# THEORETICAL NOTE

# An Evaluation of Psychophysical Models of Auditory Change Perception

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In many psychophysical experiments, the participant's task is to detect small changes along a given stimulus dimension or to identify the direction (e.g., upward vs. downward) of such changes. The results of these experiments are traditionally analyzed with a constant-variance Gaussian (CVG) model or a high-threshold (HT) model. Here, the authors demonstrate that for changes along three basic sound dimensions (frequency, intensity, and amplitude-modulation rate), such models cannot account for the observed relationship between detection thresholds and direction-identification thresholds. It is shown that two alternative models can account for this relationship. One of them is based on the idea of sensory quanta; the other assumes that small changes are detected on the basis of Poisson processes with low means. The predictions of these two models are then compared against receiver operating characteristics (ROCs) for the detection of changes in sound intensity. It is concluded that human listeners' perception of small and unidimensional acoustic changes is better described by a discrete-state Poisson model than by the more commonly used CVG model or by the less favored HT and quantum models.

Keywords: signal detection theory, threshold, discrimination, change perception, auditory perception

Detecting simple differences or unidimensional changes between sensory stimuli (e.g., changes in brightness or loudness) and identifying the direction of these changes (e.g., upward vs. downward) are two fundamental perceptual abilities. How these abilities are related to one another is an important question for psychophysicists. The answer has both theoretical and practical implications. An important practical implication relates to the choice of psychophysical paradigm for measuring justnoticeable differences (JNDs) between stimuli. In auditory psychophysics, for instance, the two-interval two-alternative forced-choice (2I2AFC) paradigm has been commonly used to measure JNDs for various sound dimensions. However, JNDs are usually defined as the smallest stimulus differences that an individual can detect with a certain level of accuracy (e.g., 70% correct). In contrast, the 2I2AFC paradigm requires the participant to identify the relative positions of the two presented stimuli along some sensory dimension or, equivalently, to identify the direction of the stimulus change. Thus, interpretations of 2I2AFC thresholds in terms of JNDs rest (in most cases, implicitly) on the assumption that thresholds for the identification of the direction of sensory changes are closely related to thresholds for the detection of those changes. Specifically, it is commonly assumed that an individual's ability to identify the direction of sensory changes is limited solely by that individual's ability to detect those changes or that as soon as a change has been detected, its direction can be identified.

Clearly, this assumption is not always warranted. For instance, Semal and Demany (2006) recently identified listeners who could detect relatively small changes in frequency (subjectively, pitch) between consecutive tones but who required changes approximately one order of magnitude larger in order to correctly identify their direction. Similar findings were obtained by Johnsrude, Penhune, and Zatorre (2000) for individuals with auditory-cortex lesions. Another example of dissociation between change detection (D) and change-direction identification (I) was provided by experiments concerning the perception of transient intensity changes in a continuous sound (Gallun, 2003; Hafter, Bonnel, Gallun, & Cohen, 1998; Macmillan, 1971, 1973). These experiments revealed that listeners

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This work was supported by the National Institutes of Health, National Institute on Deafness and other Communication Disorders Grant R01 DC 05216. We are grateful to Josh McDermott, Andrew Oxenham, and Neal Viemeister for insightful discussions. We are especially grateful to Frederick Gallun and Neil Macmillan for their detailed reading of an earlier version of the article and for the many helpful suggestions that they offered, which led to substantial improvements in both style and contents.

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are able to detect transient intensity changes with a cue that provides no information regarding change direction.

Although these findings show that in some cases, detecting a change is not sufficient for the identification of its direction, they represent exceptions. More generally, experimental data in the auditory perception<sup>1</sup> literature are consistent with the view that the ability to identify the direction of changes in sound frequency or sound intensity is limited only by the ability to detect these changes. Some information relevant to that issue comes from studies in which frequency and/or intensity discrimination thresholds measured with a 2I2AFC task (which required participants to identify the direction of stimulus change) were compared with thresholds measured in the same participants with a samedifferent (AX)<sup>2</sup> task (which required the detection of a change but not the identification of its direction). The authors of such experiments (Creelman & Macmillan, 1979; Jesteadt & Bilger, 1974; Jesteadt & Sims, 1975) intended to determine whether this relationship was consistent with the predictions of the standard constant-variance Gaussian (CVG) psychophysical model from signal detection theory (Green & Swets, 1966; Macmillan & Creelman, 2005; Wickens, 2001). In this model, the presentation of a stimulus is assumed to evoke a sensory observation contaminated by a Gaussian internal noise with zero mean and constant variance. Under the assumption that performance in the 2I2AFC and AX tasks is limited by the same internal noise and that the listener's decision strategy is optimal in the likelihood-ratio sense, the model predicts that the paradigm-independent index of sensitivity d', defined as the standardized distance between the means of the probability density functions (PDFs) corresponding to the two stimulus classes that must be discriminated, should be the same in the two tasks. As it turns out, the mean d' ratio (d' in the AX task over d' in the 2I2AFC task) measured across several studies (Creelman & Macmillan, 1979; Jesteadt & Bilger, 1974; Jesteadt & Sims, 1975; see also the compact summary of these studies in Macmillan and Creelman, 2005, p. 182) is approximately equal to 0.8. This ratio, smaller than 1, is obviously consistent with the idea that the ability to identify the direction of sensory changes is limited only by the ability to detect these changes. On the other hand, the reason why the ratio differs from 1 is not clear. One possibility is that listeners had difficulties using a stable response criterion in the AX task. Another possibility, which is more interesting, is that the CVG model does not adequately describe how human listeners detect simple auditory changes.

In the theoretical work reported here, detailed measurements of auditory D and I thresholds were used to test several psychophysical models of auditory D. The considered acoustic changes were unidimensional, and it was reasonable to assume that as soon as they were detectable, their direction could be identified; for these changes, in other words, a warranted assumption was that detection and direction identification merely represented different decision rules applied to the same sensory information (Thomas, 1985; Thomas, Gille, & Barker, 1982). The analyzed data were collected with a dual-pair psychophysical paradigm. This paradigm allowed D and I thresholds to be measured with the same stimulus design, and it had the advantage of alleviating some of the concerns usually associated with the two-interval (2I) AX design.

The outline of this article is as follows. First, the dual-pair psychophysical paradigm that was used to collect the experimental data is briefly described. Then, the predictions of two classic psychophysical models (the CVG model and the high-threshold [HT] model) regarding the relationship between D thresholds and I thresholds in the considered paradigm are derived. In the third section, these predictions are compared with the experimental data. In the fourth section, ways in which the CVG model may be reconciled with the data are explored. The fifth section is devoted to exploring alternative models, and it shows that two models, assuming quantized-Gaussian (QG; Stevens, 1972; Stevens, Morgan, & Volkmann, 1941; Stevens & Volkmann, 1940) and Poisson-distributed (Kaernbach, 1991a) decision variables, respectively, can account for the experimental data. Finally, the relative merits of the two latter models are discussed.

#### The Dual-Pair Paradigm

The experimental data that provide the empirical basis for this article were collected with a four-interval stimulus design, also known as dual pair. As the name indicates, in this design, two pairs of stimuli are presented on each trial. In one of the two pairs, the stimuli are identical; in the other, they are different. For brevity, we refer to these pairs as the same pair and the different pair. The order of presentation of the two pairs is randomized, each of the two possible orderings being as likely (a priori) as the other. In the different pair, the change between the first stimulus and the second stimulus can be either upward (e.g., the second tone has a higher intensity than the first) or downward, with equal probability. This dual-pair stimulus design can be used to measure D and I, the only difference being in the instructions given to the participant. In the D task, the participant is asked to indicate which of the two pairs contained different stimuli. In the I task, the participant must report in which direction the stimuli in the different pair changed.

The dual pair design makes it possible to measure both D and I with the same stimulus design while avoiding (or at least, alleviating) concerns regarding the influence of bias on performance. In this respect, this four-interval design is superior to the more popular two-interval AX paradigm for measuring D because the two-interval AX is notoriously susceptible to bias. In fact, the dual-pair design can be thought of as a two-interval AX design embedded in a 2I2AFC design (Noreen, 1981).

In addition to these general features, the model predictions derived below take the following methodological features into account. First, the frequency (or amplitude-modulation [AM] rate)

<sup>&</sup>lt;sup>1</sup> Our choice of focusing on audition was motivated in part by a greater familiarity with the auditory-perception literature and in part by the fact that detailed measurements of thresholds for the discrimination of changes in various sound parameters (intensity, frequency, and amplitude-modulation rate) were available to us. These empirical data, which represent a total of 1,210 threshold measurements across 11 listeners (an average of 110 threshold estimates per listener), provided a unique opportunity to distinguish between different psychophysical models, the predictions of which are not distant enough to permit statistical separation with smaller data sets.

<sup>&</sup>lt;sup>2</sup> In the same-different paradigm, also known as AX or as 2IAX paradigm, the two stimuli presented on a trial (A and B) can be either identical (AA or BB) or different (AB or BA), and the observer's task is to indicate whether the stimuli were the same or different.

of the first stimulus in each pair was randomized independently from that in the other pair. This technique, known as *roving* in the auditory psychophysics literature, is frequently used to discourage participants from comparing individual stimuli across the two pairs. When, as was the case here, the roving range is large compared with the measured thresholds, listeners are forced to rely on perceived differences between the stimuli in each pair rather than on comparisons of the individual stimuli across pairs, across trials, or with a fixed internal reference in memory. Second, thresholds in the D and I tasks were measured with an adaptive procedure that tracked the 75%-correct point on the psychometric function (Kaernbach, 1991b). Finally, to avoid some of the difficulties inherent in double-judgment psychophysics (Klein, 1985), the D and I thresholds were tested not simultaneously but in separate blocks of trials, intermingled within each test session.

