Evaluating Auditory Performance Limits: II. One-Parameter Discrimination with Random-Level Variation

Michael G. Heinz
Speech and Hearing Sciences Program, Division of Health Sciences and Technology, Massachusetts Institute of Technology, Cambridge, MA 02139, U.S.A., and Hearing Research Center, Biomedical Engineering Department, Boston University, Boston, MA 02215, U.S.A.

H. Steven Colburn
Laurel H. Carney
Hearing Research Center, Biomedical Engineering Department, Boston University, Boston, MA 02215, U.S.A.

Previous studies have combined analytical models of stochastic neural responses with signal detection theory (SDT) to predict psychophysical performance limits; however, these studies have typically been limited to simple models and simple psychophysical tasks. A companion article in this issue ("Evaluating Auditory Performance Limits: I") describes an extension of the SDT approach to allow the use of computational models that provide more accurate descriptions of neural responses. This article describes an extension to more complex psychophysical tasks. A general method is presented for evaluating psychophysical performance limits for discrimination tasks in which one stimulus parameter is randomly varied. Psychophysical experiments often randomly vary a single parameter in order to restrict the cues that are available to the subject. The method is demonstrated for the auditory task of random-level frequency discrimination using a computational auditory nerve (AN) model. Performance limits based on AN discharge times (*all-information*) are compared to performance limits based only on discharge counts (*rate place*). Both decision models are successful in predicting that random-level variation has no effect on performance in quiet, which is the typical result in psychophysical tasks with random-level variation. The distribution of information across the AN population provides insight into how different types of AN information can be used to avoid the influence of random-level variation. The rate-place model relies on comparisons between fibers above and below the tone frequency (i.e., the population response), while the all-information model does not require such across-fiber comparisons. Frequency discrimination with random-level variation in the presence of high-frequency noise is also simulated. No effect is predicted for all-information, consistent with the small effect in human

performance; however, a large effect is predicted for rate-place in noise with random-level variation.

1 Introduction

The use of signal detection theory (SDT) combined with stochastic models of neural responses has provided much insight into neural encoding of sensory stimuli (e.g., Fitzhugh, 1958; Siebert, 1965, 1968, 1970; Colburn, 1969, 1973, 1977a, 1977b, 1981; Goldstein & Srulovicz, 1977; Delgutte, 1987; Erell, 1988; see Delgutte, 1996, and Parker & Newsome, 1998, for reviews). These studies evaluated psychophysical performance limits based on the stochastic behavior of neural responses. However, the application of this approach has been limited to simple psychophysical tasks due to the use of simple analytical models and by the restricted use of SDT with these models to deterministic stimuli. Computational neural models can describe more accurate physiological responses to a much wider range of stimuli than analytical models. Previous methods that have combined SDT and computational auditory models to predict psychophysical performance have either not included physiological (internal) noise (e.g., Gresham & Collins, 1998; Huettel & Collins, 1999) or have used arbitrary internal noise that was not directly related to physiological variability (e.g., Dau, Püschel, & Kohlrausch, 1996a, 1996b; Dau, Kollmeier, & Kohlrausch, 1997a, 1997b). Our companion article in this issue ("Evaluating Auditory Performance Limits: II") describes a general method that extends previous studies that have quantified the effects of physiological noise on psychophysical performance using analytical auditory nerve (AN) models (e.g., Siebert, 1968, 1970; Colburn, 1969, 1973) to incorporate the use of computational models; however, the SDT analysis in the companion article was limited to deterministic discrimination experiments. This study extends the general SDT approach described in the companion article to allow more complicated psychophysical tasks to be evaluated, specifically discrimination tasks in which one parameter is randomly varied from trial to trial.

Many psychophysical experiments have used random variation of certain stimulus parameters in order to limit the cues available to the subject. For example, McKee, Silverman, and Nakayama (1986) observed that human visual velocity discrimination was unaffected by random variation of either contrast or temporal frequency, and concluded that performance was mediated by sensing velocity. In the auditory system, this method has been used in profile analysis experiments to demonstrate that level discrimination of a single component within a tone complex or detection of a tone in noise is not affected by the randomization of overall level, and thus these tasks can be performed without relying on an absolute energy cue (Green, Kidd, & Picardi, 1983; Kidd, Mason, Brantley, & Owen, 1989; see Green, 1988 for a review). While psychophysical performance in the presence of overall-level randomization is typically unchanged, performance based on

single neurons would likely be severely degraded. Therefore, it is important to evaluate quantitatively how physiological responses can account for behavior in these types of psychophysical tasks. Durlach, Braida, and Ito (1986) described a quantitative model for profile analysis tasks based on across-frequency-level comparisons, which included the effects of both external (stimulus) variations and internal processing noise. However, the internal noise used in their model was not directly related to the known physiological noise that exists in AN fibers, and thus was somewhat arbitrary. Huettel and Collins (1999) evaluated the information loss in physiological auditory models that resulted from randomization of phase in a tone detection in noise experiment; however, their analysis did not include internal noise. Our study here extends the analysis in the companion article, which quantified performance limits for deterministic discrimination tasks based on Poisson neural discharges, to include the effect of random stimulus variation in a single parameter on psychophysical performance limits. In order to demonstrate this method, predictions for a random-level frequency discrimination task are evaluated using the same computational AN model used in the companion study. Predictions are made for both rate-place (based on discharge counts) and all-information (based on discharge times) encoding schemes, as was done in the companion study of pure-tone frequency and level discrimination. It is often stated that listeners use rate-place information to encode frequency at high frequencies, (e.g., Wever, 1949; Moore, 1973, 1989; Dye & Hafter, 1980; Wakefield & Nelson, 1985; Javel & Mott, 1988; Pickles, 1988; Moore & Glasberg, 1989), because AN phase locking rapidly degrades above 2 to 3 kHz (Johnson, 1980; Joris, Carney, Smith, & Yin, 1994; or see Figure 1c in the companion article). This analysis illustrates quantitatively the relation between random-level frequency discrimination and fixed-level frequency and level discrimination in terms of average-rate and temporal information.

Random-level variation has been used in several auditory frequency discrimination experiments to test rate-place models for frequency encoding (Henning, 1966; Verschuure & van Meeteren, 1975; Emmerich, Ellermeier, & Butensky, 1989; Moore & Glasberg, 1989). In this task, the listener is asked to discriminate the frequency of two tones whose levels are varied randomly and independently from trial to trial. Frequency-discrimination-in-quiet could hypothetically be performed by observing the average discharge rate of a single-frequency channel tuned either above or below the tone frequency (e.g., Zwicker, 1956, 1970; Henning, 1967). Such single-channel rate-based models would be expected to be affected greatly by random-level variation because changes in level could not be discriminated from changes in frequency. Conversely, temporal models would not be expected to be affected by random-level variation.

