The magnitude and phase spectra of the h_2 s were obtained by Fourier transforming their highest-rank singular vectors [or 1st-rank singular vector (FSV)], h_2 -FSVs [Eq. 13 of companion paper (Recio-Spinoso et al. 2005)], using MATLAB function *fft*. Input to *fft* was the h_2 -FSV padded with zeroes to a total sample length of 4,096. Statistical significance of the vector strength [VS_{noise} ; obtained from 1st-order reverse correlations; see Fig. 12 of Recio-Spinoso et al. (2005)] was determined by computation of the quantity $2nVS^2$, where n is the number of spikes. Further details on the computation of the Wiener kernels and singular value decomposition are given in a companion paper (Recio-Spinoso et al. 2005).

Analysis of responses to tones

Responses to tones were analyzed using cross-correlograms (between the spike trains and the stimulus tones) and their Fourier transforms to obtain the Fourier magnitude at the stimulus frequency (R , with units of spikes/s), the vector strength (VS_{tones}), and phase (θ_{tones}) (Goldberg and Brown 1969; Mardia and Jupp 2000)

$$VS_{tones} = \frac{R}{2N_0} \quad (1)$$

$$\theta_{tones} = \arctan [\Sigma \sin(\varphi_i) / \Sigma \cos(\varphi_i)] \quad (2)$$

where N_0 is the average (i.e., DC) response rate (spikes/s) and φ_i is the phase angle of the i th spike ($0 \leq \varphi_i \leq 2\pi$).

To assess the statistical significance of phase locking of responses to tones (VS_{tones}), the statistic $2nVS^2$ was computed, where n is the number of spikes (Mardia and Jupp 2000). Except where explicitly noted, $2nVS^2 > 10.6$ for all of the tone data reported here. With $2nVS^2 > 10.6$, phase locking is significant with $P < 0.01$.

Prediction of responses to frozen noise

Peristimulus time histograms (PSTHs, *black traces* in Figs. 6–8) were constructed from 256, 512, or 1,024 responses to frozen noise stimuli with binwidth of 200 μ s (or 500 μ s for 2 low-CF fibers). Predictions were obtained by convolving in the time domain the frozen noise stimuli with zeroth-, 1st-, and 2nd-order Wiener kernels acquired at the same level of continuous Gaussian noise. Then predictions were averaged within bins corresponding to those of the PSTHs (*blue* and *red traces* in Figs. 6–8).

The ability of the kernels to account for responses to frozen noise was quantified using the *coefficient of determination* (COD)

$$\text{COD} = 1 - \left[\frac{\sum_i^N (p_i - m_i)^2}{\sum_i^N (m_i)^2} \right] \quad (3)$$

where N is the number of time bins in the measured response (the PSTH) and the predicted response, p_i is the predicted instantaneous rate in time bin i (e.g., *red traces* in Figs. 6–8), and m_i is the measured instantaneous rate in time bin i (e.g., *black traces* in Figs. 6–8). The COD is expressed in % throughout the paper.

RESULTS

We tested the validity of Wiener-kernel analysis by comparing responses to tones and frozen noise with response predictions derived from the Wiener kernels computed for the same ANFs. In addition, we compared cochlear delays derived from the Wiener kernels and from ANF responses to intense clicks with direct measurements of the corresponding delays in BM responses to tones, noise, and clicks.

Wiener-kernel predictions of ANF responses to tones

Figure 1 compares frequency tuning in responses of low- and mid-CF ANFs to tones and noise. Responses to tones are represented in Fig. 1 by their frequency–threshold tuning curves (dotted lines). Tuning in responses to low- or moderate-level noise stimuli is indicated by the magnitudes of the Fourier transforms of the 1st-order Wiener kernels (hereafter, “ h_1 s”; dashed lines) and the 1st-rank singular vectors of the 2nd-order kernels (hereafter, “ h_2 -FSVs”; continuous lines). The magnitude spectra of the h_1 s and h_2 -FSVs were very similar to each other and also similar to the frequency–threshold tuning curves (only within about 20–30 dB of CF threshold because of the limited dynamic range permitted by Wiener-kernel analysis of spike trains). When the tuning revealed by tones and noise differed significantly, the discrepancy could be explained by the fact that the kernels were occasionally measured with noise stimuli well above threshold, which result in wider bandwidths than at threshold [e.g., see Figs. 13 and 14 of the companion paper (Recio-Spinoso et al. 2005)].

For ANFs with BF > 2 kHz, the signal-to-noise ratios of the h_1 s decreased steadily as a result of the loss of phase locking, impeding the reliable measurement of frequency tuning in high-CF ANFs. For such ANFs, reliable measurements of frequency tuning in responses to noise were derived from h_2 -FSVs (Fig. 2). Figure 2 compares frequency tuning in responses to tones and noise of high-CF ANFs. In general, the magnitude spectra of h_2 -FSVs (continuous line) were very similar to the FTCs of responses to tones (dotted line) within about 20–30 dB of CF threshold.

Figure 3 explores the strength of phase locking in responses to noise and tones as a function of frequency. The thick dashed line indicates the trend line for a measure of reverse-correlation (revcor) magnitude, VS_{noise} [see Fig. 12 in the companion paper (Recio-Spinoso et al. 2005)], which is analogous to vector strength for responses to tones (Goldberg and Brown 1969). This trend line is also consistent with the vector strengths for responses to noise (VS_{noise} , diamonds) and tones (VS_{tones} , circles and squares) recorded in the same ANFs (phases plotted in Fig. 5B). Note that good matches between noise and tone data extend to at least 10.5 kHz. For comparison with the chinchilla data, Fig. 3 includes vector-strength trend lines for responses to tones in guinea pig (dashed line) and cat (dotted line) ANFs (from data of Palmer and Russell 1986 and Johnson 1980, respectively, summarized in Weiss and Rose 1988). Except for probable differences in corner frequencies, vector strength in all 3 species can be simply described as a low-pass function with high-frequency slope of roughly -18 dB/octave. The corner frequency for chinchilla ANFs is intermediate between those for cat ANFs (highest) and guinea pig (lowest).