Under those methodological circumstances, what do classic psychophysical models predict regarding the relationship between thresholds in D and I tasks?

# Predictions of the CVG Model and the HT Model

# The CVG Model

Gaussian signal-detection theory posits the existence of a continuum of sensory observations, contaminated by normally distributed internal noise (Green & Swets, 1966). In the most common instantiation of this theory, the CVG model, it is further assumed that the variance of the internal noise is constant, that is, that it is the same for all observations and does not vary over time. In addition, the Gaussian internal noises added to the observations are assumed to be uncorrelated, that is, statistically independent.

Because the dual-pair design described above involves the presentation of four stimuli on each trial, each stimulus yielding one observation, the decision space for this paradigm is four dimensional. However, in the experiments considered here, wide acrosspair roving was used to prevent listeners from taking advantage of comparisons between individual observations across the two pairs. With such roving, we can assume that the observer derives no significant information from the absolute positions of the observations or from comparisons between single observations in different pairs; only the relative positions of, or the differences between, the observations within each pair are relevant (Dai, Versfeld, & Green, 1996; Macmillan & Creelman, 2005; Macmillan, Kaplan, & Creelman, 1977; Noreen, 1981). Therefore, there is no loss of information in reducing the decision space to two axes corresponding to the signed differences between the observations in each pair. Denoting the four observations made consecutively on each trial by  $y_{11}$ ,  $y_{12}$ ,  $y_{21}$ , and  $y_{22}$ , in that order, we can plot the difference  $\Delta y_1 = y_{12} - y_{11}$  (first pair) along the x-axis, and the difference  $\Delta y_2 = y_{22} - y_{21}$  (second pair) along the y-axis of a Cartesian plane.

Figure 1 provides a schematic illustration, in this decision space, of the two-dimensional, conditional PDF of the difference variables,  $\Delta y_1$  and  $\Delta y_2$ , conditioned on the different pair being presented first and on the change being upward; accordingly, the bidimensional Gaussian PDF has a positive mean along axis  $\Delta y_1$  and a zero mean along axis  $\Delta y_2$ .<sup>3</sup> It is easy to imagine what the conditional PDFs for the other three possible stimulus configurations look like.



*Figure 1.* Schematic illustration of the decision space for the dual-pair detection and identification tasks, according to the constant-variance Gaussian model. Differences between the two observations from the first pair,  $y_{12} - y_{11}$ , are plotted along the  $\Delta y_1$  axis. Differences between the two observations from the second pair,  $y_{22} - y_{21}$ , are plotted along the  $\Delta y_2$  axis. The four quadrants (labeled P1 to P4) delimited by the major and minor diagonals correspond to different decision regions, as explained in the text. The fuzzy patch represents the two-dimensional probability density function of the decision variables (with darker areas corresponding to regions of higher probability density) for trials in which the first pair contained an upward change; accordingly, the mean is positive along the  $\Delta y_1$  axis and zero along the  $\Delta y_2$  axis. In this example, the mean of the PDF along the  $\Delta y_1$  axis was chosen so that the probability mass over quadrants P1 and P3 was equal to .75, the targeted probability of a correct response in the detection (D) task in the psychophysical experiments described in the text.

The correct-response probabilities in the D and I tasks can be found by integrating the conditional PDFs of the decision variables over regions of the decision space that correspond to a correct response. These regions depend on the decision rule used by the observer for task performance. An ideal observer uses optimal decision rules, that is, rules that maximize the probability of a

<sup>&</sup>lt;sup>3</sup> Here, as in many other applications of signal detection theory, the expected values of the observations are linearly related to the values of the relevant physical parameters, provided an appropriate choice of units for the latter. In the case of intensity, the decibel (dB) is an appropriate unit because the index of sensitivity *d'*, which is defined as the standardized distance between the expected values of the observations evoked by the two stimuli to be discriminated, increases roughly linearly with the stimulus intensity difference in dB (Buus & Florentine, 1991; Jesteadt & Bilger, 1974). For frequency difference between the two stimuli in hertz (Hz; Nelson & Freyman, 1986); we assume that the same conclusion applies for AM rate, at least in the range of rates studied here. In the experiments considered here, thresholds were measured in dB for intensity discrimination and in cents for frequency or AM-rate discrimination; small frequency differences in cents are approximately proportionally related to their counterpart in Hz.

correct response, given the constraints. For the D task with wide across-pair roving, the optimal decision rule consists of selecting the pair for which the magnitude (i.e., absolute value) of the difference between the observations is largest (Macmillan et al., 1977; Noreen, 1981; Rousseau & Ennis, 2001). According to this rule, the observer chooses Pair 1 if the point defined by the differences between the observations in each pair falls inside quadrant P1 or P3 and chooses Pair 2 if it falls inside quadrant P2 or P4. Therefore, under the CVG model, the probability of a correct response in the D task can be calculated as the integral, over the region corresponding to quadrants P1 and P3, of the joint PDF shown in Figure 1, which corresponds to the case in which an upward change occurred in the first pair.<sup>4</sup> Macmillan et al. (1977; see also Micheyl & Messing, 2006) provided a formula for this integral as a function of *d*'; this equation is

$$PC_{DCVG} = \left[\Phi\left(\frac{d'}{2}\right)\right]^2 + \left[1 - \Phi\left(\frac{d'}{2}\right)\right]^2, \quad (1)$$

where  $PC_{DCVG}$  denotes the proportion of correct responses in the D task under the CVG model, and  $\Phi(x)$  denotes the cumulative standard normal function, defined as the integral from  $-\infty$  to x of the Gaussian function, with zero mean and unit variance. The converse equation, which gives d' as a function of  $PC_{DCVG}$  is

$$d' = 2\Phi^{-1} \left( \frac{1}{2} + \sqrt{\frac{PC_{DCVG}}{2} - \frac{1}{4}} \right), \tag{2}$$

where  $\Phi^{-1}$  denotes the inverse cumulative standard normal function. According to this equation, when  $PC_{DCVG}$  equals .75 (the probability of correct responses corresponding to threshold in the experimental data used here), d' in the D task equals approximately 2.10.

For the I task, an intuitive strategy is to select the pair in which the magnitude of the difference between the two observations is largest, to respond "up" if the signed difference between these observations is positive, and to respond "down," if otherwise. Going through the four quadrants of Figure 1, which illustrates the PDF of the decision variables for the case of an upward change in the first pair, we find that correct responses will occur in this case whenever the point  $(\Delta y_1, \Delta y_2)$  falls in the half-plane formed by the quadrants P1 and P2. Thus, the decision rule may be reformulated as follows: Respond "up" if  $\Delta y_1 > -\Delta y_2$ ; otherwise, respond "down." Note that this can be rewritten as respond "up" if  $\Delta y_1 + \Delta y_2 > 0$ , providing another description of the same decision rule. As it turns out, this decision rule is optimal in a likelihood-ratio sense. Using this decision rule, we can derive the probability of responding correctly in the I task under the CVG model; it is

$$PC_{ICVG} = \Phi\left(\frac{d'}{2}\right). \tag{3}$$

Note that this equation is identical to that defining the relation between d' and the probability of a correct response of an unbiased observer in the single-interval (yes–no) task (Green & Swets, 1966; Macmillan & Creelman, 2005). Equation 3 can be used to determine that the value of d' corresponding to a correct-response probability of .75 in the I task is approximately 1.34. This is roughly 1.56 times smaller than the value found for the D task with Equation 2. Thus, according to the CVG model, thresholds should be approximately 56% larger in the D task than in the I task.

# The HT Model

HT theory posits the existence of a sensory threshold that can never be exceeded in the absence of a signal (for a review of the theory, see Green & Swets, 1966; Macmillan & Creelman, 2005; Wickens, 2001). In the case of discrimination, the signal is defined as the physical difference,  $\Delta$ , between the two stimuli to be discriminated. The theory further posits the existence of two internal states: a nondetect state, which occurs whenever the signal does not exceed the threshold, and a detect state, which occurs whenever the signal exceeds the threshold. Participants left in the nondetect state take a guess, which in the absence of bias is equally likely to be either response alternative.

A slight complication arises from the fact that with the experimental design considered in this note,  $\Delta$  can be either positive or negative. Although the sign of  $\Delta$  is irrelevant for the D task, it is crucial for the I task. Therefore, we must assume two types of detect states: a detect+ state, which corresponds to the detection of an upward change, and a detect- state, which corresponds to the detection of a downward change. The three internal states, detect-, nondetect, and detect+ are separated by two thresholds. For simplicity, these thresholds are assumed to be positioned symmetrically around zero, along the relevant physical axis.

The HT model assumes that the threshold will never be exceeded in the absence of a change. If an upward change is never registered in a same pair, that is, a pair of identical stimuli, it is logical to assume that such a change is also never registered in presence of a downward change. Thus, according to this model, whenever a change has been detected, the direction of that change should be readily identified.