Several studies have observed an effect of random-level variation on frequency discrimination (e.g., Henning, 1966; Emmerich et al., 1989); however, the observed effect of random-level variation is likely to be largely due to

pitch shifts associated with the changes in level over the broad range of level variation used in these studies (Verschuure & van Meeteren, 1975; Emmerich et al., 1989). Moore and Glasberg (1989) measured frequency discrimination as a function of frequency with a smaller range of random-level variation and observed virtually no effect. Moore and Glasberg also measured frequency discrimination in the presence of high-frequency noise that was used to mask the characteristic frequencies (CF, the most sensitive frequency of the AN fiber) above the tone frequency. This experiment was designed to test the idea that rate-place models could avoid the effect of random-level variation by comparing information from CFs above and below the tone frequency. A small but significant effect of adding the high-frequency noise was observed, with a slightly larger effect when the noise was added to the random-level condition. Despite a similar magnitude of effect at all tone frequencies, Moore and Glasberg (1989) concluded that their results were consistent with the "duplex theory" for frequency encoding (Wever, 1949), that is, that rate-place information is used at high frequencies and temporal information is used at low frequencies. The results in this study question this conclusion by quantifying that there is insufficient rate-place information in the AN model to account for human performance with random-level variation under the assumption that the high-frequency noise masks all CFs above the tone frequency.

In addition to the specific results on the auditory task of random-level frequency discrimination, the current study is also a presentation of general methods for using SDT and computational neural models to address quantitatively questions of general interest to theoretical neuroscience. These methods are applicable to any sensory system for which there are statistical descriptions of neural responses as a function of the relevant stimulus parameters.

2 General Methods

2.1 Computational Auditory-Nerve Model. The computational AN model used in this study was the same model described in the companion study.[1] This AN model was a simplified version of a previous nonlinear AN model (Carney, 1993) and was used in order to simplify the verification of the computational SDT methods. The major components of the AN model are summarized below (see the companion article for a detailed description, and Ruggero, 1992, for a review of basic AN responses).

The initial model stage was a linear fourth-order gamma-tone filter bank, which was used to represent the frequency selectivity of AN fibers. Model filter bandwidths were based on psychophysical estimates of human bandwidths from Glasberg and Moore (1990). Each bandpass filter was followed

---

[1] Code for the AN model used in the study is available online at http://earlab.bu.edu/.

by a memoryless, asymmetric, saturating nonlinearity, which represents the mechano-electric transduction of the inner hair cell (IHC). All AN model fibers had a rate threshold of roughly 0 dB SPL, a spontaneous rate of 50 spikes per second, and a maximum sustained rate of roughly 200 spikes per second. The model dynamic range for sustained rate was roughly 20–30 dB, and the dynamic range for onset rate was much larger. The high-spontaneous-rate (HSR), low-threshold fibers described by the AN model represent the majority (61%) of the total AN population (Liberman, 1978). Medium- (23%) and low-SR (16%) fibers, which have higher thresholds and larger dynamic ranges, are not included in the model. The rolloff in phase locking was chosen to be consistent with all species discussed in Weiss and Rose (1988), and the cutoff frequency matched data from cat (Johnson, 1980). Neural adaptation was introduced through a simple three-stage diffusion model for the IHC-AN synapse based on data from Westerman and Smith (1988). The output of the ith AN model fiber represents the instantaneous discharge rate $r_i(t, f, L)$ of an individual high-spontaneous-rate, low-threshold AN fiber in response to an arbitrary stimulus. The AN discharges are assumed to be produced by a population of conditionally independent, nonstationary Poisson processes with rate functions described by $r_i(t, f, L)$ (see the companion article).

2.2 Signal Detection Theory. The application of SDT in this study is extended from the companion study to evaluate psychophysical tasks in which a single parameter is randomly varied. Performance limits are evaluated for both rate-place and all-information models and compared to data from human listeners. *Rate-place* predictions are based on the assumption that the population of AN-fiber discharge counts $\{K_i\}$ over the duration of the stimulus is the only information used by the listener. In contrast, the *all-information* predictions are based on the assumption that the listener uses the population of discharge times and counts $\{t^i_1, \ldots, t^i_{K_i}\}$, where t^i_j represents the jth discharge from the ith AN fiber. The contribution of temporal information in the responses can be inferred by comparing the predictions of the rate-place and all-information models. The all-information model does not assume any specific forms of temporal processing, such as calculating synchrony coefficients or creating interval histograms, and thus provides an absolute limit on achievable performance given the total information available in the AN.

3 General Analytical Results: One-Parameter Discrimination with One Unwanted Random Parameter

3.1 Overview of Basic Result. The use of SDT with stochastic models of neural responses has never been applied to the class of psychophysical tasks that randomly vary one parameter in order to restrict the cues that are

available to the subject. The SDT analysis of a general one-parameter discrimination experiment with one unwanted random parameter is a straightforward extension of the Cramér-Rao-bound analysis described in the companion article to the multiple-parameter case, as described in section 3.2. In this study, the analysis is described in terms of a random-level frequency-discrimination task. A performance limit for the just-noticeable difference in frequency for this task can be calculated as

$$\Delta f_{JND} = \left\{ E_L \left\{ \sum_i \left(\delta_f'[CF_i] \right)^2 \right\} - \frac{\left\{ E_L \left(\sum_i \delta_{Lf}'[CF_i] \right) \right\}^2}{E_L \left\{ \sum_i \left(\delta_L'[CF_i] \right)^2 \right\} + API_L} \right\}^{-\frac{1}{2}}, \quad (3.1)$$

where E_L denotes the expected value over the random-level range, $(\delta_f'[CF_i])^2$ and $(\delta_L'[CF_i])^2$ represent, for the ith fiber, the normalized sensitivities to changes in frequency and level, respectively, API_L represents the a priori information about level (e.g., the random-level range), and $\delta_{Lf}'[CF_i]$ represents the cross-interaction between changes in level and frequency on the ith AN fiber (see section 3.2 and the companion article). The normalized sensitivities and the cross-interaction terms in equation 3.1 can be evaluated in terms of the time-varying discharge rate $r_i(t, f, L)$ for each AN fiber. Thus, equation 3.1 can be used with any AN model (e.g., analytical or computational) and is applicable to any single-parameter discrimination experiment with one randomized parameter. This analysis is also applicable to any sensory system for which the statistics of the neural responses can be described as a function of the stimulus parameters of interest.