The correspondence between Wiener kernels and the FTCs for responses to tones is further explored in Fig. 4. Figure 4A shows that the CFs for responses to tones were nearly the same as the best frequencies (BFs) of responses to noise measured from revcors, h_1 s and h_2 s in the same ANFs. [We distinguish between CF, the frequency that yields the most sensitive responses at threshold levels in normal adult cochleae, and BF, the frequency of peak sensitivity. Each ANF has a unique CF but has various BFs that depend on cochlear maturity (Overstreet et al. 2002) or health and stimulus level.] It is apparent from Fig. 4A that, in spite of decreasing signal-to-noise ratio as a function of increasing BF, BFs could be reliably determined from windowed h_1 s [see Fig. 10B of companion paper (Recio-Spinoso et al. 2005)] in many ANFs with BF as high as 10 kHz.

Figure 4B compares the sharpness of tuning of responses to tones and noise, measured as Q_{10dB} (CF or BF divided by the bandwidth of tuning at +10 dB re CF or BF threshold). In general, responses to noise and tone stimuli revealed frequency tuning that varied similarly with CF. However, the sharpness of tuning of many high-CF ANFs was underestimated by the h_1 s (closed circles in Fig. 4B) as a result of their poor signal-to-noise ratio [Fig. 2; see also Fig. 12 of companion paper (Recio-Spinoso et al. 2005)].

Figure 5A compares the phases of responses to tones (open circles) and noise (lines, from the Fourier transforms of revcors) for several low-CF ANFs. It is evident that noise and tone stimulation yielded very similar response phases, both at CF (filled circles) and at higher and lower frequencies.

Timing information from the near-CF responses of high-CF ANFs (Fig. 5B) was obtained from the h_2 -FSVs [see *red traces* of Figs. 4A and 9, and *color traces* of Fig. 14A of companion paper (Recio-Spinoso et al. 2005)]. In 7 of these ANFs, responses to tones were also measured at CF and/or at other frequencies. [The strength of phase locking (*vector strength*) for each of the responses to tones of the ANFs of Fig. 5B is indicated in Fig. 3.] All but one of the responses to tones of the 4 ANFs with CFs <6 kHz exhibited highly significant phase locking ($2nVS^2 > 10.6$; $P < 0.005$) but the ANFs with CFs >6 kHz were not significantly phase locked. Nevertheless, Fig. 5B shows that the phases of responses to tones with frequency >6 kHz (open symbols) were very similar to the phases of responses to noise (lines, from the Fourier transforms of the h_2 -FSVs) at the same frequencies. On average, the phases of responses to tones of the ANFs of Fig. 5B differed from the phases of the corresponding responses to noise, at the same frequencies and comparable stimulus levels, by only $21 \pm 20^\circ$ ($n = 7$).

To summarize: 1st- and 2nd-order Wiener kernels of responses to noise correctly predicted the frequency tuning (Figs. 1–4) and timing characteristics (Fig. 5) of responses to tones, regardless of ANF CF.

Wiener-kernel predictions of ANF responses to frozen noise

We further assessed the ability of Wiener analysis to characterize ANF responses by testing the accuracy with which the kernels predicted responses to a short sample of white Gaussian noise (“frozen noise”). Thirty-eight ANFs (CFs: 109 Hz to 14 kHz) were stimulated with many repetitions of the frozen noise (illustrated at the *top* of Figs. 6–8). Responses of the same ANFs were also elicited using white Gaussian noise of long duration, presented at the same spectral level as the frozen noise. Wiener kernels computed from the long-duration noise were used to predict the average responses to the short-duration frozen noise. The predicted waveforms were synthesized by summing h_0 (i.e., the average response rate) and the 1st- and/or 2nd-order functionals [i.e., the convolutions of the h_1 s and h_2 s with the frozen-noise waveform (Marmarelis and Marmarelis 1978; Schetzen 1989)].

The *black traces* of Fig. 6, A–D show the PSTH for the responses of a representative low-CF ANF to many repetitions of the frozen noise. The histogram consisted of an oscillation with periodicity corresponding to CF (109 Hz). The responses predicted by h_0 and h_1 individually are shown in Fig. 6A (*green* and *blue traces*, respectively). It is apparent that the waveform predicted by h_1 accounts for much of the response, its major deficiency being that it is not rectified. The absence of rectification is ameliorated by including h_0 (Fig. 6A, *green trace*) in the prediction (Fig. 6C, *blue trace*). Figure 6B shows the individual contribution of h_2 . When this contribution is added to that of h_0 and h_1 , the predicted response (Fig. 6D, *red trace*) improves further and closely approximates the actual response histogram.

The panels of Fig. 7 show the PSTH (*black trace*) for responses of a representative high-CF ANF to many repetitions of the frozen noise. In contrast with the responses of low-CF fibers to the same stimulus (Fig. 6), the fine structure of the histograms of Fig. 7 is unrelated to CF. The fine structure probably bears a relation to the average frequency of the random amplitude modulation expected from a narrow bandpass filter stimulated by white noise (Rice 1954; Ruggero 1973). The responses predicted by h_0 and h_2 are shown individually in Fig. 7A (*green* and *red traces*, respectively). Their joint prediction (*red trace* in Fig. 7B) accounts for most of the features of the histogram.

The ability of the kernels to account for responses to frozen noise was quantified using the COD (see Eq. 3 in METHODS). The COD equals 100% for a perfect prediction. The CODs for the predictions based on the kernels individually or jointly are indicated in red in Figs. 6–8. [The initial 7 ms of the responses were excluded from the computations of the CODs (see *blue bars* in Fig. 8) because the Wiener kernels, inasmuch as they are based on well-adapted ANF responses during continuous noise stimulation, cannot predict the response onsets.] In the case of the ANF of Fig. 6, with the lowest CF in our sample, the CODs for the joint predictions of h_0 , h_1 , and h_2 averaged 83%. In other words, the 3 kernels jointly predicted 83% of the features of the response histograms. In the case of the high-CF ANF of Fig. 7, h_0 and h_2 jointly predicted 85% of the measured response. [Note that the sum of the individual CODs (i.e., those computed separately for h_0 , h_1 , or h_2) is not the same as the COD for their joint prediction.]

Figure 8 compares the measured responses to frozen noise (*black traces*) and the responses predicted by the Wiener kernels (*red traces*) for 10 ANFs with widely ranging CFs (392 Hz–11.5 kHz). The responses to the frozen noise differed between low- and high-CF ANFs in that

the carrier was absent from the latter, but all responses, regardless of CF, were well matched by predictions based on the Wiener kernels.