To account for the probabilistic nature of detection or discrimination, HT theory posits that thresholds fluctuate over time. Thus, associated with each  $\Delta$ , there is a certain probability,  $P_D(\Delta)$ , that the observer is in one of the two detect states and a probability of  $1 - P_D(\Delta)$  that he or she is in the nondetect state. Because for the same pair,  $\Delta = 0$ , and because according to the theory the threshold can never be exceeded in the absence of the signal, the same pair can never leave the observer in the detect state. Therefore, at the end of a trial in the dual-pair paradigm, the HT observer can find himself or herself in one of the following three situations: (a) he or she detected an upward change in one of the two pairs, (b) he or she detected a downward change in one of the two pairs, (c) he or she failed to detect a change. In cases a and b, the response of the listener in the D task should obviously correspond to the pair in which a change was detected; in those cases, the probability of a correct response is 1. In case c, the listener is forced to guess, and the probability of a correct response is .5. For the I task, the response of the listener should, according to the model, correspond to the perceived direction of the change in cases a and b; in case c, the listener should, again, guess. It follows that under this model the predicted probability of a correct response in the I task is the

<sup>&</sup>lt;sup>4</sup> The integration does not need to be carried out for the other possible stimulus configurations and response regions because the PDFs and regions are symmetric.

same as that in the D task.<sup>5</sup> Thus, unlike the CVG model, the HT model predicts that the threshold in the I task should be the same as the threshold in the D task, that is, a D/I threshold ratio of 1.

# Comparison of Model Predictions and Experimental Data

To test the predictions of the two above-described models, we reanalyzed data collected in a series of experiments concerning detection and direction identification of changes in frequency, intensity, and AM rate. The vast majority of these data was reported in an earlier article (Semal & Demany, 2006). Although that article is entitled "Individual Differences in the Sensitivity to Pitch Direction," it contains data on intensity and AM-rate discrimination in addition to frequency discrimination, and we strongly encourage readers to look into it for details regarding how the discrimination thresholds on which the D/I threshold ratios reported here were measured. It is important to note that Semal and Demany's (2006) article was primarily focused on listeners who exhibited unusually large thresholds in the discrimination of the direction of frequency changes (i.e., the I task); these listeners were recruited especially for the purpose of that study and are not representative of those tested in the vast majority of earlier studies on frequency discrimination. In contrast, here, we were specifically interested in listeners who did not exhibit a conspicuous deficit in the identification of the direction of frequency changes and whose thresholds in this task are normal in the sense that they are in line with those typically reported in the psychoacoustical literature.<sup>6</sup> Additional data on frequency discrimination, which were collected by the same authors using the same paradigm as in their original study but which were not reported in the 2006 article, were also included in the present analysis; these supplementary data are as of yet unpublished. Overall, the data analyzed here represent a total of 1,210 threshold measurements (460 for frequency discrimination, 630 for intensity discrimination, and 120 for AM-rate discrimination) from 11 different listeners.

The geometric means and ranges of the D and I thresholds for frequency, intensity, and AM-rate discrimination that were used in the analyses described below are indicated in Table 1. For frequency discrimination, the mean D and I thresholds (expressed in musical cents; 1 cent = 1/100 semitone = 1/1,200 octave) correspond to frequency differences of less than 1%. For AM-rate discrimination, the thresholds (also expressed in cents) are very much larger, as expected from previous studies on AM perception (Formby, 1985; Hanna, 1992). For intensity discrimination, the thresholds were around 2 dB. In comparing these thresholds with those obtained in earlier studies, it is important to note that the thresholds reported here were measured with a wide roving range, which explains why they are somewhat larger than those reported in earlier studies with no (or smaller) roving. The frequency and intensity discrimination thresholds reported here are generally consistent with those measured in other studies with roving (e.g., Berliner & Durlach, 1973; Demany & Semal, 2005). It is important to note that for each of the three dimensions considered, thresholds in the D task were larger, on average, than thresholds in the I task.

For each listener, we computed the mean ratio between the thresholds measured in the D task and the thresholds measured in the I task.<sup>7</sup> Statistical bootstrap (Efron & Tibshirani, 1993) was used to estimate the 95% confidence intervals around these mean D/I threshold ratios.<sup>8</sup> Figure 2 shows the mean D/I ratios. Each

circle corresponds to the estimated D/I ratio for a given listener (identified by a specific letter) and a given acoustic dimension, along with the associated 95% confidence intervals. The predictions of the CVG and HT models, which correspond to D/I ratios of 1.56 and 1.00, are indicated by horizontal solid lines. It can be seen that 17 of the 18 D/I ratios displayed in Figure 2 fall between 1.0 (the prediction of HT theory) and 1.56 (the prediction of the CVG model); the exception (Participant J, frequency discrimination) is a D/I ratio of 1.57. In view of their confidence intervals, 8 D/I ratios are statistically consistent with the CVG model and are not statistically consistent with the HT model, 6 go in the opposite direction, and the remaining 4 are inconsistent with both models. Further statistical evidence that the data do not agree with the prediction of either model is provided by a simple sign test: If the CVG model were correct, the mean D/I ratios should fluctuate

<sup>6</sup> As mentioned in the introduction, some of the listeners tested by Semal and Demany (2006) had unusual perceptual difficulties in identifying the direction of changes in frequency; they could detect relatively small changes in frequency but needed much larger frequency differences before they could reliably identify the direction of these changes. Judging from the results of other studies in the literature, which generally found comparable thresholds (or performance) in the detection and the identification of frequency changes (Creelman & Macmillan, 1979; Jesteadt & Bilger, 1974; Nelson et al., 1983; Sek & Moore, 1995), such listeners appear to be atypical. Accordingly, in the present reanalysis, we decided that for frequency discrimination, we would include only the data from the three listeners (L1, L2, and L3) who had the smallest thresholds in Semal and Demany's (2006) study. In 2007, four other listeners were tested in exactly the same conditions. The data of these listeners were included into the reanalysis. As a result, data from seven listeners are presented for frequency discrimination. Finally, we also excluded Semal and Demany's frequency discrimination data for pure tones with very low frequencies (<120 Hz) because, in that case, the frequency changes may have been systematically associated with changes in sensation level and loudness, making it difficult to assess which perceptual cue (or cues) was used by the listeners.

<sup>7</sup> For consistency with the way in which the thresholds were originally measured, the mean ratios were computed with the geometric mean rather than the arithmetic average.

<sup>8</sup> The technical details of the bootstrapping procedure are as follows: First, the D and I thresholds measured in the considered listener were log-transformed. Then, they were independently resampled, with replacement, a large number of times (N = 100,000), keeping the same sample size as the original sample. The arithmetic average of the log-transformed values in each sample was then computed, still separately for the D and I tasks, and the difference between the resulting averages (taken pairwise, in the order in which the samples were generated) was computed, resulting in a single series of 100,000 differences. The statistical distribution of these differences was used in order to estimate the 95% confidence intervals. To increase the stability and accuracy of the estimate, the distribution was first fitted with a Gaussian with a maximum-likelihood fitting procedure. The confidence interval was determined by adding or subtracting 1.96 times the standard deviation of the best-fitting Gaussian to or from its mean. Finally, the resulting values were transformed back from log to linear space.

<sup>&</sup>lt;sup>5</sup> These probabilities can be computed as  $PC_{IHT} = PC_{DHT} = P_D(\Delta) + [1 - P_D(\Delta)]/2$ . The threshold corresponding to the proportion of correct responses targeted by the tracking procedure, here .75, should equal that  $\Delta$  for which  $P_D(\Delta) + [1 - P_D(\Delta)]/2$  equals .75, which simplifies to  $P_D(\Delta) = .5$ ; the value of  $\Delta$  that satisfies this equation can be found by inverting the function relating  $\Delta$  to  $P_D$ .

| Across Participants Geometric Mean | s and Ranges of the | Thresholds Measured in the I | <b>)</b> Task and the |
|------------------------------------|---------------------|------------------------------|-----------------------|
| I Task                             |                     |                              |                       |

| Task   | Frequency discrimination |                       | Intensity discrimination |                    | AM-rate discrimination |                            |
|--------|--------------------------|-----------------------|--------------------------|--------------------|------------------------|----------------------------|
|        | М                        | Range                 | M                        | Range              | М                      | Range                      |
| D<br>I | 13.7<br>9.9              | 10.3–14.8<br>8.8–11.0 | 2.2<br>1.8               | 1.2–4.2<br>0.9–3.9 | 184.3<br>155.2         | 152.0–223.4<br>110.7–208.4 |

*Note.* Frequency discrimination is in cents and intensity discrimination is in decibels. D = detection; I = identification; and AM = amplitude modulation.

around 1.56, with roughly half of them below that value and with the other half above it. Instead, 17 out of the 18 measured mean D/I ratios were lower than 1.56, an outcome that has a negligible probability of occurring (p < .0001) under the hypothesis that the underlying mean D/I ratio is 1.56. For the HT model, the outcome is even clearer: None of the mean D/I ratios is lower than 1.

Although a trend is apparent for D/I ratios to be higher (and closer to the prediction of the CVG model) for frequency discrimination than for the other two acoustic dimensions tested, the mean difference between the D/I ratios for frequency discrimination and intensity discrimination failed to reach statistical significance; t(12) = 1.99, p = .069. Thus, it is not clear that the relationship between D and I thresholds really differs across auditory domains; this is a question for future studies. Assuming for now that the fluctuations in the mean D/I ratios across acoustic dimensions merely reflect random variability across and/or within listeners, it is interesting to pool the data to compute the grand average (geometric mean) D/I ratio, across all acoustic dimensions and listeners. The result is a D/I ratio of 1.27. This value, which is indicated by the horizontal dashed line in Figure 2, falls almost exactly halfway between the predictions of the HT and CVG



*Figure 2.* Mean individual detection/identification (D/I) threshold ratios measured in 11 listeners (A, B, C, ... K) for three sound attributes (frequency, intensity, and amplitude modulation [AM] rate). Values greater than 1.0 indicate that the threshold for detection of a change is higher than the threshold for the identification of the direction of the change. Note that only two listeners (A and B) were tested on all three attributes. Error bars indicate the 95% confidence intervals around the mean ratios, estimated with statistical resampling (bootstrap). The two solid horizontal lines indicate the predictions of the constant-variance Gaussian model (a ratio of 1.56) and of the high-threshold model (a ratio of 1.00). The geometric mean of the 18 plotted D/I ratios is indicated by a dashed line.

models, making it difficult to favor one model over the other. Judging from the confidence-interval bars in Figure 2, a model that would be able to predict a D/I ratio of 1.27 would be statistically consistent with the vast majority of the data points shown in this figure: 16 out of the 18 confidence intervals encompass this value.