This general form of the relation between the performance limit and the relevant information quantities provides insight into the influence of random-level variation on the ability to perform frequency discrimination. Equation 3.1 illustrates that the neural information available about changes in frequency in the random-level experiment is equal to the average (over level) of the information available for fixed-level frequency discrimination, $E_L\{\sum_i(\delta_f'[CF_i])^2\}$, minus the amount of information that is lost due to the random-level variation. The numerator of the second term, $\{E_L(\sum_i \delta_{Lf}'[CF_i])\}^2$, represents the square of the average total correlation between the effect of changes in frequency and changes in level on the neural observations. If changes in level influence the observations in the same way as changes in frequency, then the information about changes in frequency is reduced in the presence of random-level variation. The denominator of the second term, $E_L\{\sum_i(\delta_L'[CF_i])^2\} + API_L$, is a normalization factor that represents the total information available about changes in level. The first term in the denominator is the average information about level from the AN observations, while the second term is the a priori information available about level from the limited random-level range. Thus, if the frequency-level cross term (the numerator) is comparable to the level information

(the denominator), then the random-level variation term (the subtracted term in equation 3.1) could be comparable to the first term and influence frequency-discrimination performance. The analysis thus illustrates the relation between information for random-level frequency discrimination and the information for fixed-level frequency and level discrimination.

3.2 Mathematical Analysis. In this section, the analysis leading to equation 3.1 is presented. In a random-level frequency discrimination experiment, the observations (Poisson discharge times on M AN fibers, $\mathcal{T} = \{t_1^i, \ldots, t_{K_i}^i; i = 1, \ldots, M\}$, where t_j^i represents the jth discharge on the ith fiber), are influenced by both the nonrandom, unknown frequency f and the random level L. The form of an optimal processor in this case can be theoretically derived using a likelihood-ratio test (LRT), in which the likelihood of the observations given frequency is integrated over the uncertainty in level for both hypotheses, Δf and $f + \Delta f$ (van Trees, 1968). However, the integrals over level (of the joint probability density of the conditionally independent AN fibers) in both the numerator and the denominator of the likelihood ratio prohibit simplification of the decision variable into a form for which performance can be evaluated analytically. An alternative to the LRT for evaluating psychophysical performance limits is the Cramér-Rao bound from estimation theory (Siebert, 1968, 1970; see the companion article), which provides a lower bound on the variance of any unbiased estimator. We demonstrated in the companion article that for deterministic discrimination experiments, where the independence of AN fibers permits simplification of the decision variable derived from the LRT, the Cramér-Rao bound on performance was met with equality by the LRT processor. Thus, the Cramér-Rao bound was used in the study presented here to calculate performance limits because performance evaluation of the optimal processor derived from the LRT is not easily calculated analytically for a one-parameter discrimination task in which an unwanted parameter is randomly varied. It is possible to evaluate the performance of the LRT processor using numerical simulations (e.g., Gresham & Collins, 1998; Huettel & Collins, 1999); however, in the case here for which performance based on the total population of 30,000 AN fibers is desired, such simulations would be arduous given the across-fiber correlations created by the random stimulus variability.

The Cramér-Rao bound for estimating a vector of random parameters ($N = 2$ in this case) can be used in this case (Cramér, 1951; see van Trees, 1968, pp. 84–85). In general, the information available to an observer to estimate a random parameter is the sum of the a priori information based on the known distribution of the parameter and the information available from the data. In order to treat the frequency parameter as nonrandom but unknown, the a priori information is set to zero. The Cramér-Rao bound provides a lower bound on the variance of any unbiased estimate of f, in

the presence of randomized level L, and is given by

$$
\frac{1}{\sigma_{\hat{f}}^2} \le E_{L,\mathcal{T}} \left\{ \left[\frac{\partial}{\partial f} \ln p \left(\mathcal{T} | L; f \right) \right]^2 \right\}
$$

$$
- \frac{\left(E_{L,\mathcal{T}} \left\{ \left[\frac{\partial}{\partial L} \ln p \left(\mathcal{T} | L; f \right) \right] \left[\frac{\partial}{\partial f} \ln p \left(\mathcal{T} | L; f \right) \right] \right\} \right)^2}{E_{L,\mathcal{T}} \left\{ \left[\frac{\partial}{\partial L} \ln p \left(\mathcal{T} | L; f \right) \right]^2 \right\} + E_L \left\{ \left[\frac{\partial}{\partial L} \ln p \left(L \right) \right]^2 \right\}}, \tag{3.2}
$$

where $E_{L,\mathcal{T}}$ indicates the expectation over both the random-level L and the random observations $\mathcal{T}$, and $p(L)$ is the probability density used to specify the random-level distribution and determines the a priori information for level. Equation 3.2 can be written in a more useful form using iterated expectations:

$$
\frac{1}{\sigma_{\hat{f}}^2} \le E_L \left(E_{\mathcal{T}} \left\{ \left[\frac{\partial}{\partial f} \ln p \left(\mathcal{T} | L; f \right) \right]^2 \middle| L \right\} \right)
$$

$$
- \frac{\left[E_L \left(E_{\mathcal{T}} \left\{ \left[\frac{\partial}{\partial L} \ln p \left(\mathcal{T} | L; f \right) \right] \left[\frac{\partial}{\partial f} \ln p \left(\mathcal{T} | L; f \right) \right] \middle| L \right\} \right) \right]^2}{E_L \left(E_{\mathcal{T}} \left\{ \left[\frac{\partial}{\partial L} \ln p \left(\mathcal{T} | L; f \right) \right]^2 \middle| L \right\} \right) + E_L \left\{ \left[\frac{\partial}{\partial L} \ln p \left(L \right) \right]^2 \right\}}. \tag{3.3}
$$

The probability density of the observed Poisson discharge times on all fibers is the product of the densities for individual fibers, assuming each fiber is conditionally independent given L (see Parzen, 1962; Snyder & Miller, 1991; Rieke, Warland, de Ruyter van Steveninck, & Bialek, 1997). Conditional independence results from the assumption that each AN fiber has an independent discharge-generating mechanism and that correlation between AN fibers results only from a common stimulus drive (see the companion article). The conditional expectations with respect to $\mathcal{T}$ are of a form that has been previously evaluated for Poisson observations (Siebert, 1970; see the companion article).