Figure 9 summarizes the quality of predictions based on the kernels for the entire data set of 38 ANFs stimulated with frozen noise. Triangles and open and closed circles in Fig. 9A indicate, respectively, the CODs for the predictions based individually on h_0 , h_1 , and h_2 . In the case of ANFs innervating apical regions of the cochlea, h_0 , h_1 , and h_2 contributed roughly equally, between 10 and 40%, to the overall prediction of the response histograms. The contributions of h_0 varied widely in high-CF ANFs and were, on average, marginally larger than those in low-CF ANFs. The contributions of the h_1 s were relatively constant in low-CF ANFs but insignificant in high-CF ANFs (dashed line). The contributions of h_2 grew monotonically as a function of increasing CF (dotted line). For most high-CF ANFs, the contributions of h_2 were dominant, typically accounting for $\geq 50\%$ of the responses.

The CODs for the joint predictions of the 3 kernels are shown in Fig. 9B (closed circles). On average, h_0 , h_1 , and h_2 accounted jointly for $77.4 \pm 9.7\%$ ($n = 38$) of the responses of chinchilla ANFs, regardless of CF (dashed line). For low-CF ANFs (CF < 2.7 kHz), the CODs for the 1st- and 2nd-order predictions averaged 65.3 and 75.1%, respectively. For high-CF ANFs (CF > 2.7 kHz), the CODs for the 1st- and 2nd-order predictions were 45.8 and 78.6% on average. In other words, the 2nd-order predictions improved the 1st-order predictions by amounts that grew as a function of increasing CF.

Interestingly, it was possible to obtain fairly accurate predictions of the responses to frozen noise by using h_0 s and h_1 s jointly with severely reduced versions of h_2 , constructed on the basis of either the h_2 -FSV alone or the singular vectors with 1st and 2nd ranks. Figure 9C shows that the predictions based on the FSV alone (upward triangles) accounted for 71.6% of the response features (i.e., only slightly worse than the predictions based on the complete h_2 s) and predictions based on reduced h_2 s constructed from the 2 highest ranked singular vectors (i.e., 1st and 2nd ranks; downward triangles) were similar. However, the former (reduced h_2 s based on the FSVs alone) yielded better predictions than the latter for low-CF ANFs and worse predictions for high-CF ANFs. These results are consistent with the finding that the singular vectors of rank other than 1st for low-CF ANFs and ranks other than 1st or 2nd for high-CF ANFs represent spurious features accompanying poor h_2 signal-to-noise ratios [Fig. 7B of companion paper (Recio-Spinoso et al. 2005)].

DISCUSSION

Relationship between h_1 s and responses to tones of low-CF ANFs

The close match between the magnitude spectra of the h_1 s and the tips of the frequency–threshold tuning curves of low-CF ANFs in chinchilla (Figs. 1 and 4) is consistent with previous findings for low-CF ANFs of cat (de Boer 1969, 1973; Evans 1977), guinea pig (Harrison and Evans 1982), and rat (Møller 1978). In all 4 species, the frequency–threshold tuning curves of low-CF ANFs are closely approximated (over a limited, 20- to 30-dB range) by h_1 s estimated using noise levels near threshold.

Comparisons between phases of h_1 s and responses to tones of low-CF ANFs have not been carried out previously. The present results for chinchilla (Fig. 5A) demonstrate that the phases and group delays of h_1 s and responses to tones are similar when measured in the same ANFs.

Validation of 2nd-order Wiener analysis: prediction of frequency tuning of high-CF ANFs

No previous investigation in a mammalian species has compared the frequency tuning or the phases of responses to noise of high-CF ANFs with those of responses to tones. The present

results in chinchilla show that, within 20–30 dB of CF threshold, the frequency tuning of high-CF ANFs can be measured equally well with h_2 s and FTCs of responses to tones (Figs. 2 and 4). However, the h_2 s based on stimulation with low-to-moderate level noise (as we used in the present investigation) provide no information on the high-threshold tails of frequency–threshold tuning curves of high-CF ANF responses to tones.

Validation of 2nd-order Wiener analysis: prediction of phases of responses to high-frequency tones of high-CF ANFs

In the companion paper we demonstrated that h_2 s [and also h_1 s to some extent, Figs. 9, 10B, 11, and 12 of Recio-Spinoso et al. (2005)] can provide timing information on the responses of most ANFs, regardless of CF. The present results show that, at least in some high-CF ANFs, the strength of phase locking is sufficient (diamonds in Fig. 2) to permit measuring the phases of responses to tones with frequency as high as 10 kHz. In these high-CF ANFs, the absolute phases (Fig. 5B), the phase-versus-frequency functions, and thus also the group delays (Fig. 13B), of high-frequency responses to tones and noise are very similar.

With but a single (and probably questionable) exception (Teich et al. 1993), phase-locked responses to tones with frequency as high as 10 kHz (e.g., Fig. 5B) have not been previously demonstrated in ANFs in any mammalian species. Nevertheless, Fig. 3 shows that the rate of decay of phase-locking strength as a function of increasing frequency in chinchilla is roughly consistent with previous results in guinea pig and cat. It has been suggested that residual phase locking for high-frequency stimuli provides significant temporal information and, in humans, plays an important role in encoding frequencies at least ≤ 10 kHz (Heinz et al. 2001).

Validation of 2nd-order Wiener analysis: predictions of responses to frozen noise

The present results demonstrate that predictions of responses of low-CF ANFs based jointly on h_0 , h_1 , and h_2 are far superior to those based on h_1 alone (Figs. 6–8). In fact, most aspects of the responses of low-CF ANFs to frozen noise, including rectification, are closely approximated by predictions based on the first 3 kernels, jointly accounting for 60–90% of the responses (vs. 30–40% accounted for by h_1 alone).

Wickesberg et al. (1984) were the first to use h_2 s for the study of auditory neurons in the cat cochlear nucleus. They estimated the quality of predictions of responses to noise on the basis of h_0 , h_1 , and h_2 . Even when conditions were optimal, as illustrated in their Fig. 2 (Wickesberg et al. 1984), the 3 kernels jointly predicted <50% of the responses of low-CF neurons and “... the addition of the second kernel improved a prediction based on the zero- and first-order kernels, but not by very much.” In contrast, our general finding for chinchilla low-CF ANFs is that 2nd-order predictions (based on the 3 kernels) *almost always* improved the 1st-order predictions (based solely on h_0 and h_1).