In summary, neither the HT model nor the CVG model provides a satisfactory account of the observed relationship between the measured D and I thresholds. Although the HT model predicts a D/I ratio of 1.00, which is significantly lower than more than half of the measured mean D/I ratios, the CVG model predicts a ratio of 1.56, which is significantly higher than more than half of the measured mean D/I ratios. Overall, the mean measured D/I ratio falls almost exactly between the predictions of these two models. This makes it difficult to favor one model over the other, and it suggests that in fact, neither of these two models based on widespread assumptions is consistent with the experimental data.

# Can the CVG Model Be Reconciled With the Data?

In this section, we explore whether and how the CVG model can be modified to yield predicted D/I ratios between 1.00 and 1.56, consistent with the empirical data. The CVG model is characterized by several assumptions. In particular, in this model, it is assumed that the sensory observations on a trial are contaminated by additive Gaussian noises, which are uncorrelated and which have a constant variance. Moreover, the relationships between d'and the probability of a correct response for the D and I tasks, as given in Equations 1 and 3, are based on the assumption that the observer is unbiased, that is, the observer has no a priori preference for either response alternative. Departures from these assumptions affect the predictions of the model and can in some cases yield smaller predicted D/I threshold ratios.

Some intuition into which changes in model assumptions are likely to yield predicted D/I ratios lower than 1.56 can be gained by considering the geometry of the decision space illustrated in Figure 1. Any geometric transformation of PDF or decision axes that increases the probability mass in quadrant P1 or P3 relative to that in quadrants P2 or P4 contributes to lower predicted threshold in the D task relative to that in the I task. To limit the number of possible transformations, we considered only linear transformations (i.e., stretchings and/or rotations of the PDF or decision axis) that had a relatively simple interpretation. For instance, horizontal stretching of the PDF corresponds to an increase in the variance of the internal noise associated with the sensory trace evoked by the first pair, which might be due to memory noise (as discussed

Table 1

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below); a stretch and a 45° rotation of the PDF reflects correlation between the decision variables, due possibly to fluctuating bias (as discussed below).

To compute how such modifications affected the predicted D/I ratios, we ran a series of computer experiments simulating the behavior of a virtual listener in the D and I tasks with modified versions of the original CVG model. Our main findings are summarized below.

#### Nonconstant Internal-Noise Variance?

The CVG model assumes that the variance of the internal noise that contaminates the sensory observations remains constant over time. There are at least two reasons why this assumption might not hold. The first relates to the possible influence of memory on sensory representations. According to the CVG model, correct performance in the D and I tasks requires comparing a quantity derived from the two observations in the first pair with one derived from the two observations in the second pair. Thus, it requires that the observer hold in memory the first quantity, or the original observations from which it derives, until the second quantity can be computed. Retention in memory is not perfect. Stochastic diffusion models of memory assume that sensory traces undergo a random walk, which may be modeled as a linear increase in internal noise variance as a function of time (Kinchla & Smyzer, 1967). According to this type of model, the variance of the internal noise associated with the difference between the observations in the first pair should be larger than that associated with the difference between the observations in the second pair. Monte-Carlo simulations showed that systematic differences in internal noise magnitude between the first and the second pairs could produce D/I threshold ratios lower than 1.56. However, these simulations also revealed that in order for the predicted D/I ratio to equal 1.27 (the mean D/I ratio measured based on the experimental data), the standard deviation of the internal noise had to change (increase or decrease) by a factor of approximately 4 between the first pair and the second pair.<sup>9</sup> Assuming that such a difference in internal-noise magnitude between the sensory representations of the differences in the two pairs was due entirely to sensory-trace diffusion occurring between the offset of the first pair and that of the second (i.e., an interval of 1.45 s), and that trace variance increases linearly as a function of time, this should translate into an approximately fourfold decrease in d' in a 2I2AFC task as the delay between the two stimuli is increased from 0.55 s to 2 s. Clément et al. (1999) found that d' decreased by a factor of about 2 as the delay between the two sounds that listeners had to discriminate increased from 0.5 s to 2 s. Thus, memory noise does not provide a plausible explanation for why thresholds in the D task are only 27% larger than thresholds in the I task, on average.

A second reason why the magnitude of the internal noise added to the observations could differ between the two pairs relates to the use of across-pair roving. As mentioned earlier, the data in Figure 2 were obtained in experiments in which the frequency (or AM rate) of the stimuli was roved over a relatively wide range across pairs to discourage listeners from comparing individual observations between the two pairs on a trial. Although data in the literature (Buus & Florentine, 1991; Jesteadt & Bilger, 1974; Nelson & Freyman, 1986) indicate that frequency and intensity JNDs do not vary markedly over the frequency range used as roving range here (400–2,400 Hz), it is possible that even small or moderate differences in internal-noise variance across pairs due to roving contributed to significantly reduce D/I ratios. To investigate this possibility, we ran Monte-Carlo simulations in which the standard deviation of the noise added to the sensory observations varied randomly across pairs, being drawn from a probability distribution that was uniform on a logarithmic axis (consistent with the use of uniform roving on a semitone frequency scale in the experiments). The simulation results revealed that such across-pair fluctuations in internal-noise magnitude could indeed produce smaller predicted D/I ratios.<sup>10</sup> However, they also revealed that for this effect to explain D/I ratios as small as 1.27, it was necessary to assume that the standard deviation of the internal-noise varied by a factor of more than 100 across the roving range. Such a large variation in internal-noise magnitude would lead to wide variations in frequency or intensity JNDs across the considered frequency range (400-2,400 Hz), inconsistent with psychophysical data in the literature (Buus & Florentine, 1991; Jesteadt & Bilger, 1974; Nelson & Freyman, 1986). Thus, roving-related fluctuations in internal-noise magnitude cannot plausibly explain the finding of smaller than expected D/I ratios.

#### Response Bias?

Another way in which the CVG model can be altered to yield lower D/I ratios involves introducing bias into the decision. In general, the proportion of correct responses achieved by a biased observer is lower than that achieved by an unbiased observer. Thus, a simple way to reduce the D/I ratio predicted by the CVG model is to assume that listeners are not unbiased and that the bias affects only the I task or, at least, that its influence on thresholds is larger in this task than in the D task. The simplest form of bias corresponds to a constant a priori preference for one of the two response alternatives. For instance, some listeners may be more inclined to choose the upward direction than to choose the downward direction; for other listeners, the converse may be true. In fact, an analysis of the trial-by-trial data collected for some of the listeners whose data are shown in Figure 2 showed no such bias. Instead, the listeners' responses were equally distributed between upward and downward, as they should be, given that these stimulus alternatives were equally likely a priori. Thus, this simple form of bias can be ruled out.

A subtler form of bias, which cannot be ruled out so easily, consists of fluctuations in the position of the internal criterion across trials. Such bias may occur as a result of the observer's response to the

<sup>&</sup>lt;sup>9</sup> The D/I ratio was similarly reduced if the noise variance was larger in the second pair than in the first pair. However, it is difficult to think of a reason why this might have occurred in actual listeners.

<sup>&</sup>lt;sup>10</sup> In these simulations and in those described hereafter, unless otherwise mentioned, the assumed decision rules were as specified above. These rules did not always lead to optimal (maximum-likelihood) decisions. However, in most of the cases studied, it was reasonable to assume that the observer was unable to adapt the decision strategy for best performance, either due to incomplete information about the stimulus or because the optimal rule was too sophisticated. The situation of across-pair fluctuations in internal variance considered here is a case in point. In that situation, the optimal strategy required the observer to memorize all possible distributions of the noise, conditioned on the stimulus frequency, and to select the appropriate distribution based on the current estimate of the stimulus frequency.

current trial being influenced by his or her response to the previous trial or, if feedback is given (as was the case in the experiments considered here), by the outcome of that trial, that is, whether the response was correct or incorrect (Treisman & Williams, 1984). For example, the participant may be inclined to choose the same response as that given on the previous trial if that preceding response turned out to be correct. Although the precise generating mechanisms of this fluctuating bias cannot be determined on the basis of the data currently available, the fact that the stimulus alternative presented on a given trial did not depend on that presented on the previous trial makes it possible to model this type of bias as a random variation of the decision criterion. Moreover, although variable across trials, the direction and magnitude of the shift may to a first approximation be regarded as constant within a trial. As a result, this form of fluctuating bias introduces some correlation between the decision variables derived from the different observations or pairs of observations on a trial; the assumption of statistical independence, which was made in the original CVG model, is violated.