A lower bound on the just noticeable difference (JND) Δf_{JND} is equal to the minimum standard deviation of any estimator based on the observations, where threshold is defined as 75% correct in a two-interval, two-alternative forced-choice task (Green & Swets, 1966; Siebert, 1968, 1970). This threshold definition corresponds to $d' = 1$, where $d' = \Delta f_{JND} / \sigma_{\hat{f}}$. Thus, a performance limit on the JND based on the population of AN fibers is given by

$$
\frac{1}{(\Delta f_{JND})^2} = E_L \left\{ \sum_i \int_0^T \frac{1}{r_i(t, f, L)} \left[\frac{\partial r_i(t, f, L)}{\partial f} \right]^2 dt \right\}
$$

$$
- \frac{\left(E_L \left\{ \sum_i \int_0^T \frac{1}{r_i(t, f, L)} \left[\frac{\partial r_i(t, f, L)}{\partial L} \frac{\partial r_i(t, f, L)}{\partial f} \right] dt \right\} \right)^2}{E_L \left\{ \sum_i \int_0^T \frac{1}{r_i(t, f, L)} \left[\frac{\partial r_i(t, f, L)}{\partial L} \right]^2 dt \right\} + E_L \left\{ \left[\frac{\partial \ln p_L(L)}{\partial L} \right]^2 \right\}}, \tag{3.4}
$$

where the conditional expectations in equation 3.3 were evaluated by using the Poisson probability densities, as described in the companion article. Equation 3.4 describes a performance limit for discriminating frequency in the presence of random-level variation based on the AN population response in terms of the time-varying discharge rates $r_i(t, f, L)$. Following the notation used in the companion article,

$$(\delta'_f[CF_i])^2 \triangleq \int_0^T \frac{1}{r_i(t, f, L)} \left[\frac{\partial r_i(t, f, L)}{\partial f} \right]^2 dt, \tag{3.5}$$

and

$$(\delta'_L[CF_i])^2 \triangleq \int_0^T \frac{1}{r_i(t, f, L)} \left[\frac{\partial r_i(t, f, L)}{\partial L} \right]^2 dt. \tag{3.6}$$

The quantities $(\delta'_f[CF_i])^2$ and $(\delta'_L[CF_i])^2$ represent the information available on the ith fiber about frequency f and level L, respectively, and are shown in the companion article to represent normalized sensitivities, defined as the sensitivity d' per unit f or L (also see Durlach & Braida, 1969; Braida & Durlach, 1988). Similarly, the cross-interaction term is defined as

$$\delta'_{Lf}[CF_i] \triangleq \int_0^T \frac{1}{r_i(t, f, L)} \left[\frac{\partial r_i(t, f, L)}{\partial L} \frac{\partial r_i(t, f, L)}{\partial f} \right] dt, \tag{3.7}$$

and represents the correlation between changes in level and changes in frequency on the ith fiber. Based on this notation, equation 3.4 is equivalent to equation 3.1, where API_L represents the a priori information available about level (e.g., from the range of levels used in the random variation of level).[2]

4 Computational Methods: Use of Auditory Nerve Models

All predictions in this study were made using the computational AN model in the identical manner used in the companion article. Briefly, predictions are based on the total population of high-spontaneous-rate (HSR) AN fibers, which are simulated using 60 model CFs ranging from 100 Hz to 10 kHz. The model CFs are uniformly spaced in location according to a human cochlear map (Greenwood, 1990). In order to account for the total number

---

[2] A gaussian distribution was used to calculate API_L due to the analytical difficulty for a uniform distribution that results from the undefined derivative with respect to L for levels at the edges of a uniform distribution. The a priori information for level was calculated to be $API_L = 2\pi/R^2$ for a gaussian distribution with a variance of $R^2/2\pi$, where R represents the random-level range in dB. A gaussian distribution with variance $R^2/2\pi$ has the same equivalent-rectangular width as a uniform distribution with random-level range R.

of AN fibers in the HSR population, predictions are based on a population of 12,200 total HSR fibers, where each of the 60 model responses represents roughly 200 conditionally independent AN fibers. Tone frequencies were always chosen to be equal to one of the 60 model CFs. Stimulus duration was defined as the duration between half-amplitude points on the stimulus envelope. All rise/fall ramps were generated from raised cosine functions. The temporal window in the all-information analysis included the model response beginning at stimulus onset and ending 25 ms after stimulus offset, in order to allow for the response delay and the transient onset and offset responses associated with AN fibers over the range of CFs and stimulus parameters used in this study. Predictions for the rate-place encoding scheme were based on the average discharge rate across the entire temporal analysis window (i.e., including the extra 25 ms after the nominal offset of the stimulus).

5 Computational Results

5.1 Random-Level Frequency Discrimination in Quiet. Predictions of performance limits for the random-level frequency discrimination task were calculated using equation 3.1 for the same values of frequency, level, and duration we used in the companion article. A random-level range was uniformly distributed and centered around the nominal level for each condition. For all conditions, there was no effect of random-level variation for the rate-place or all-information schemes for either a 6 dB or a 20 dB random-level range (neither shown).[3] This result is consistent with human performance measured by Moore and Glasberg (1989), in which no effect of random-level variation was observed with a 6 dB range. Conversely, Emmerich et al. (1989) observed a factor of three degradation in human performance when measured with a 20 dB random-level range; however, they showed that much of this effect was due to the confounding role of level-dependent shifts in pitch (Verschuure & van Meeteren, 1975), which are not likely to be produced by the simplified AN model used in this study. The results for both rate-place and all-information models thus support the idea that there is no effect of random-level variation on frequency discrimination when a small enough random-level range is used to avoid the influence of level-dependent-pitch effects (Moore & Glasberg, 1989).

In order to illustrate how each encoding scheme can discriminate frequency accurately in the presence of random-level variation, the distribu-

---

[3] The effect of random-level variation was evaluated by comparing random-level performance (given by equation 3.1) to average (across level) fixed-level performance (determined by the first term in equation 3.1, $E_L\{\sum_i (\delta'_f[CF_i])^2\}$). This comparison avoids any potential effect of variation in performance across the levels within the random-level range, which could result in a difference between fixed-level performance and average fixed-level performance that was not truly an effect of random-level variation.
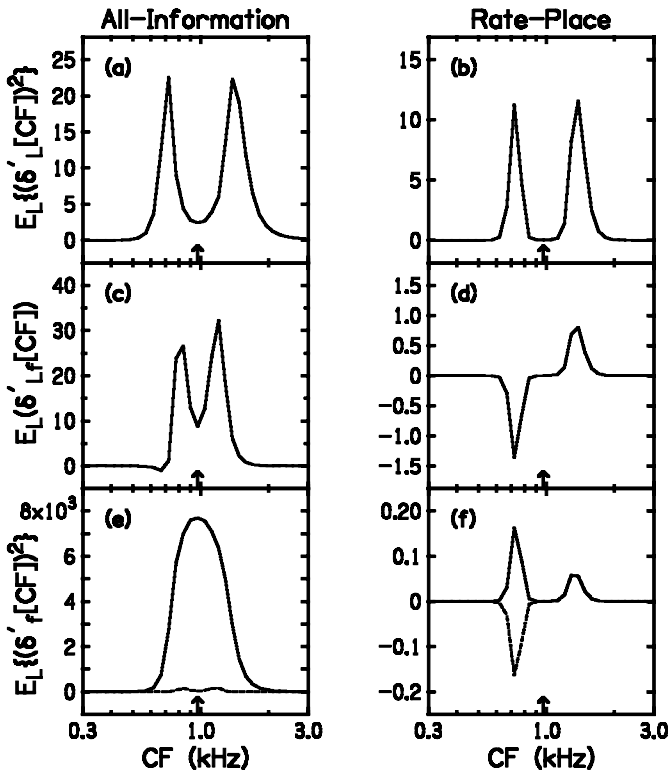
Figure 1: Information responsible for performance limits for a random-level frequency discrimination task for $f = 970$ Hz (indicated by arrows), $L = 40$ dB SPL, $T = 200$ ms (20 ms rise/fall), and a 6 dB random-level range. The left and right columns illustrate information from the all-information and rate-place encoding schemes, respectively. The top panel represents the average level information $E_L\{(\delta'_L[CF])^2\}$ available for each AN model fiber. The middle panel shows the average cross-interaction between level and frequency for each AN fiber, $E_L(\delta'_{Lf}[CF])$. In the bottom panel, the average information available for fixed-level frequency discrimination, $E_L\{(\delta'_f[CF])^2\}$, is shown by the solid line. The dashed line illustrates the information for estimating frequency based on individual AN fibers that is lost due to the random-level variation (the second term in equation 3.1). The amount of lost information (a positive quantity) is plotted so that CFs that have negative correlation between changes in level and changes in frequency have a negative value (for illustrative purposes only).