The single previous use of h_2 s to study mammalian ANFs (in gerbil; Lewis et al. 2002) did not evaluate systematically the quality of response predictions based, either individually or jointly, on h_0 , h_1 , and h_2 , apparently because the h_2 s measured in gerbil were excessively contaminated by noise (Recio-Spinoso et al. 2005; see also p. 220 of Lewis et al. 2002).

Comparison of onset latencies in responses to noise and clicks

For linear systems, h_1 is identical to the unit impulse response (or its approximation, the response to intense clicks). In the case of ANFs, the compressive growth of the underlying BM responses and the rectifying nature of the spike-generating process conspire to substantially distort the responses to clicks (e.g., Goblick Jr. and Pfeiffer 1969; Lin and Guinan Jr. 2000). Nevertheless, it is reasonable to expect some similarity between the features of ANF responses

to clicks and Wiener kernels. Figure 10A presents the onset latencies, or signal-front delays, of responses to intense rarefaction clicks of 420 ANFs recorded in 29 chinchillas [previously reported in partial form; see Fig. 10 of Ruggero and Rich (1987)]. To facilitate comparison between the onset latencies of responses to clicks and noise (Fig. 15A of the companion paper), dashed trend lines are indicated for the 2 sets of data. The solid trend line is a fit to the responses to clicks based on one previously published for low-CF chinchilla ANFs (Ruggero and Rich 1987) but modified to take into account BM responses to clicks at high-CF cochlear sites (see Fig. 13A). The dashed lines were fitted separately to the signal-front delays of Wiener kernels for ANFs with BFs lower and higher than 2.7 kHz [from Fig. 15A of the companion paper (Recio-Spinoso et al. 2005)]. Figure 10A makes it clear that for ANFs with BF < 2.7 kHz there is an excellent match between the onset latencies of responses to clicks and Wiener kernels of responses to noise. The match is also good for BFs > 5 kHz but poorer for intermediate BFs because of an apparent discontinuity at 2.7 kHz of the function relating Wiener kernel signal-front delays to BF [see Fig. 15 and corresponding discussion in companion paper (Recio-Spinoso et al. 2005)].

Figure 10B presents the onset latencies of responses to intense condensation clicks. The trend line, obtained by adding 0.5BF periods to the fit function for intense rarefaction clicks (i.e., solid line in Fig. 10A), satisfactorily matches the latencies to condensation clicks for BFs > 350 Hz but overestimates those latencies for BFs < 350 Hz. This we attribute to the presence of “glides,” from high to low frequencies, at the onset of the Wiener kernels of ANFs with BFs < 350 Hz [see Fig. 17A of companion paper (Recio-Spinoso et al. 2005)].

Estimation of cochlear filter delays as a function of BF

The availability of estimates of near-BF group delays [Fig. 15B of companion paper (Recio-Spinoso et al. 2005)] and signal-front delays (Fig. 10A) throughout the entire range of BFs of chinchilla ANFs permits the assessment of cochlear filter delays as a function of BF (or, equivalently) cochlear position. Cochlear filter delays are defined as the portion of the near-BF group delay that exceeds the signal-front delay (Goldstein et al. 1971; Ruggero 1980). The filter delays were computed by subtracting the trend function for signal-front delays of responses to clicks (solid line in Fig. 10A) from the Wiener-kernel group delays (from Fig. 15B of companion paper). [Note that those group delays were computed from responses to the lowest available noise levels. In equivalent rectangular bands, the noise levels exceeded by only about 10 dB the thresholds of responses to CF tones; see Fig. 16 of the companion paper (Recio-Spinoso et al. 2005).] The filter delays are plotted as a function of BF in Fig. 11, A and B with units of time (ms) and BF periods, respectively. In units of time (Fig. 11A), filter delay decreases monotonically with increasing BF. In period units (Fig. 11B), filter delay monotonically *increases* with increasing BF. Such dependencies of filter delay on BF are consistent with the well-known increase of sharpness of tuning (in terms of Q_{10}) as a function of increasing BF (Fig. 4B).

Comparison between responses to broadband stimuli of ANFs and BM sites of the chinchilla cochlea

Wiener kernels computed from responses to noise of high-CF ANFs differ fundamentally from their counterparts in the vibratory responses of the BM sites at the base of the chinchilla cochlea in that 1) BM h_1 s (Recio et al. 1997) are prominent and closely resemble BM responses to clicks (Recio et al. 1998), whereas the h_1 s of high-CF ANF responses are nearly buried in the baseline noise [Fig. 2; see also Fig. 10 of Recio-Spinoso et al. (2005)]; and 2) BM h_2 s are very small or insignificant (Recio et al. 1997), whereas the h_2 s of ANF responses are prominent (Recio-Spinoso et al. 2005).

The insignificance of h_2 s in BM vibrations indicate that these contain only small amounts of even-order distortion (Recio et al. 1997). This is consistent with the dearth of harmonic distortion in BM responses to tones at basal cochlear sites in chinchilla (Ruggero et al. 1997) and guinea pig (Cooper 1998) and with the similarity between BM h_1 s and responses to clicks (Recio et al. 1998). These quasi-linear relations, which may seem paradoxical in the context of the prominent level- and frequency-dependent compressive nonlinearities of BM vibrations (Robles and Ruggero 2001), constitute a striking, albeit poorly understood, aspect of cochlear mechanics (see de Boer 1993; Recio et al. 1998; Zwislocki et al. 1997). Because the even-order nonlinearities revealed by the h_2 s of high-CF ANFs do not arise in BM nonlinearities, they must arise at more central stages of cochlear signal encoding, including transduction currents and the generation of DC receptor potentials at the inner hair cells, as well as synaptic transmission, all processes characterized by asymmetrical input-output functions that produce rectification and/or other even-order nonlinearities (reviewed in Ruggero 1992).

Figure 12A compares the h_2 -FSV of an ANF (CF: 9.5 kHz) and the h_1 for a BM site with similar CF (Recio et al. 1997). The same acoustic system and similar-level noise stimuli were used in recordings from 2 different chinchillas. The h_2 -FSV from the ANF and the BM h_1 strongly resemble each other but the former is delayed relative to the latter.