A schematic illustration of this effect is provided in Figure 3. The situation illustrated in this figure is that in which an upward change occurred in the first pair, and the task is to identify the direction of the change. For this task, a random shift of the criterion is mathematically equivalent to an addition of the same random value to the two decision variables,  $\Delta y_1$  and  $\Delta y_2$ . Figure 3 shows how this modifies the joint PDF. The contour of the PDF, which was circular in Figure 1, is now elongated along the major



*Figure 3.* Decision space for the constant-variance Gaussian model with fluctuating bias added to the decision variables,  $\Delta y_1$  and  $\Delta y_2$ . In this example, the bias-related noise has a normal distribution with a standard deviation twice as large as that of the sensory noise. As manifested by the elliptical shape of the probability density function and its diagonal orientation, this type of bias introduces a correlation between the two decision variables. This correlation contributes to reduce the proportion of correct responses, compared with the case in which no such bias is present (Figure 1).

diagonal of the decision plane, reflecting a positive correlation between the two decision variables. This transformation affects the way in which the mass of the PDF is shared among the four quadrants. The effect may be depicted schematically as an increase in the proportion of the mass in the half-plane formed by P4 and P3 at the expense of that in the half-plane formed by P1 and P2. Assuming that the observer is unable to adjust his or her decision strategy to take into account the correlation between the decision variables, the predicted proportion of correct responses in the I task is still given, as in Figure 1, by the proportion of the probability mass contained in quadrants P1 and P2, relative to that contained in quadrants P3 and P4. An increase in the mass in P3 at the expense of P2 translates into a decrease of the predicted proportion correct for the I task and, therefore, in a smaller predicted D/I ratio.

Figure 4 shows how the D/I ratio predicted by a modified CVG model based on this assumption of fluctuating bias in the I task depends on the standard deviation of the bias-related noise relative to that of the sensory noise. As the relative magnitude of the fluctuating bias increases from zero to infinity, the predicted D/I ratio decreases from 1.56 to 1.00. For the D/I ratio predicted by the model to equal the mean measured D/I ratio (1.27), the bias-related noise must have approximately the same standard deviation as the sensory noise.

To summarize, D/I ratios lower than 1.56 can be accounted for by assuming a CVG observer with a fluctuating bias toward the upward response or the downward response in the I task. However, it is important to note that this is an ad hoc assumption. The data presented in this note provide no evidence for or against such fluctuating bias, affecting selectively the decision between the upward and the downward responses. One might equally well assume that a similar fluctuating bias also affected the decision between the first and the second pairs in the D task, leading the listener to favor the first interval on some trials and the second interval on other trials. Such bias would reduce the proportion of correct responses in the D task, thereby contributing to bring the D/I ratio back toward its original value of 1.56. Thus, an explanation of the results in Figure 2 in terms of fluctuating bias remains largely speculative.

# Nonlinear Psychometric Functions?

A third way in which D/I ratios lower than 1.56 might be explained without completely abandoning the CVG model involves violating the assumption of linear psychometric functions. So far, we have assumed in all mathematical derivations and simulations that d' was proportional to the physical difference (in cents, or in dB) between the stimuli to be compared. This assumption is supported by results in the psychoacoustical literature (Buus & Florentine, 1991; Nelson & Freyman, 1986; Turner & Nelson, 1982).<sup>11</sup> However, due to variability in the psychophysical measures, the experimental evidence is necessarily limited, and it cannot be used to rule out moderate deviations from linearity. Therefore, one may wonder how deviations from the assumption

<sup>&</sup>lt;sup>11</sup> In the case of frequency discrimination, Turner and Nelson (1982) and Nelson and Freyman (1986) conclude that *d'* is proportional to the frequency difference in Hertz. Here, frequency differences were measured in musical cents rather than in Hertz. However, for very small frequency differences, such as the thresholds displayed in the second column of Table 1, differences in Hertz and in cents are proportional to each other and, therefore, equivalent.



*Figure 4.* Influence of the magnitude of the bias toward one of the two response alternatives in the detection (D) task on the detection/ identification (D/I) threshold ratios predictions of the constant-variance Gaussian model. The magnitude (i.e., standard deviation) of the bias is expressed relative to that of the sensory noise. Pc = proportion of correct responses.

of linear psychometric functions influence the D/I ratio predictions of the CVG model and, more specifically, whether moderate deviations may in fact result in substantially lower predicted values, consistent with those shown in Figure 2.

To investigate this possibility, we ran additional Monte-Carlo simulations with the basic CVG model, this time assuming that the relationship between d' and stimulus difference  $\Delta$  followed a power law  $(d' = \Delta^k)$  instead of a linear relationship. The power law is often used to model psychometric functions (Gescheider, 1997; Hartmann, 1998). It presents the advantage over other elementary mathematical functions, such as the logarithmic and exponential, that it can assume either convex or concave shapes, depending on whether the value of the exponent, k, is larger or smaller than unity. In the simulations, this value was varied systematically until the D/I ratio predicted by the simulated CVG model was consistent with the mean ratio measured in the psychophysical experiments: 1.27. The results revealed that for this to be the case, the exponent in the power-law function had to be about 1.85. Such an exponent results in a substantial deviation from linearity in the shape of the psychometric function. This outcome is inconsistent with the psychophysical results reported by Turner and Nelson (1982) or Nelson and Freyman (1986) for frequency discrimination and by Buus and Florentine (1991) for intensity discrimination. (We are not aware of relevant experimental data in the case of AM-rate discrimination).

# Alternative Models

The observation that the CVG model cannot easily be reconciled with the experimental data leads us to consider other types of psychophysical models. The observation that all but one of the mean D/I ratios shown in Figure 2 fall between the predictions of the HT and CVG models suggests that listeners' behavior in the D and I tasks might be adequately captured by a model that combines some of the features of these two types of models. In this section, we briefly describe two such models. The first was obtained by appending a quantization stage to the CVG model; the resulting model is referred to as the QG model. The second model is a pure discrete-state model inspired by neurophysiological observations, which suggests that the perception of stimulus changes may be mediated at the neural level by the relative activations of neurons that are selectively sensitive to increments or decrements, whose spike-count output follows a Poisson distribution.

# A QG Model

The idea of quantized sensory representations is not new. Following Boring (Boring, 1926), Stevens and colleagues (Stevens, 1972; Stevens et al., 1941; Stevens & Volkmann, 1940) and others (Miller & Garner, 1944; Larkin and Norman, 1964) argued for a quantum model of sensory discrimination. The QG model, which we consider here, assumes an initial stage in which, as in the CVG model, the sensory activity evoked by the stimuli is modeled as a Gaussian-distributed random quantity along a continuous axis. This first stage is followed by a second one, in which the continuous sensory activity from the first stage is quantized. It is assumed that the participant only has access to the output of the latter stage; therefore, his or her decisions are based on an imperfect, quantized representation of the stimuli. This idea is represented schematically in Figure 5. Due to the quantization operation, the decision space for this model is a discrete version of that for the CVG model shown in Figure 1.

By varying the size of the quantization steps relative to the magnitude of the internal Gaussian noise, one can generate predicted D/I ratios that range from 1 to 1.56, as shown in Figure 6. This can be understood by considering that when the size of the quantization steps is large relative to the magnitude of the internal Gaussian noise, the QG model is essentially equivalent to a twostate HT model. On the other hand, if the quantization steps are made infinitely small, the QG model becomes equivalent to the CVG model.

From this point of view, the HT and CVG models described in earlier sections can be thought of as extreme cases on a continuum going from two to an infinitely large number of possible internal states. The results shown in Figure 2 suggest that human observers stand between these two extremes: They behave as if their decisions were based on a finite number of states, although more states than assumed by the HT model. The simulation results shown in Figure 6 indicate that in order for the QG model to predict a D/I ratio equal to the mean D/I ratio measured experimentally (1.27), the size of the quantization step (or quantum) must be between 2 and 3 times larger than the standard deviation of the internal Gaussian noise. (Figure 5 was produced assuming a quantum size equal to 3 times the standard deviation of the internal Gaussian noise).

It is worth noting that Stevens and Volkmann (1940) and Stevens (1972) reached a different conclusion regarding the relative size of the quantum, compared with other sources of noise affecting the observer's responses in sensory discrimination experiments. These authors concluded that the quantum size was probably smaller than that of the other sources of noise, explaining why quantization effects are usually difficult to observe. Following this line of reasoning, one might object that if, as indicated by our simulation results, the quantum size is several times the standard deviation of the prequantization noise, this should produce visible steps in psychometric functions for frequency and intensity discrimination, whereas in most published reports of such functions, such steps are not clearly apparent.<sup>12</sup> A possible explanation for this lack of evidence for a quantization operation in psychometric data is that the standard deviation of the additional sensory noise introduced by the quantization operation is only  $1/\sqrt{12}$  of the quantum size. This means that even if the size of the quanta is up to 3.5 times the standard deviation of the Gaussian sensory



Figure 5. Schematic illustration of the sensory-observation process and decision space for the quantized-Gaussian (QG) model. Top: This is a schematic representation of the physical and sensory scales. A stimulus with a certain value on a physical scale, x, evokes a sensory response on a continuous sensory scale, y. As in the constant-variance Gaussian (CVG) model, this sensory response is contaminated by Gaussian noise. However, in the QG model, the observer only has access to a quantized representation of the sensory activity, as represented by the discrete scale, q. In this example, the size of the quanta was chosen to equal 3 times the standard deviation of the Gaussian sensory noise. In addition, we purposefully chose a case in which sensory activity on the continuous scale, y, falls close to the border between two quanta, to illustrate the fact that a given stimulus value does not always result in the activation of the same quantum. Bottom: This is the two-dimensional decision space for the QG model. This can be compared with the decision space for the CVG model illustrated in Figure 1. As in that figure, the situation illustrated is one in which an upward change occurred in the first pair. Here, the probability of a correct response is computed as a sum over quadrants P1 and P3 for the detection (D) task and quadrants P1 and P2 for the identification (I) task. For quanta that are cut through by one or two diagonals, decisions are determined by guessing. In this example, the physical difference,  $\Delta$ , between the two stimuli was set to 2.1 times the standard deviation of the Gaussian sensory noise, so that the proportion correct in the D task equals approximately .75.