tion of information quantities in equation 3.1 across the population of AN fibers is shown in Figure 1. The first row shows the average information about level available for each CF, $E_L\{(\delta'_L[CF])^2\}$. The second row shows the

average cross-interaction term as a function of CF, $E_L(\delta'_{Lf}[CF])$. The average fixed-level information about frequency for each AN fiber, $E_L\{(\delta'_f[CF])^2\}$, is shown by the solid line in the bottom row. The dashed line in the bottom row illustrates the average frequency information that is lost due to the random-level variation based on estimating frequency from single AN fibers (i.e., the second term in equation 3.1 evaluated for single CFs, and with $API_L = 0$). The amount of lost information is plotted so that CFs that have a negative correlation between changes in level and frequency have a negative value. This is solely for illustrative purposes, as the second term in equation 3.1 is always positive because it is the ratio of a squared value and a positive information quantity.

The curves in the bottom panel of Figure 1 illustrate how both encoding schemes overcome the influence of random-level variation. In the all-information scheme, each fiber possesses significantly more information for estimating frequency than is lost due to the random-level variation (compare the solid and dashed lines in Figure 1, bottom left). However, the situation with single-fiber rate-place information is very different. The average amount of rate-place information on a single fiber that is lost due to random-level variation is equal to the average amount of information available for estimating frequency with fixed level (compare the solid and dashed lines in Figure 1, bottom right). However, when the population response is considered, there is no effect of random-level variation for the rate-place scheme due to the opposite polarity of the cross-interaction term above and below the frequency of the tone (see the middle panel of Figure 1). The lack of an effect for the rate-place population response can be seen (see equation 3.1) to result from the summation of the cross-interaction term $\delta'_{Lf}[CF]$ over all CFs prior to squaring the total interaction. The rate-place cross-interaction profile is an odd function around the frequency of the tone (see Figure 1, middle panel), and thus the positive interaction above the frequency of the tone cancels the negative interaction below the frequency of the tone so that the overall effect of random-level variation is negligible. The shape of the rate-place cross-interaction profile results directly from the frequency tuning associated with AN fibers and quantifies the significance of the fundamental relation between frequency and level discrimination discussed by Siebert (1968).

In summary, single AN fibers in the all-information scheme can perform random-level frequency discrimination equally as well as fixed-level frequency discrimination. In contrast, it is not possible to discriminate frequency in the presence of random-level variation based on rate-place information from a single AN fiber. However, a rate-place model that compared information in CFs above and below the frequency of the tone could make use of the opposite interaction to separate the effect of changes in level from the effect of changes in frequency, and thereby discriminate frequency in the presence of random-level variation.

5.2 Random-Level Frequency Discrimination in Noise. Moore and Glasberg (1989) measured human frequency discrimination performance in four conditions in order to test the duplex theory of frequency coding, that is, that rate-place information is used at high frequencies while temporal information is used at low frequencies. They reported performance as a function of frequency for four conditions:

1. Fixed-level frequency discrimination in quiet

2. Random-level frequency discrimination in quiet

3. Fixed-level frequency discrimination with a high-frequency noise masker that spanned from $1.1f$ to $1.4f$

4. Random-level frequency discrimination in the presence of the high-frequency noise

Moore and Glasberg suggested that if the high-frequency noise were assumed to mask completely all CFs above the frequency of the tone, then the performance of a rate-place model should be significantly affected by randomizing the level of the tone in the presence of the noise.

The random-level frequency discrimination analysis in this study was used to simulate all four conditions from Moore and Glasberg (1989). The first two conditions have been described above, while the conditions that included the high-frequency noise were simulated by considering the information from CFs only below the frequency of the tone. While this simulated effect of the noise masker is extreme (e.g., given the effects of suppression; Sachs & Kiang, 1968; Delgutte, 1990; Ruggero, Robles, & Rich, 1992), this simulation directly mimics the assumption that was made by Moore and Glasberg (1989) and has been often used to interpret psychophysical experiments with noise maskers (e.g., Viemeister, 1983). Thus, performance limits predicted with this simulation are based on information in model CFs below and equal to the tone frequency, which are the only source of information under the assumption used by Moore and Glasberg (1989) to interpret their psychophysical experiment.