Figure 12B presents the Fourier magnitudes of the BM h_1 of Fig. 12A and of other h_1 s measured for higher-level stimuli at the same BM site. It is clear from Fig. 12B that BM and ANF responses of similar CF exhibited similar frequency tuning when stimulated by noise presented at low stimulus levels. For higher stimulus levels, the BM responses had increasingly broader tuning. A similar trend exists in responses to noise of ANFs [Figs. 11 and 12 of companion paper (Recio-Spinoso et al. 2005)], presumably as a result of the corresponding changes in BM vibrations.

Relative timing of BM vibrations and ANF responses to noise: estimation of synaptic and neural delays

The timing of responses to clicks and other transient stimuli, as well as Wiener kernels in the time domain, may be characterized by their signal-front and near-CF group delays (Ruggero 1980, 1994). The near-CF group delay is identical to the weighted-average group delay (i.e., the average of the slopes of the phase-vs.-frequency curves weighted according to spectral magnitude) of well-tuned responses and corresponds to the center of gravity of responses to transient stimuli (Goldstein et al. 1971; Ruggero 1980). In the case of low-level stimuli, the weighted-average group delay gives the slope of the phase-versus-frequency curve near CF (Ruggero 1994). We use here the near-CF group delays and the signal-front delays of responses of the BM and of ANFs to estimate the synaptic delay intervening between cochlear mechanical vibrations and the generation of spikes in ANFs.

In the companion paper, we presented near-CF group delays of chinchilla ANF responses to noise, computed from the phase-versus-frequency curves of h_2 -FSVs [Fig. 15B of Recio-Spinoso et al. (2005)]. The trend line representing those data [derived from responses to low-level noise stimuli; see Fig. 16 of companion paper (Recio-Spinoso et al. 2005)] is reproduced in Fig. 13B (dashed line), which also includes a trend line (dotted line) for the near-CF group delays computed from phase-versus-frequency curves of chinchilla ANF responses to tones (Temchin and Ruggero 2001). The group delays for responses to tones (dotted line) and noise (continuous line) varied similarly as a function of CF but the former were somewhat shorter. The group-delay differences between the responses to tones and noise probably reflect the unequal stimulus levels (tones were presented at 60–70 dB, whereas noise stimuli were presented at near-threshold levels) and are consistent with the well-known inverse variation of

group delays of ANF and BM vibrations as a function of stimulus intensity [e.g., Figs. 13 and 14 of the companion paper (Recio-Spinoso et al. 2005) and Fig. 1 of Ruggero (1994)].

The symbols in Fig. 13B depict near-CF group delays derived from cochlear mechanical responses at basal (Narayan and Ruggero 2000; Recio et al. 1997, 1998; Ruggero et al. 1997, 2000) and apical (Cooper 1997) sites of the chinchilla cochlea, with the upper and lower brackets indicating the range of group delays for near-threshold and intense stimuli, respectively. [Other phase-vs.-frequency curves for responses to tones at basal BM sites of the chinchilla cochlea have been published (Rhode and Recio 2000) but are not shown in Fig. 13B because they are available only for relatively intense stimuli (70 dB).] The synaptic and neural delays intervening between cochlear vibrations at the 3.5- and 14-mm sites of the chinchilla cochlea and the arrival of action potentials at a microelectrode near ANFs with appropriate CFs can be estimated by measuring the time differences between the trend lines for ANF responses and the symbols indicating BM vibrations. The solid black line, which is identical to the dashed curve but displaced downward by 1 ms, fits the BM data very well, indicating that on average action potentials arrive at the microelectrode in the auditory nerve about 1 ms after transduction in inner hair cells is initiated by deflection of their stereocilia. The 1-ms delay is identical to previous estimates for chinchilla ANFs from our laboratory (Ruggero and Rich 1987; Ruggero et al. 1996b) but somewhat longer than the synaptic delay (700–800 μ s) estimated in the guinea pig cochlea (Palmer and Russell 1986).

Figure 13A compares the latencies of signal-front delays in ANFs and at the BM. The dashed line indicates the trend of the latencies of ANF responses to intense rarefaction clicks (from Fig. 10A). After subtracting 1 ms to compensate for synaptic/neural delays, the BM signal-front delays derived from ANF responses (continuous line) match almost perfectly the latencies directly measured in cochlear (BM and tectorial-membrane) responses to intense rarefaction clicks. This match supports the conclusion based on group delays (Fig. 13B) that a frequency-independent delay amounting to 1 ms intervenes between cochlea mechanical vibrations and the initiation of nerve impulses.

Finally, Fig. 14 compares the frequency glides observed in h_2 -FSVs of ANFs and basilar membrane responses. The line is the trend line taken from Fig. 17 of the companion paper (Recio-Spinoso et al. 2005) and the symbols represent basilar membrane data obtained at several sites of the chinchilla cochlea. There is an excellent match between the neural and BM data in that both sets of data indicate high-to-low frequency glides for CFs <1 kHz and low-to-high glides for higher CFs. Interestingly, the neural data for CFs >4 kHz also support the contention, based on BM data, that the “relative amount of FM ... decreases with increasing CF” at the base of the cochlea (Recio and Rhode 2000).

Do 2nd-order Wiener kernels yield accurate absolute phases?

Although 2nd-order Wiener kernels are capable of revealing timing information otherwise masked by low-pass filtering, such as in the receptor potentials of inner hair cells [see Figs. 5B and 6 of companion paper (Recio-Spinoso et al. 2005)], it is not clear whether they can also compensate for the effects of neural time jitter. In particular, the excellent match between the high-frequency phases of responses to tones and noise in the same ANFs (Fig. 5B) does not necessarily imply that population averages of ANF response phases can yield unambiguous information about high-frequency cochlear responses phases. The deleterious effect of time jitter is probably minimal when comparing high-frequency phases of responses to tones and/or noise recorded at slightly different times from the same ANFs, and may be altogether absent in comparisons of *relative* phases (e.g., for different frequencies in a single spike train). As a result, near-CF group delays (Fig. 13B) computed from ANF phase-versus-frequency curves faithfully reflect the group delay of the antecedent basilar-membrane vibrations (see *Relative*

timing of BM vibrations and ANF responses to noise: estimation of synaptic and neural delays, above). In contrast, the varying time jitters of recordings from *different* ANFs (even those innervating the same inner hair cell) may hopelessly scramble the response phases, thus preventing the use of averaging for extracting meaningful *absolute cochlear phases* at high frequencies. Indeed, plots of absolute phases versus BF [not shown either in this or the companion paper (Recio-Spinoso et al. 2005)] exhibit great scatter and it is doubtful that statistical trends computed from such plots are reliable. We are now investigating this issue, which we consider unresolved.