*Figure 6.* Detection/identification (D/I) ratio predicted by the quantum model as a function of the quantum size relative to the standard deviation of the prequantization noise. The vertical dotted line shows the relative quantum size corresponding to the case of a quantization noise with a standard deviation equal to that of the prequantization noise, as discussed in the text. Pc = proportion of correct responses.

noise, the quantization operation will contribute less noise than there already is in the system. Thus, a quantum size between 2 and 3 times larger than the standard deviation of the prequantization noise, as indicated by our results, might not produce detectable steps in psychometric functions, at least under usual testing conditions.

To summarize, the simulation results indicate that D/I threshold ratios comprised between 1.00 and 1.56 can be predicted by a model based on the assumption that listeners only have access to a quantized representation of Gaussian sensory observations. From this point of view, the experimental data are consistent with the general idea behind the psychophysical quantum theory (Stevens & Volkmann, 1940).

# A Neurophysiologically Inspired Poisson Model

The second model considered here is based on the idea (supported by experimental data, in the auditory domain as well as the visual domain) that some neurons in the central nervous system respond with an increased firing rate when a stimulus changes in a given direction. Psychophysical observations reported by Demany and Ramos (2005) provide strong evidence for the existence of automatic and direction-sensitive frequency-shift detectors in the human auditory system. This study showed that a sequence of two pure tones differing in frequency and separated by a 500-ms silent delay can elicit a percept of directional pitch shift, even when the pitch of the first tone is not consciously audible.

<sup>&</sup>lt;sup>12</sup> Although Stevens and colleagues (Stevens, 1972; Stevens et al., 1941; Stevens & Volkmann, 1940) did claim that under some specific experimental conditions, linear steps are apparent in psychometric functions in various visual and auditory perception tasks, this claim was questioned in subsequent publications, on the basis of methodological considerations (Corso, 1973; Green & Swets, 1966).

The model that we propose here involves a neural increment detector, which compares the two stimuli in a pair, whose mean firing rate increases monotonically with the difference in intensity or frequency,  $\Delta$ , between these stimuli, but only if this difference is positive (i.e.,  $\Delta > 0$ ). For simplicity, we assume that when  $\Delta$  is relatively small, as is typically the case near discrimination threshold, the mean firing rate of the detector increases linearly with  $\Delta$ . For negative physical differences (i.e.,  $\Delta < 0$ ), the output of this detector is distributed following the same distribution as for physically identical stimuli (i.e.,  $\Delta = 0$ ), reflecting the fact that the detector is insensitive to decrements. Furthermore, it is assumed that the output of this detector can be modeled as a Poisson process with a driving rate  $\mu_0$  for identical stimuli or decrements, and  $\mu =$  $\mu_0 + \alpha \Delta$  for increments (with  $\alpha$  a constant). Poisson processes are frequently used as an approximate model of neural spiking, and accordingly, the Poisson distribution is commonly used as an approximate model of the distribution of spike counts (Rieke, Warland, de Ruyter van Steveninck, & Bialek, 1997).

In addition to this increment detector, the model contains a decrement detector, which produces a Poisson-distributed output with mean rate  $\mu_0$  for  $\Delta \ge 0$ , and mean rate  $\mu = \mu_0 + \alpha |\Delta|$  for  $\Delta < 0$ . The difference between the outputs of these increment and decrement detectors is used to decide whether a change occurred, and if a change did occur, to decide in which direction it was. Accordingly, the decision space for this model resembles that for the Gaussian and QG models, in that the decision variables are differences between random variables derived from the first and the second pairs; however, instead of having a Gaussian or QG distribution, here, the decision variables have a distribution given by the difference between two Poisson-distributed random variables. Examples of such Poisson-difference distributions are shown in Figure 7. The two panels in this figure show how the decision variables are distributed for same trials (upper panel) and different trials (lower panel), assuming a Poisson process with a



*Figure 7.* Example probability distributions for the difference between observations decision variable in the Poisson model. The two panels in this figure show how the decision variables are distributed (A) on same trials and (B) on different trials. These distributions are for a Poisson process with a mean spontaneous rate,  $\mu_0$ , of 0.8 spikes per second and a mean evoked rate of 2.9 spikes per second.

mean spontaneous rate,  $\mu_0$ , of 0.8 spikes per second and a mean evoked rate of 2.9 spikes per second. As can be seen, the two distributions have different spreads; this results from the fact that the variance of a Poisson-distributed random variable increases with the mean.

The critical variable, in this model, is the mean spontaneous rate,  $\mu_0$ , of the increment and decrement detectors; for simplicity, this rate is assumed to be the same for the two types of detectors. As the mean spontaneous rate increases, and the mean evoked rate increases beyond it, the probability distribution of the difference between the output of the two types of detectors tends toward a Gaussian distribution and the D/I predicted by this Poisson model tends toward that of the CVG model. In Figure 8, we show how the D/I threshold ratio predicted by the Poisson model depends on the mean spontaneous rate,  $\mu_0$ . For each value of  $\mu_0$  we determined the value of the evoked rate,  $\mu_D$ , which yielded a predicted proportion of correct responses of .75 in the D task, and the value of evoked rate,  $\mu_{I}$ , corresponding to the same proportion correct in the I task. The D/I ratio was then calculated as  $(\mu_D - \mu_0)/(\mu_I - \mu_0)$ . These results confirm that this Poisson model can predict D/I ratios lower than 1.56, and they reveal that such ratios result from relatively low spontaneous rates: D/I ratios below 1.4 require a mean spontaneous rate of approximately 1 or less.

# Receiver Operating Characteristics for D: A Further Test of the Models

The above simulation results reveal that a discrete Poisson model, or a hybrid (continuous-discrete) QG model, provides a more satisfactory account of the empirical D/I threshold ratio data shown in Figure 2 than the HT and CVG models. However, it may be argued that the former two models are ad hoc and that although they originate in earlier work independent from the present one (e.g., Green and Swets, 1966; Egan, 1975; Kaernbach, 1991a), they were only invoked here because it was suspected that they would resolve the particular problem under consideration. Therefore, it was desirable to consider additional experimental data, besides D/I ratios, to further evaluate whether the Poisson and QG models provide more adequate models of how sensory changes are perceived.

Receiver operating characteristics (ROCs), which represent the probability of a false alarm as a function of the probability of a hit for different values of the criterion (Green & Swets, 1966; Egan, 1975), provide such data. A landmark of the Poisson model is that it can account for experimental findings of asymmetric ROCs in yes–no signal-D tasks (Egan, 1975; Kaernbach, 1991a; Swets, Tanner, & Birdsall, 1961). This stems from the Poisson distribution being asymmetric and from its variance increasing with its mean. In contrast to the Poisson model, the CVG model predicts symmetric ROC curves, at least for the yes–no D task. Therefore, ROCs provide a way of distinguishing the Poisson model from the CVG model.

One complication, which must be taken into account here, stems from the fact that we are not dealing simply with detection, but with D. More precisely, we are dealing with the detection of discrete sensory changes. The paradigm of choice for measuring this ability is not the yes-no paradigm, for which the above distinction between CVG and Poisson models has been established, but rather the two-interval, same-different (2IAX) para-



*Figure 8.* Detection/identification (D/I) ratios for decisions based on Poisson increment and decrement detectors as a function of the mean spontaneous rate at the output of the detector. Pc = proportion of correct responses.

digm. For that paradigm, the CVG model can actually predict asymmetric ROCs in some situations (see, e.g., Dai et al. 1996; Hautus, Irwin, & Sutherland, 1994). This is the case, in particular, for experiments in which the stimuli are roved over a relatively wide range across trials, as commonly done to force listeners to compare the two stimuli presented on each trial rather than rely on a long-term memory trace. In this situation, the ROCs predicted by the CVG model are slightly asymmetric about the minor diagonal (Dai et al. 1996).<sup>13</sup> This makes the task of distinguishing between the CVG model and the Poisson model less straightforward, because asymmetric ROCs are now expected for both models (Kaernbach, 2008). Fortunately, there is a simple way to overcome this problem. The CVG model only predicts asymmetric ROCs in the 2IAX paradigm if the direction of the change is not known in advance by the observer. If the observer knows the direction of the change in advance, the asymmetry is eliminated. This is because knowing the direction of the change eliminates the need for an optimal CVG observer to base his decisions on the absolute value (or any other nonmonotonic transformation) of the difference between the sensory observations evoked by the two stimuli presented on a trial. Instead, the CVG observer can now decide between same and different on the basis of the signed (as opposed to the unsigned) difference between the two observations. This decision strategy is formally equivalent to the differencing strategy for the 2I2AFC paradigm, which we mentioned earlier, except for the placement of the criterion: Assuming a balanced design (with equal a priori probabilities and symmetric payoffs), the optimal placement of the criterion in the 2I2AFC paradigm corresponds to the origin (zero) of the decision axis; in contrast, in the directionknown 2IAX paradigm, the optimal placement of the criterion corresponds to a positive value for trials on which the direction of the change is upward," and to a negative value for trials on which the direction is downward. In both cases, the criterion should be positioned halfway between the means of the difference distributions corresponding to same and different trials. Therefore, if in a 2IAX experiment the change between the two stimuli in the different pairs always has the same direction, and listeners are aware of this fact, ROCs should be symmetric under the CVG model. Because, on the other hand, the Poisson model still predicts asymmetric ROCs, this provides a way of distinguishing between the CVG model and the Poisson model in a D setting.