The group mean results from Moore and Glasberg (1989) are shown in Figure 2a, the all-information predictions in Figure 2b, and the rate-place predictions in Figure 2c. Psychophysical performance is plotted in terms of the normalized JND in frequency $\frac{\Delta f}{f}$, where higher JNDs correspond to worse performance. (Comparisons between human performance and predicted performance limits are made in terms of both absolute values and trends, as discussed in section 2.2 in the companion article.) If the performance limits are uniformly better than human performance (i.e., parallel to human performance across the entire range of stimulus parameters), then it can be hypothesized that AN information is used in a (uniformly) inefficient manner. On the other hand, if the performance limits exceed human performance in a nonuniform way, and there is no realistic processor
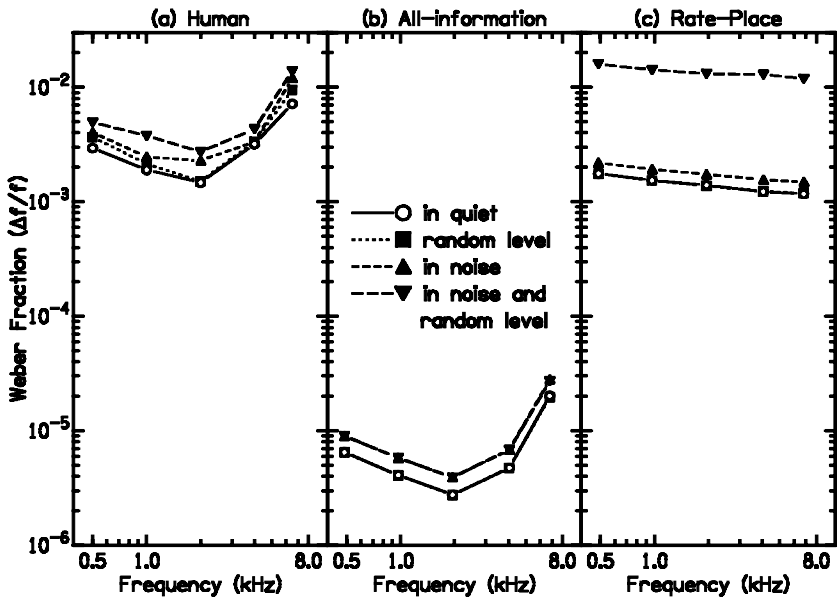
Figure 2: Comparison between human performance and predicted performance limits for the random-level frequency-discrimination conditions reported by Moore and Glasberg (1989). The Weber fraction $\Delta f/f$ is plotted as a function of frequency in each panel. (a) Human performance. (b) All-information predictions. (c) Rate-place predictions. Condition 1 (open circles): fixed-level frequency discrimination in quiet. Condition 2 (filled squares): random-level frequency discrimination in quiet. Condition 3 (filled upward triangles): fixed-level frequency discrimination in the presence of high-frequency noise. Condition 4 (filled downward triangles): random-level frequency discrimination in high-frequency noise. Human data are for $L = 70$ dB SPL, T=200 ms (10 ms rise/fall), 6-dB random-level range, and overall noise level of 75 dB SPL (Moore & Glasberg, 1989). Model predictions are for $L = 40$ dB SPL, $T = 200$ ms (20 ms rise/fall), and 6 dB random-level range.

that would be nonuniformly inefficient in the required manner, then a fairly strong hypothesis can be made that the information provided in the AN is sufficient but not likely to account solely for human performance. Finally, if human performance is superior to the performance limits, then this result states that there is insufficient information represented by the model of the peripheral transformations to account for human performance.

In general, predicted rate-place performance limits (see Figure 2c) are closer to the absolute values of human performance (see Figure 2a), but do not match the trends in human performance as a function of frequency, particularly at high frequencies. In contrast, predicted all-information per-

Table 1: Average Ratio Between Thresholds in Conditions 2–4 Relative to Condition 1 (Frequency Discrimination in Quiet).

	Human	Model	
Condition	Moore and Glasberg (1989)	All-Information	Rate-Place
Random level (condition 2)	1.15[a]	1.00	1.00
In noise (condition 3)	1.37	1.41	1.26
Random level in noise (condition 4)	1.65	1.40	9.68

Notes: Conditions are defined in the text and the caption to Figure 2.
[a] Not statistically significant.

formance limits (see Figure 2b) match the trends in human performance versus frequency, but are significantly better than the absolute values of human performance.

The effects of the different conditions used by Moore and Glasberg (1989) on human performance were relatively small, especially compared with the factor-of-five degradation in performance between 2 and 6.5 kHz in all four conditions (see Figure 2a). Moore and Glasberg reported that there was no statistically significant interaction between condition and frequency, as indicated by the roughly parallel shifts of the curves for the different conditions in Figure 2a. Table 1 shows the average factor across frequency by which thresholds for each condition became worse relative to frequency discrimination in quiet (condition 1) for human and model performance. Moore and Glasberg reported that there was not a statistically significant difference between frequency discrimination in quiet and with a random level (between conditions 1 and 2). Human thresholds became worse by an average factor of 1.37 (statistically significant) for the in-noise condition, while the most significant effect was seen for the random-level in noise condition in which performance became worse by an average factor of 1.65.

Both all-information (see Figure 2b) and rate-place predictions (see Figure 2c) in quiet were unaffected by random-level variation, as described above. The simulated effect of adding the high-frequency noise for the fixed-level task resulted in similar increases in predicted thresholds for both the rate-place and all-information encoding schemes (see Figures 2b and 2c). The increase is consistent with the removal of roughly one half of the available information (see the solid curve in the bottom panels of Figure 1) and the resultant increase in threshold by a factor of $\sqrt{2}$, and is similar to the size of the observed effect in the human data. The only relative difference between the rate-place and all-information predictions was for the random-level in-noise condition. All-information thresholds were worse than condition 1 by a factor of 1.40; there was no effect of imposing random-level variation in the presence of high-frequency noise (conditions 3 and 4 were identical;

see Figure 2b and Table 1). In contrast, the rate-place thresholds increased by a factor of 9.68 compared to frequency discrimination in quiet (see Figure 2c and Table 1). The large, predicted increase in rate-place thresholds for the random-level in-noise condition compared to the noise-alone condition is due to the inability of the rate-place model to compare CFs above and below the tone frequency (see Figure 1). This large effect is inconsistent with the small effect observed in human performance at all frequencies.

6 Discussion

This study describes an extension of SDT analysis of stochastic neural models to psychophysical tasks in which one stimulus parameter is randomly varied in order to restrict the cues available to the subject. Frequency-discrimination performance limits based on either the population of discharge counts (rate-place) or discharge times (all-information) of high-spontaneous-rate, low-threshold AN fibers were unaffected by random-level variation, consistent with human performance. The distributions of frequency and level information across the AN population demonstrated how both rate-place and all-information encoding schemes avoid the effect of random-level variation in quiet. Predictions were also made for random-level frequency discrimination in the presence of high-frequency noise, based on the simplified assumption that the noise masker acts to eliminate all information above the frequency of the tone.

When the simple model of the effect of noise masking is used, the predictions for the random-level frequency discrimination in noise experiment (see Figure 2) are inconsistent with human data if rate-place coding of frequency is assumed. The predicted effect in rate-place performance of adding random-level variation in the presence of high-frequency noise (see Figure 2c) is much larger than the small effect observed in human performance (see Figure 2a); Moore and Glasberg (1989). In fact, there is insufficient rate-place information in the total AN model population to account for human performance in the random-level-in-noise condition. The cause of the large reduction in information in the random-level-in-noise condition is the inability of the rate-place model to compare CFs above and below the tone frequency. Medium- and low-spontaneous-rate (SR) AN fibers, which have higher thresholds and broader dynamic ranges than the high-SR, low-threshold fibers included in our AN model, would not be expected to alter significantly the fundamental relation between frequency and level discrimination that underlies the behavior of the rate-place predictions. Neither an increase in the total number of AN fibers nor an alteration of the innervation density across CF would reduce the large discrepancy (factor of 9.68) between rate-place JNDs for the in-quiet and random-level-in-noise conditions. The implications of less easily quantified alterations to the AN model for the assumed effect of the masking noise are discussed below.