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FIG 1.

Frequency tuning of responses to tones and noise recorded in the same low-characteristic frequency (CF) auditory-nerve fibers (ANFs). Responses to tone pips are represented by their frequency-threshold tuning curves (dotted lines). Responses to noise are represented by the magnitudes of the Fourier transforms of the windowed 1st-order kernel (h_1 s; dashed lines) and the 2nd-order kernel– first-rank singular vector (h_2 -FSVs; solid lines). Windowing procedure [Fig. 10 of Recio-Spinoso et al. (2005)] does not affect the h_1 waveforms of low-CF ANFs but may reduce h_1 noisiness in the case of high-CF ANFs. CF, CF threshold (Th), noise spectral pressure level at CF, and noise total pressure in equivalent rectangular bandwidth (ERB; between parentheses) are given below in order of increasing CF. A: CF = 100 Hz, Th = 35 dB SPL, 18 dB SPL/Hz (37 dB SPL); CF = 173 Hz, Th = 43 dB SPL, 46 dB SPL/Hz (69 dB SPL); CF = 463 Hz, Th = 19 dB SPL, 0 dB SPL/Hz (22 dB SPL); CF = 678 Hz, Th = 9 dB SPL, -6 dB SPL/Hz (18 dB SPL); CF = 890 Hz, Th = 5 dB SPL, -20 dB SPL/Hz (4 dB SPL). B: CF = 1,195 Hz, Th = 21 dB SPL, 3 dB SPL/Hz (30 dB SPL); CF = 2,048 Hz, Th = 19 dB SPL, 4 dB SPL/Hz (29 dB SPL); CF = 2,652 Hz, Th = 28 dB SPL, 14 dB SPL/Hz (42 dB SPL); CF = 3,621 Hz, Th = 18 dB SPL, 7 dB SPL/Hz (35 dB SPL); CF = 4,569 Hz, Th = 10 dB SPL, -6 dB SPL/Hz (22 dB SPL).

FIG 2.

Frequency tuning of responses to tones and noise recorded in the same high-CF ANFs. Responses to tone pips are represented by the frequency–threshold tuning curves (dotted lines). Responses to noise are represented by the magnitudes of the Fourier transforms of the h_2 -FSVs (solid lines). CF, CF threshold, noise spectral pressure level at CF, and noise total pressure in ERB (between parentheses) are given below in the order of increasing CF. CF = 5,151 Hz, Th = 9 dB SPL, -4 dB SPL/Hz (25 dB SPL); CF = 6,173 Hz, Th = 21 dB SPL, -5 dB SPL/Hz (22 dB SPL); CF = 11,160 Hz, Th = 9 dB SPL, -20 dB SPL/Hz (11 dB SPL); CF = 13,924 Hz, Th = 15 dB SPL, -9 dB SPL/Hz (22 dB SPL).

FIG 3.

Strength of phase locking as a function of CF in ANF responses to noise and tones. Thick dashed line indicates the trend of the magnitude of the 1st-order cross-correlograms (revcors) normalized to stimulus amplitude [from Fig. 12 of the companion paper (Recio-Spinoso et al. 2005)]. This measure is the noise-response analog of vector strength for responses to tones (Goldberg and Brown 1969). Also shown are vector strengths for near-CF tone (diamonds) and noise (triangles) data obtained from 7 fibers (identified as *B1–B7*) in 2 chinchillas. (Corresponding phases are shown in Fig. 5*B*; see also the legend of Fig. 5 for ANF sensitivity and noise levels.) Squares indicate vector strengths for non-CF tone data from fibers *B1* and *B3* of Fig. 5*B*; *B1*: CF = 3,646 Hz, tones at 1,890 Hz (68 dB SPL) and 5,500 Hz (67 dB SPL); *B3*: CF = 4,927 Hz, tones at 1,000 Hz (61 dB SPL) and at 6,500 Hz (58 dB SPL). Diamonds and triangles represent, respectively, the vector strength of responses to CF tones and the normalized magnitudes of responses to noise measured in the same ANFs. For all but one tone response of ANFs *B1–B4*, phase locking was statistically significant ($2nVS^2 > 10$; $P < 0.005$). Tone responses of ANFs *B5–B7* were not significantly phase locked in a statistical sense. Also shown are trend lines for vector strength at CF computed from responses to tones in cat (dotted line) and guinea pig (dashed line), taken from Fig. 3 of Weiss and Rose (1988), which summarized data of Johnson (1980) and Palmer and Russell (1986).

FIG 4.

Frequency tuning measured with tones and with noise. *A*: peak frequencies [best frequencies (BFs)] of the windowed h_1 s [closed circles; see Fig. 10*B* of the companion paper (Recio-Spinoso et al. 2005)] and the h_2 -FSVs (open circles) are plotted against the CFs of the frequency-threshold tuning curves for responses to tones. Also shown are “revcors” (triangles) from ANFs for which 2nd-order kernels were unavailable (M. A. Ruggero and N. C. Rich, unpublished data). CFs were not available for some ANFs. *B*: sharpness of tuning of responses to tones (squares) or noise (open and closed circles) are expressed as Q_{10dB} and plotted against h_2 -FSV BF.

FIG 5.