The above rationale led us to analyze ROC data obtained in a 2IAX intensity-discrimination experiment in which the change in intensity between the two tones presented on different trials could only be downward. Note that intensity is the dimension for which we previously found D/I ratios to be the lowest, on average (Figure 2), consistent with a Poisson process having a relatively low mean. Therefore, it is for this dimension that one should expect the most asymmetric ROC curves, if the Poisson model accurately describes the D process. This provides ideal conditions for testing which of the two rival models, CVG and Poisson, is most consistent with empirical ROCs.

Listeners rated their certitude regarding the occurrence of a change between the stimuli with six response categories: "very sure yes," "sure yes," "maybe yes," "maybe no," "sure no," and "very sure no." A multiple-response monetary payoff matrix was used to entice listeners to vary their criteria for deciding between the different response categories over a relatively broad range, going from most conservative (i.e., trying to limit the number of false alarms) to most liberal (i.e., trying to achieve a high hit rate). The ROC data measured across five listeners by this technique are shown as symbols in Figure 9. The best-fitting predictions of the CVG model and Poisson model are shown as dashed and solid curves, respectively. As can be seen, the best-fitting asymmetric ROC produced by the Poisson model provides a better fit to the empirical data than does the best-fitting symmetric ROC produced by the CVG model (model comparison: log of Poisson/CVG likelihood ratio = 75.5; p < .0001).<sup>14</sup> It is interesting to note that the best-fitting Poisson model had a mean spontaneous rate, µ0, of approximately 0.8, and an evoked mean rate of approximately 2.6. Based on the data shown in Figure 8, which illustrate how the mean D/I ratio predicted by the Poisson model depends on the mean spontaneous rate, a mean spontaneous rate of 0.8 corre-

<sup>&</sup>lt;sup>13</sup> Why the CVG model predicts asymmetric ROCs in 2IAX experiments with roving can be understood by considering that in this situation the optimal decision rule is based on the absolute value of the difference between the sensory observations; this is the so-called differencing strategy for the 2IAX paradigm. Whereas the distributions of the original sensory observations are equal-variance Gaussian, the distributions of the absolute value of the difference between the observations on same and different trials are not.

<sup>&</sup>lt;sup>14</sup> This *p* value was computed as p = 1 - K(x, n), where K(x, n) denotes the cumulative chi-square distribution with *n* degrees of freedom, evaluated at *x*. Here, *x* was equal to  $2\log(\lambda_1/\lambda_2)$ , with  $\lambda_1$  and  $\lambda_2$  denoting the likelihoods of the data under the two considered models: Poisson and CVG, respectively. The number of degrees of freedom, *n*, was calculated as the difference between the number of free parameters of the CVG model, 1 (*d'*), and the number of degrees of freedom for the Poisson model, 2 (mean and evoked spontaneous rates); thus, *n* was equal to 1. This calculation relies on a convenient result in probability theory, which says that the statistic,  $2\log(\lambda_1/\lambda_2)$ , or twice the logarithm of the likelihood ratio, is asymptotically chi-square distributed with degrees of freedom equal to the difference in the number of free parameters of the two models being compared.



*Figure 9.* Receiver operating characteristics (ROCs) predicted by the constant-variance Gaussian (CVG) and Poisson models compared with human data. The crosses show mean hit and false-alarm probabilities measured in five human listeners performing a 2IAX intensity-discrimination task in which the direction of intensity changes (downward) was constant and known to the listener (see text for details). The dashed curve shows the best-fitting ROC curve produced by the CVG model, which under such testing conditions can only yield symmetric ROCs. The solid lines indicate the best-fitting ROC obtained with the Poisson model described in the text. As can be seen, the latter predicts an asymmetric ROC, which more accurately fits the data than does the symmetric ROC produced by the CVG model.

sponds to a mean D/I ratio slightly below 1.4. This value is somewhat larger than the mean empirical D/I ratio computed from the data displayed in Figure 2, which was 1.27. However, in view of the inter- and intraindividual variability in the psychophysical data, our estimates of the Poisson-model parameters derived from the D/I data are in reasonably good agreement with those derived from the ROC data.

So far, this section has focused exclusively on the Poisson and CVG models. One remaining question is whether the ROC data can also be used to distinguish the Poisson model from the other two models that were shown earlier to account for the empirical threshold-ratio data, namely the modified Gaussian model with fluctuating bias, and the QG model. The former is easy to rule out because it assumed that a fluctuating bias was present only in the I task. For the D task, the predictions of that model are exactly the same as those of the CVG model. Consequently, we turn our attention to the QG model. To investigate whether and how well this model could explain the ROC data, we ran simulations with different quantum sizes (relative to the magnitude of the prequantization internal noise), until the best possible match between measured and predicted ROCs was achieved. The results of this analysis revealed that the QG model could produce asymmetric ROCs, if the quantum size was sufficiently large. This can be understood by considering that as the quantum size increases, the Gaussian internal-noise distribution is sampled more and more coarsely. For very large quantum sizes, the number of relevant internal states in the QG model is relatively small, yielding ROCs with visible edges. Occasionally, depending on the exact relationship between the quanta and the prequantization noise, the main edge in the predicted ROC falls below the minor diagonal, as observed in the empirical ROC data. However, this requires a specific relationship between the quanta and the prequantization noise; in practice, this requirement is unlikely to be met consistently. Moreover, we found that in order to account for a substantial departure from symmetry in the predicted ROCs, the quantum size must be very large compared with the standard deviation of the prequantization noise. Specifically, our simulation results revealed that in order to account for the asymmetry observed in the empirical ROC data in Figure 9, the quantum size must be roughly 8 times larger than the standard deviation of the prequantization noise. This factor of 8 is considerably larger than the factor that we arrived at earlier on the basis of empirical D/I ratios, which indicated an average quantum size at most 3 times larger than the prequantization noise. A quantum size 8 times larger than the prequantization noise is inconsistent, not only with this earlier result, but also with other data in the literature (cf. our earlier discussion of the consequences of a large quantum size on psychometric functions).

To summarize the results and arguments presented in this section, the Poisson model correctly predicts that ROCs for the detection of sensory changes having a fixed and known direction are asymmetric. In addition to being qualitatively consistent with empirical ROC data, the predictions of this model are in better quantitative agreement with the data than are those of the various other models considered in this work. Further study is required to determine whether these findings, which concern changes in sound intensity, hold for other dimensions of auditory perception and for other sensory modalities. However, combined with our previous demonstration that the Poisson model can account for the observed relationship between D and I thresholds, these results pinpoint this model as a more adequate description of the perceptual and/or neural processes involved in the perception of simple sensory changes than the HT, CVG, or QG model.

# Conclusions

A statistical analysis of detailed measurements of thresholds for the detection of simple changes in auditory stimuli and thresholds for the identification of the direction of these changes measured under identical stimulus conditions in the same listeners revealed that the relationship between these thresholds departed significantly from the predictions of two common psychophysical models, the CVG model and the HT model. However, remarkably, for the three acoustic dimensions studied (intensity, frequency, and AM rate) and for all but one of the 11 listeners tested, the mean measured D/I threshold ratios fell between the predictions of these two models. This led us to consider the possibility that a hybrid model combining early Gaussian sensory observations with a later quantization stage (the QG model) or a discrete-state model with a larger number of internal states than the basic HT model (the Poisson model) might adequately capture the behavior of human listeners in the D and I tasks. This possibility was confirmed by simulation results: Both the QG and Poisson model were able to

produce D/I threshold ratios between 1.00 and 1.56, as observed in humans. To further evaluate the different models, we analyzed ROC data collected under conditions in which the direction of the sensory change was fixed and known to the listener. These ROC data were best accounted for (both qualitatively and quantitatively) by the Poisson model.

Gaussian models have usually been favored over discrete-state models because of their ability to fit empirical ROC curves better than their historic competitor, the dual-state HT model. However, as noted by Green and Swets (1966), ROCs typically contain a handful of data points, and discrete-state models with at least as many internal states as the number of data points can fit such empirical ROCs as well as the Gaussian model. The QG model and the Poisson model described in this article fall into this category. The Poisson model presents the advantage that it can accommodate asymmetric empirical ROCs (Kaernbach, 1991a). Future studies involving detailed measurements of ROCs for the detection of changes in sound intensity or frequency under stimulus conditions similar to those considered here may provide further arguments for or against this model.

Another argument that is often used to justify the Gaussian assumption is that by the central-limit theorem, the distribution of the sum of a large number of random variables tends toward a Gaussian. However, this statistical theorem applies specifically to large numbers of statistically independent sources of variability combined additively. Research on the neural underpinnings of perception conducted during the past decades indicates that the neural responses that are combined to arrive at a perceptual decision are usually correlated rather than independent (Averbeck, Latham, & Pouget, 2006; Zohary, Shadlen, & Newsome, 1994). Moreover, neural responses may be combined in complex nonlinear ways rather than additively. The view that perception ultimately relies on discrete quantities is consistent with a wealth of neurophysiological observations, including, in particular, findings indicating that perceptual decisions may be based on the correlated spike counts of a relatively limited number of neurons (Shadlen & Newsome, 1998). In this respect, the Poisson model of D and I described here is particularly attractive because of its neurophysiological plausibility and simplicity.

Another argument in support of the QG and Poisson models stems from the introspective fact that physically identical sounds are often perceived as identical. According to a model in which sensory observations are continuous and contaminated by Gaussian internal noise, the sensory observations evoked by two physically identical stimuli have an infinitely small probability of being exactly identical, due to the influence of internal noise. By contrast, in discrete-state models, the probability that two physically identical stimuli evoke strictly identical percepts is not negligible. To reconcile the CVG model with introspection, one would have to assume that the participant does not have conscious access to the true sensory observations but does have access only to the decisions that were reached after comparing these observations with an internal criterion. This is tantamount to assuming that the decisions of the participant rest on a quantized (discrete) representation of the stimuli.