The inconsistency between the effect of random-level variation with a noise masker for the rate-place model and human performance occurs for all frequencies. This finding, combined with the finding by Moore and Glasberg (1989) that there was no statistically significant interaction between the effects of conditions 1 through 4 (see Figure 2) and frequency suggests that a single encoding scheme is responsible for performance at all frequencies, rather than the duplex theory often invoked to explain frequency encoding (e.g., Wever, 1949; Moore, 1973; Dye & Hafter, 1980; Wakefield & Nelson, 1985; Moore & Glasberg, 1989). As we discussed in the companion article, rate-place performance in quiet is closer to human performance than all-information performance in terms of absolute performance level. However, the trends in rate-place performance versus frequency are inconsistent with human performance at high frequencies, converse to the duplex theory. This strong discrepancy between the trends in rate-place and human performance is shown in this study to exist for all four frequency-discrimination conditions described by Moore and Glasberg (1989). In contrast to rate-place, all-information performance limits match the trends in human performance across all frequencies and all four conditions. Notably, and contrary to general beliefs (e.g., Moore, 1973, 1989; Dye & Hafter, 1980; Wakefield & Nelson, 1985; Javel & Mott, 1988; Pickles, 1988; Moore & Glasberg, 1989), there is significant temporal information in the AN at high frequencies for all four conditions in this study. Also, this study shows that all-information performance limits are unaffected by random-level variation in quiet and in the presence of high-frequency noise (see Figure 2), consistent with the small effects on human performance.

The computational AN model used in this study did not include several important aspects of AN responses that could affect the predictions for the masking conditions. The absence of suppression (i.e., nonlinear interactions between different CFs; Sachs & Kiang, 1968; Delgutte, 1990; Ruggero et al., 1992) in our model prohibits the accurate simulation of AN responses to complex stimuli (e.g., noise stimuli). Suppression could potentially produce effects that contradict the assumption that the high-frequency noise acts to mask completely all AN fibers with CF above the tone frequency. Another potentially significant limitation of the current AN model is the exclusion of high-threshold AN fibers with low and medium spontaneous rates (Liberman, 1978). Low- and medium-spontaneous-rate AN fibers (16% and 23% of the AN population, respectively) have been suggested to contribute to level encoding at higher levels (e.g., Colburn, 1981; Delgutte, 1987; Winter & Palmer, 1991), and therefore should be included in future AN models to quantify the effects of masking noise. In addition, a significant extension of the SDT analysis is necessary in order accurately to evaluate psychophysical tasks with complex random stimuli, such as noise (Heinz, 2000). Future studies using more complex AN models and SDT analyses will evaluate the validity of common assumptions regarding the effects of masking noise on auditory information.

7 Conclusion

1. Signal detection theory can be used to quantify the effects of both physiological noise and stimulus variation on psychophysical performance limits in discrimination experiments with random variation in one stimulus parameter.

2. Frequency-discrimination performance limits based on the population of AN discharge counts (rate-place) or based on discharge times on individual AN fibers are unaffected by random-level variation in quiet.

3. There is insufficient rate-place information in this AN model to account for human performance in a random-level frequency-discrimination task with high-frequency noise based on a common psychophysical assumption for the effects of noise maskers.

4. All-information performance limits with high-frequency noise are unaffected by random-level variation, consistent with human performance.

The primary goal of this study was to demonstrate a method for relating stochastic neural responses to behavior in psychophysical tasks that include random variation of one stimulus parameter. This method was demonstrated for the auditory task of random-level frequency discrimination but is applicable to any psychophysical discrimination experiment in which one parameter is randomly varied. The analysis presented applies to any sensory system for which there are models that describe the statistical properties of neural responses to the relevant stimuli. Equation 3.1 is valid for any neural model, while some of the analysis in section 3.2 is specific for neural responses that are well described statistically by conditionally independent, nonstationary Poisson processes. Thus, the study describes a general modeling approach for quantitatively relating physiological responses to behavior in complex psychophysical tasks that are often used to test neural encoding hypotheses.

Acknowledgments

References

Braida, L. D., & Durlach, N. I. (1988). Peripheral and central factors in intensity perception. In G. M. Edelman, W. E. Gall, & W. M. Cowan (Eds.), *Auditory function: Neurobiological bases of hearing* (pp. 559–583). New York: Wiley.

Carney, L. H. (1993). A model for the responses of low-frequency auditory-nerve fibers in cat. *J. Acoust. Soc. Am., 93*, 401–417.

Colburn, H. S. (1969). *Some physiological limitations on binaural performance*. Unpublished doctoral dissertation, Massachusetts Institute of Technology, Cambridge, MA.

Colburn, H. S. (1973). Theory of binaural interaction based on auditory-nerve data. I. General strategy and preliminary results on interaural discrimination. *J. Acoust. Soc. Am., 54*, 1458–1470.

Colburn, H. S. (1977a). Theory of binaural interaction based on auditory-nerve data. II. Detection of tones in noise. *J. Acoust. Soc. Am., 61*, 525–533.

Colburn, H. S. (1977b). *Theory of binaural interaction based on auditory-nerve data. II. Detection of tones in noise. Supplementary material* (AIP Document No. PAPS JASMA-61-525-98). Available online at: http://www.aip.org/epaps/howorder.html.

Colburn, H. S. (1981). *Intensity perception: Relation of intensity discrimination to auditory-nerve firing patterns* (Internal Memorandum). Cambridge, MA: Research Laboratory of Electronics, Massachusetts Institute of Technology.

Cramér, H. (1951). *Mathematical methods of statistics*. Princeton, New Jersey: Princeton University Press.

Dau, T., Kollmeier, B., & Kohlrausch, A. (1997a). Modeling auditory processing of amplitude modulation. I. Detection and masking with narrow-band carriers. *J. Acoust. Soc. Am., 102*, 2892–2905.

Dau, T., Kollmeier, B., & Kohlrausch, A. (1997b). Modeling auditory processing of amplitude modulation. II. Spectral and temporal integration. *J. Acoust. Soc. Am., 102*, 2906–2919.

Dau, T., Püschel, D., & Kohlrausch, A. (1996a). A quantitative model of the "effective" signal processing in the auditory system I. Model structure. *J. Acoust. Soc. Am., 99*, 3615–3622.

Dau, T., Püschel, D., & Kohlrausch, A. (1996b). A quantitative model of the "effective" signal processing in the auditory system II. Simulations and measurements. *J. Acoust. Soc. Am., 99*, 3623–3631.

Delgutte, B. (1987). Peripheral auditory processing of speech information: Implications from a physiological study of intensity discrimination. In M. E. H. Schouten (Ed.), *The psychophysics of speech perception* (pp. 333–353). Dordrecht: Nijhoff.