Phases of responses to tones and noise recorded in the same ANFs. Lines indicate the phases of responses to noise, as a function of frequency. Filled symbols indicate the phase at BF. Open symbols indicate responses to tones of the same ANFs. *A*: comparisons of the phases of responses derived from 1st-order kernels and responses to tones in low-CF ANFs in 2 chinchillas. CF, CF threshold, noise spectral pressure level at CF, noise total pressure in ERB (between parentheses), and tone levels were as follows. *A1*: 267 Hz, 31 dB SPL; noise: 33 dB SPL/Hz (56 dB SPL); tones: 30 dB SPL. *A2*: 534 Hz, 34 dB SPL; noise: 30 dB SPL/Hz (55 dB SPL); tones: 20 dB SPL. *A3*: 739 Hz, 23 dB SPL; noise: 51 dB SPL/Hz (76 dB SPL); tones: 40 dB SPL. *A4*: 1,682 Hz, 50 dB SPL; noise: 29 dB SPL/Hz (57 dB SPL); tones: 40 dB SPL. *A5*: 1,835 Hz, 33 dB SPL; noise: 10 dB SPL/Hz (36 dB SPL); tones: 40 dB SPL. *A6*: 1,958 Hz, 43 dB SPL; noise: 20 dB SPL/Hz (45 dB SPL); tones: 30 dB SPL. *B*: comparisons of the phases of responses to noise and tones in high-CF ANFs from 2 other chinchillas. Phases of responses to noise were derived from the FSVs of h_2 with polarities chosen to match those of the windowed h_1 s [see Fig. 10*B* of Recio-Spinoso et al. (2005)]. Phases of responses to tones were computed with Eq. 2. CF, CF threshold; noise spectral levels at CF, and total pressure in ERB (between parentheses); tone levels and duration (*t*), and number of spikes (*N*) in responses to tones were as follows. *B1*: CF: 3,646 Hz, 7 dB SPL; noise: -2 dB SPL/Hz (26 dB SPL); tones: 3,650 Hz, 17–37 dB SPL (*t* = 168 s; *n* = 30,692, 29,745, 29,207). *B2*: CF: 4,627 Hz, 10 dB SPL; noise: -3 dB SPL/Hz (25 dB SPL); tones: 4,630 Hz, 5–25 dB SPL (*t* = 235, 175, 225 s; *n* = 31,886, 27,271, 34,860); *B3*: CF: 4,937 Hz, 7 dB SPL; noise: -6 dB SPL/Hz (23 dB SPL);

tones: 4,940 Hz, 10–30 dB SPL ($t = 175$ s; $n = 25,791, 25,649, 24,006$); *B4*: CF: 5,746 Hz, 19 dB SPL; noise: 25 dB SPL/Hz (55 dB SPL); tones: 5,750 Hz, 24–34 dB SPL ($t = 295$ s; $n = 8,870, 20,275$); *B5*: CF: 6,403 Hz, 21 dB SPL; noise: –5 dB SPL/Hz (22 dB SPL); tones: 6,400 Hz, 15 dB SPL ($t = 175$ s, $n = 5,811$); *B6*: CF: 8,861 Hz, 3 dB SPL; noise: –6 dB SPL/Hz (25 dB SPL); tones: 8,850 Hz, 31 dB SPL ($t = 230$ s, $n = 29,893$); *B7*: CF: 10,538 Hz, 10 dB SPL; noise: –10 dB SPL/Hz (19 dB SPL); tones: 10,000 Hz, 16 dB SPL ($t = 70$ s, $n = 6,275$). Three data points (*B2*, *B3*, and *B4*) were shifted rightward by 50 Hz to avoid complete overlapping.

FIG 6.

Wiener-kernel predictions of responses to frozen noise for a low-CF ANF. Averaged responses to 256 repetitions of a frozen noise sample (illustrated at *top*) are indicated by peristimulus time histograms (PSTHs; *black traces* in A–D). Response predicted by h_0 (i.e., the mean rate) is indicated by the *green trace* in A. Response predicted by h_1 individually is indicated by the *blue trace* in A. Response predicted by h_2 individually is indicated by the *red trace* in B. C: *red trace* indicates the response predicted by h_0 and h_1 jointly. D: *red trace* indicates the joint prediction by all 3 kernels. Binwidth = 500 μ s. Goodness of the predictions is indicated as the *coefficient of determination* (COD, in %) in each panel. $h_0 = 119.2$ spikes/s. Stimulus level for both frozen and continuous Gaussian noise was 18 dB SPL/Hz (37 dB SPL in ERB). Kernels

for the same fiber are shown in Fig. 8 (#1) of the companion paper (Recio-Spinoso et al. 2005).

FIG 7.

Wiener-kernel predictions of responses to frozen noise for a high-CF ANF. Averaged responses to 512 repetitions of a frozen noise sample (illustrated at *top*) are indicated by PSTHs (*black traces* in A and B). Responses predicted individually by h_0 and h_1 are indicated in A by the *green* and *red* traces, respectively. Responses predicted jointly by h_0 and h_2 are indicated in B (*red trace*). Binwidth = 200 μ s. Goodness of the predictions is indicated as CODs (in %) in each panel. $h_0 = 152.6$ spikes/s. Stimulus level for both frozen and continuous Gaussian noise was -5 dB SPL/Hz (24 dB SPL in ERB). Kernels of the same fiber are shown in Fig. 9 (#7) of the companion paper (Recio-Spinoso et al. 2005).

FIG 8.

Wiener-kernel predictions of ANF responses to frozen noise. Averaged responses to many presentations of a frozen noise sample (illustrated at *top*) are indicated by PSTHs (*black traces*). ANFs had CFs between 0.4 and 11.5 kHz. Responses predicted jointly by the Wiener kernels are indicated by the *red traces*. Binwidth = 200 μ s. Blue bars indicate the time window used for COD computation. CF thresholds, noise spectral pressure levels at CF, and noise total pressure in ERB (in parenthesis) in order of increasing CF: 28 dB SPL, 8 dB SPL/Hz (30 dB SPL); 37 dB SPL, 15 dB SPL/Hz (37 dB SPL); 23 dB SPL, 10 dB SPL/Hz (33 dB SPL); 26 dB SPL, 24 dB SPL/Hz (50 dB SPL); 28 dB SPL, 14 dB SPL/Hz (42 dB SPL); 22 dB SPL, 4 dB SPL/Hz (33 dB SPL); 15 dB SPL, -5 dB SPL/Hz (24 dB SPL); 9 dB SPL, minus; 18 dB

SPL/Hz (10 dB SPL); 10 dB SPL, minus; 18 dB SPL/Hz (12 dB SPL); 9 dB SPL, minus; 20 dB SPL/Hz (11 dB SPL).

FIG 9.