On the basis of these results and considerations, we suggest that discrete-state models, and in particular, a Poisson model, describe more adequately than does the CVG model the processes involved in the perception of simple changes in auditory stimuli. Of course, it would be interesting to know whether such a conclusion is valid for auditory dimensions not considered here (for instance, sound localization) and to see whether a similar conclusion can be drawn for other sensory modalities. It is therefore hoped that the analysis described in this article will spark further empirical studies concerning, especially, the relationship between D and I.

# References

- Averbeck, B. B., Latham, P. E., & Pouget, A. (2006, May 7). Neural correlations, population coding and computation. *Nature Reviews Neuroscience*, 7, 358–366.
- Berliner, J. E., & Durlach, N. I. (1973). Intensity perception: IV. Resolution in roving-level discrimination. *Journal of the Acoustical Society of America*, 53, 1270–1287.
- Boring, E. G. (1926). Auditory theory with special reference to intensity, volume, and localization. *American Journal of Psychology*, 37, 157– 188.
- Buus, S., & Florentine, M. (1991). Psychometric functions for level discrimination. *Journal of the Acoustical Society of America*, 90, 1371– 1380.
- Clément, S., Demany, L., & Semal, C. (1999). Memory for pitch versus memory for loudness. *Journal of the Acoustical Society of America*, 106, 2805–2811.
- Corso, J. F. (1973). Neural quantum controversy in sensory psychology. *Science*, 181, 467–469.
- Creelman, C. D., & Macmillan, N. A. (1979). Auditory phase and frequency discrimination: A comparison of nine procedures. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 146–156.
- Dai, H., Versfeld, N. J., & Green, D. M. (1996). The optimum decision rules in the same-different paradigm. *Perception & Psychphysics*, 58, 1–9.
- Demany, L., & Ramos, C. (2005). On the binding of successive sounds: Perceiving shifts in nonperceived pitches. *Journal of the Acoustical Society of America*, 117, 833–841.
- Demany, L., & Semal, C. (2005). The slow formation of a pitch percept beyond the ending time of a short tone burst. *Perception & Psychophysics*, 67, 1376–1383.
- Efron, B., & Tibshirani, R. (1993). *An introduction to the bootstrap*. New York: Chapman and Hall/CRC.
- Egan, J. P. (1975). Signal detection theory and ROC analysis. New York: Academic Press.
- Formby, C. (1985). Differential sensitivity to tonal frequency and to the rate of amplitude modulation of broadband noise by normally hearing listeners. *Journal of the Acoustical Society of America*, 78, 70–77.
- Gallun, F. J. (2003). The role of stimulus envelope in the detection of brief increments in the intensity of a tone. Unpublished doctoral dissertation, University of California, Berkeley.
- Gescheider, G. A. (1997). *Psychophysics. The fundamentals.* Mahwah, NJ: Erlbaum.
- Green, D. M., & Swets, J. A. (1966). Signal detection theory and psychophysics. New York: Krieger.
- Hafter, E. R., Bonnel, A.-M., Gallun, E., & Cohen, E. (1998). A role for memory in divided attention between two independent stimuli. In A. R. Palmer, A. Rees, A. Q. Summerfield, & R. Meddis (Eds.), *Psychophysical and physiological advances in hearing* (pp. 228–238). London: Whurr.
- Hanna, T. E. (1992). Discrimination and identification of modulation rate using a noise carrier. *Journal of the Acoustical Society of America*, 91, 2122–2128.
- Hartmann, W. M. (1998). Signals, sound, and sensation. New York: Springer.
- Hautus, M. J., Irwin, R. J., & Sutherland, S. (1994). Relativity of judgments

about sound amplitude and the asymmetry of the same-different ROC. *The Quarterly Journal of Experimental Psychology: Section A*, *47*, 1035–1045.

- Jesteadt, W., & Bilger, R. C. (1974). Intensity and frequency discrimination in one- and two-interval paradigms. *Journal of the Acoustical Society of America*, 55, 1266–1276.
- Jesteadt, W., & Sims, S. L. (1975). Decision processes in frequency discrimination. *Journal of the Acoustical Society of America*, 57, 1161– 1168.
- Johnsrude, I. S., Penhune, V. B., & Zatorre, R. J. (2000). Functional specificity in the right human auditory cortex for perceiving pitch direction. *Brain*, 123, 155–163.
- Kaernbach, C. (1991a). Poisson signal-detection theory: Link between threshold models and the Gaussian assumption. *Perception & Psychophysics*, 50, 498–506.
- Kaernbach, C. (1991b). Simple adaptive testing with the weighted up-down method. *Perception & Psychophysics*, 49, 227–229.
- Kaernbach, C. (2008). *Poisson processes in change detection*. Manuscript in preparation.
- Kinchla, R., & Smyzer, F. (1967). A diffusion model of perceptual memory. Perception & Psychophysics, 2, 219–229.
- Klein, S. A. (1985). Double-judgment psychophysics: Problems and solutions. *Journal of the Optical Society of America A*, *2*, 1560–1585.
- Larkin, W. D., Norman, D. A. (1964). An extension and experimental analysis of the neural quantum theory. In R. C. Atkinson (Ed.), *Studies* in mathematical psychology, Palo Alto, CA: Stanford University Press.
- Macmillan, N. A. (1971). Detection and recognition of increments and decrements in auditory intensity. *Perception & Psychophysics*, 10, 233– 238.
- Macmillan, N. A. (1973). Detection and recognition of intensity changes in tone and noise: The detection-recognition disparity. *Perception & Psychophysics*, 13, 67–75.
- Macmillan, N. A., & Creelman, C. D. (2005). Detection theory: A user's guide. Mahwah, NJ: Erlbaum.
- Macmillan, N., Kaplan, H., & Creelman, D. (1977). The psychophysics of categorical perception. *Psychological Review*, 84, 452–471.
- Micheyl, C., & Messing, D. P. (2006). Likelihood ratio, optimal decision rules, and correct response probabilities in a signal detection theoretic, equal-variance Gaussian model of the observer in the 4IAX paradigm. *Perception & Psychophysics*, 68, 725–735.
- Miller, G. A., & Garner, W. R. (1944). Effects of random presentation on the psychometric function: Implications for a quantal theory of discrimination. *The American Journal of Psychology*, 57, 451–467.
- Nelson, D. A., & Freyman, R. L. (1986). Psychometric functions for frequency discrimination from listeners with sensorineural hearing loss. *Journal of the Acoustical Society of America*, 79, 799–805.
- Noreen, D. (1981). Optimal decision rules for some common psychophysical paradigms. In S. Grossberg (Ed.), *Mathematical psychology and psychophysiology: Proceedings of the Symposium in Applied Mathematics of the American Mathematical Society and the Society for Industrial*

*and Applied Mathematics* (Vol. 13, pp. 237–279). Providence, RI: American Mathematical Society.

- Nelson, D. A., Stanton, M. E. & Freyman, R. L. (1983). A general equation describing frequency discrimination as a function of frequency and sensation level. *Journal of the Acoustic Society of America*, 73, 2117– 2123.
- Rieke, F., Warland, D., de Ruyter van Steveninck, R., & Bialek, W. (1997). *Spikes: Exploring the neural code*. Cambridge, MA: MIT Press.
- Rousseau, B., & Ennis, D. M. (2001). A Thurstonian model for the dual pair (4IAX) discrimination method. *Perception & Psychophysics*, 63, 1083–1090.
- Sek, A., & Moore, B. C. (1995). Frequency discrimination as a function of frequency, measured in several ways. *Journal of the Acoustical Society* of America, 97, 2479–2486.
- Semal, C., & Demany, L. (2006). Individual differences in the sensitivity to pitch direction. *Journal of the Acoustical Society of America*, 120, 3907–3915.
- Shadlen, M. N., & Newsome, W. T. (1998). The variable discharge of cortical neurons: Implications for connectivity, computation, and information coding. *Journal of Neuroscience*, 18, 3870–3896.
- Stevens, S. S. (1972, September 1). A neural quantum in sensory discrimination. Science, 177, 749–762.
- Stevens, S. S., Morgan, C. T., & Volkmann, J. (1941). Theory of the neural quantum in the discrimination of loudness and pitch. *The American Journal of Psychology*, 54, 315–335.
- Stevens, S. S., & Volkmann, J. (1940, December 20). The quantum of sensory discrimination. *Science*, 92, 583–585.
- Swets, J. A., Tanner, W. P., & Birdsall, T. G. (1961). Decision processes in perception. *Psychological Review*, 61, 301–340.
- Thomas, J. P. (1985). Detection and identification: How are they related? *Journal of the Optical Society of America A*, 2, 1457–1467.
- Thomas, J. P., Gille, J., & Barker, R. A. (1982). Simultaneous visual detection and identification: Theory and data. *Journal of the Optical Society of America A*, 72, 1642–1651.
- Treisman, M., & Williams, T. C. (1984). A theory of criterion setting with an application to sequential dependencies. *Psychological Review*, 91, 68–111.
- Turner, C. W., & Nelson, D. A. (1982). Frequency discrimination in regions of normal and impaired sensitivity. *Journal of Speech and Hearing Research*, 25, 34–41.
- Wickens, T. (2001). Elementary signal detection theory. Oxford, England: Oxford University Press.
- Zohary, E., Shadlen, M. N., & Newsome, W. T. (1994, July 14). Correlated neuronal discharge rate and its implications for psychophysical performance. *Nature*, 370, 140–143.

Received November 27, 2007 Revision received June 6, 2008

Accepted June 7, 2008 ■