Delgutte, B. (1990). Two-tone rate suppression in auditory-nerve fibers: Dependence on suppressor frequency and level. *Hear. Res., 49*, 225–246.

Delgutte, B. (1996). Physiological models for basic auditory percepts. In H. L. Hawkins, T. A. McMullen, A. N. Popper, & R. R. Fay (Eds.), *Auditory computation* (pp. 157–220). New York: Springer-Verlag.

Durlach, N. I., & Braida, L. D. (1969). Intensity perception I: Preliminary theory of intensity resolution. *J. Acoust. Soc. Am., 46*, 372–383.

Durlach, N. I., Braida, L. D., & Ito, Y. (1986). Towards a model for discrimination of broadband signals. *J. Acoust. Soc. Am., 80*, 63–72.

Dye, R. H., & Hafter, E. R. (1980). Just-noticeable differences of frequency for masked tones. *J. Acoust. Soc. Am., 67*, 1746–1753.

Emmerich, D. S., Ellermeier, W., & Butensky, B. (1989). A reexamination of the frequency discrimination of random-amplitude tones, and a test of Henning's modified energy-detector model. *J. Acoust. Soc. Am., 85*, 1653–1659.

Erell, A. (1988). Rate coding model for discrimination of simple tones in the presence of noise. *J. Acoust. Soc. Am., 84*, 204–214.

Fitzhugh, R. (1958). A statistical analyser for optic nerve messages. *J. Gen. Physiol., 41*, 675–692.

Glasberg, B. R., & Moore, B. C. J. (1990). Derivation of auditory filter shapes from notched-noise data. *Hear. Res., 47*, 103–138.

Goldstein, J. L., & Srulovicz, P. (1977). Auditory-nerve spike intervals as an adequate basis for aural spectrum analysis. In E. F. Evans & J. P. Wilson (Eds.), *Psychophysics and physiology of hearing* (pp. 337–347). New York: Academic Press.

Green, D. M. (1988). *Profile analysis: Auditory intensity discrimination*. New York: Oxford University Press.

Green, D. M., Kidd, G., Jr., & Picardi, M. C. (1983). Successive versus simultaneous comparison in auditory intensity discrimination. *J. Acoust. Soc. Am., 73*, 639–643.

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Greenwood, D. D. (1990). A cochlear frequency-position function for several species—29 years later. *J. Acoust. Soc. Am., 87*, 2592–2605.

Gresham, L. C., & Collins, L. M. (1998). Analysis of the performance of a model-based optimal auditory signal processor. *J. Acoust. Soc. Am., 103*, 2520–2529.

Heinz, M. G. (2000). *Quantifying the effects of the cochlear amplifier on temporal and average-rate information in the auditory nerve*. Unpublished doctoral dissertation, Massachusetts Institute of Technology, Cambridge, MA.

Henning, G. B. (1966). Frequency discrimination of random amplitude tones. *J. Acoust. Soc. Am., 39*, 336–339.

Henning, G. B. (1967). A model for auditory discrimination and detection. *J. Acoust. Soc. Am., 42*, 1325–1334.

Huettel, L. G., & Collins, L. M. (1999). Using computational auditory models to predict simultaneous masking data: Model comparison. *IEEE Trans. Biomed. Eng., 46*, 1432–1440.

Javel, E., & Mott, J. B. (1988). Physiological and psychophysical correlates of temporal processing in hearing. *Hear. Res., 34*, 275–294.

Johnson, D. H. (1980). The relationship between spike rate and synchrony in responses of auditory-nerve fibers to single tones. *J. Acoust. Soc. Am., 68*, 1115–1122.

Joris, P. X., Carney, L. H., Smith, P. H., & Yin, T. C. T. (1994). Enhancement of neural synchrony in the anteroventral cochlear nucleus. I. Responses to tones at the characteristic frequency. *J. Neurophysiol., 71*, 1022–1036.

Kidd, G., Jr., Mason, C. R., Brantley, M. A., & Owen, G. A. (1989). Roving-level tone-in-noise detection. *J. Acoust. Soc. Am., 86*, 1310–1317.

Liberman, M. C. (1978). Auditory-nerve response from cats raised in a low-noise chamber. *J. Acoust. Soc. Am., 63*, 442–455.

McKee, S. P., Silverman, G. H., & Nakayama, K. (1986). Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Res., 26*, 609–619.

Moore, B. C. J. (1973). Frequency difference limens for short-duration tones. *J. Acoust. Soc. Am., 54*, 610–619.

Moore, B. C. J. (1989). *An introduction to the psychology of hearing*. New York: Academic Press.

Moore, B. C. J., & Glasberg, B. R. (1989). Mechanisms underlying the frequency discrimination of pulsed tones and the detection of frequency modulation. *J. Acoust. Soc. Am., 86*, 1722–1732.

Parker, A. J., & Newsome, W. T. (1998). Sense and the single neuron: Probing the physiology of perception. *Annu. Rev. Neurosci., 21*, 227–277.

Parzen, E. (1962). *Stochastic processes*. San Francisco: Holden-Day.

Pickles, J. O. (1988). *An introduction to the physiology of hearing*. New York: Academic Press.

Rieke, F., Warland, D., de Ruyter van Steveninck, R., & Bialek, W. (1997). *Spikes: Exploring the neural code*. Cambridge, MA: MIT Press.

Ruggero, M. A. (1992). Physiology and coding of sound in the auditory nerve. In A. N. Popper, & R. R. Fay (Eds.), *The mammalian auditory pathway: Neurophysiology* (pp. 34–93). New York: Springer-Verlag.

Ruggero, M. A., Robles, L., & Rich, N. C. (1992). Two-tone suppression in the basilar membrane of the cochlea: Mechanical basis of auditory-nerve rate suppression. *J. Neurophysiol., 68*, 1087–1099.

Sachs, M. B., & Kiang, N. Y. S. (1968). Two-tone inhibition in auditory-nerve fibers. *J. Acoust. Soc. Am., 43*, 1120–1128.

Siebert, W. M. (1965). Some implication of the stochastic behavior of primary auditory neurons. *Kybernetik, 2*, 206–215.

Siebert, W. M. (1968). Stimulus transformation in the peripheral auditory system. In P. A. Kolers & M. Eden (Eds.), *Recognizing patterns* (pp. 104–133). Cambridge, MA: MIT Press.

Siebert, W. M. (1970). Frequency discrimination in the auditory system: Place or periodicity mechanisms? *Proc. IEEE, 58*, 723–730.

Snyder, D. L., & Miller, M. I. (1991). *Random point processes in time and space*. New York: Springer-Verlag.

van Trees, H. L. (1968). *Detection, estimation, and modulation theory: Part I*. New York: Wiley.