Quantitative estimates of the quality of predictions of responses to frozen noise based on Wiener-kernel analysis. Quality of the predictions of responses from 38 ANFs from 4 chinchillas is quantified using the COD (expressed as a percentage; see Eq. 3). Abscissa indicates CF. Noise spectral pressure level at CF averaged 1.6 ± 14.5 dB SPL/Hz ($n = 38$); equivalently, noise total pressure in ERB 29.2 ± 13.8 dB SPL. **A:** CODs for the individual predictions of h_0 , h_1 , and h_2 are indicated by the triangles and the open and closed circles, respectively. A smoothed step function (dashed line) accurately fits the variation with log CF of the COD based solely on h_1 ($r^2 = 0.98$). A linear function of log CF (dotted line) fits somewhat less well ($r^2 = 0.64$) the variation with CF of the COD based solely on h_2 . **B:** CODs for predictions based on h_0 individually (triangles), h_0 and h_1 jointly (open circles), and by all 3 kernels jointly (closed circles). Bracketed closed circle at right and the dashed line indicate

the average COD for predictions based on all 3 kernels jointly, $\pm$ SD ($77.4 \pm 9.7\%$, $n = 38$).
C: COD for the joint predictions of h_0 , h_1 , and a reduced h_2 . Reduced h_2 s were constructed on the basis of the 2 highest-rank singular vectors (downward triangles) or the h_2 -FSV only (upward triangles). Bracketed upward triangle at *right* and the dashed line indicate the average COD for predictions based on zeroth-, 1st-, and reduced (h_2 -FSV only) 2nd-order kernel, $\pm$ SD ($71.6 \pm 10.8\%$, $n = 38$). See text for details.

FIG 10.

Onset latencies of ANF responses to rarefaction and condensation clicks. Latencies τ were obtained from compound PSTHs (binwidth: 40 μ s) of responses to intense (peak: about 104 dB SPL) clicks [M. A. Ruggero, N. C. Rich and A. N. Temchin, unpublished data; partially reported in Ruggero and Rich (1987)]. *A*: onset latencies of responses to intense rarefaction clicks. Solid fit line is: $\tau \text{ (ms)} = 1.244 + 2.402e^{-1.699CF} + 0.083e^{-0.269CF}$. Dashed trend lines are linear-log fits of signal-front delays from h_2 -FSVs computed from responses to noise [see Fig. 15A of the companion paper (Recio-Spinoso et al. 2005)]. *B*: onset latencies of responses to intense condensation clicks. Dashed fit line is the trend line of A plus 0.5CF period.

FIG 11.

Filter delay of low-level basilar-membrane (BM) responses. BM filter delays were obtained by subtracting signal-front delays (i.e., the latencies of ANF responses to intense rarefaction clicks) from the near-BF group delays of Wiener kernels of responses to low-level noise. Distance scale was computed from the BFs using Greenwood's cochlear map for chinchilla (Greenwood 1990). *A*: filter delay expressed in milliseconds. Trend line is the difference: trend line of Fig. 15B of the companion paper (Recio-Spinoso et al. 2005) minus trend line of Fig. 10A. *B*: filter delay expressed as periods of BF.

FIG 12.

Comparison between the responses to noise of an ANF and a BM site with similar CFs. BM data are from cochlea L160, taken from Fig. 1 of Recio et al. (1997). BM site, located some 3.5 mm from the extreme basal end of the cochlea, and the ANF (from another animal) both had a CF of about 9.5 kHz. Noise levels are indicated near each response as a spectral level at CF, in dB SPL/Hz, and as a total pressure in ERB (between parentheses). *A*: time-domain comparison; the 1st-order kernel of BM vibration responses (thin line) and the FSV of the 2nd-order kernel of an ANF (thick line). *B*: frequency-domain comparison: the Fourier magnitudes of the h₁s of BM responses to noise presented at several levels (thin lines) and the h₂-FSV of ANF responses (thick line). All neural and mechanical data were normalized to their respective peak magnitudes. CF threshold = -3 dB SPL; spontaneous rate = 149.2/s; h₀ = 137.3/s.

FIG 13.

Onset latencies and near-CF group delays of responses of ANFs and BM sites in the chinchilla cochlea. A: dashed line is the central tendency for the onsets of chinchilla ANF responses to intense rarefaction clicks (τ_{front} from Fig. 11A), which is also replotted after downward displacement by 1 ms (solid line). Filled square indicates the onset latency of h_1 s at a BM site with CF = 9 kHz (Recio et al. 1997). Open circle (Recio et al. 1998) and squares (Recio and Rhode 2000) indicate latencies of BM responses to clicks at basal sites of the chinchilla cochlea. Filled circle indicates the latency of the “slow” component of click-evoked tectorial-membrane vibrations at a site located some 14 mm from the basal end of the chinchilla cochlea (Cooper and Rhode 1996). Distance scale was computed using Greenwood’s map for the chinchilla cochlea (Greenwood 1990). Continuous trend line (BM τ_{front}) is the equation: τ_{front} (ms) =

$0.018 + 2.4e^{-1.70CF} + 0.083e^{-0.27CF}$. *B*: dashed line represents the central tendency of the near-CF group delays (τ_{BFGD}) of the h_2 -FSVs of ANFs [corrected for a 0.225-ms acoustic/equipment delay but otherwise identical to curve of Fig. 15*B* of the companion paper (Recio-Spinoso et al. 2005)]. For high-CF BM vibrations, group delays were measured from h_1 s of responses to noise and from responses to tones (Narayan and Ruggero 2000; Recio and Rhode 2000; Recio et al. 1997; Ruggero et al. 1997, 2000). Low-CF mechanical group delay (filled circle) represents tone-evoked vibrations at a site of the tectorial membrane (CF = 500 Hz) located 14 mm from the base of the chinchilla cochlea [from Fig. 1*F* of Cooper (1997)]. Continuous line, identical to the dashed line but displaced downward by exactly 1 ms, indicates the equation $\tau_{BFGD} \text{ (ms)} = 0.496 + 1.863CF^{-0.771}$. Dotted line indicates a trend line computed from responses to tones at 60 or 70 dB SPL of ANFs with CFs <3 kHz (Temchin and Ruggero 2001). Some data points with CFs around 9–10 kHz region are slightly shifted to avoid overlapping.

FIG 14.

Frequency glides in ANF and BM responses. Trend line is taken from Fig. 17C of the companion paper (Recio-Spinoso et al. 2005). A dimensionless glide slope was computed by dividing the slope expressed in kHz/ms by BF^2 (i.e., kHz^2); see Fig. 17 of companion paper (Recio-Spinoso et al. 2005) for details. BM data computed from Fig. 4 of Ruggero et al. (1996a); Fig. 6A of Recio et al. (1998); Fig. 4B of Recio and Rhode (2000); Fig. 5 of Cooper and Rhode (1996). Downward triangle represents BM response (L160) shown in Fig. 12A.