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Increment detection of bandlimited noises in the chinchilla

William P. Shofner, William A. Yost and Stanley Sheft

Parmlly Hearing Institute, Loyola University Chicago, Chicago, Illinois, USA

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A positive reinforcement, adaptive tracking procedure was used to study the intensity discrimination abilities of six chinchillas to noise signals. Increment detection thresholds were obtained using a two-down, one-up tracking rule. The effect of overall noise masker level and the effect of noise bandwidth on increment detection thresholds were studied. The continuous noise masker and the signal increment had equal bandwidths. Increment detection thresholds are independent of overall level for wideband noise; the asymptotic DL for wideband noise is 1.334 dB. In addition, increment detection thresholds decrease as the bandwidth of the noise increases. The observed slope of the bandwidth function for the chinchilla is independent of overall level and is around -2.8 dB/decade. The slope of the bandwidth function obtained for the chinchilla is similar to values reported for human subjects under similar conditions, but is less than the slope predicted by the ideal energy detector model.

Intensity discrimination; Chinchilla; Noise; Bandwidth

Introduction

The detection of changes in the level of a sound is one of the fundamental abilities of the auditory system. Intensity discrimination by human subjects has long been studied under a variety of stimulus conditions, and more recently, psychophysical studies of intensity discrimination have been carried out in a wide variety of animal models (for review of data see Fay, 1988). While the chinchilla has become popular in recent years as an animal model for human hearing, there have been only two psychophysical studies investigating intensity discrimination in chinchillas.

Saunders et al. (1987) measured the difference limen (DL) in the chinchilla for tones and found that as the standard intensity increased up to 30 dB SL, there was a decrease in the DL, but that DLs remained constant at approximately 3.5–4.0 dB above 30 dB SL. Moreover, there was no effect of tone frequency on DL. Using a wideband noise, Salvi et al. (1982) found that the DL computed from the peak-to-trough ratio at amplitude modulation detection threshold was around 1.5 dB. While the DL has traditionally been calculated from amplitude modulation detection, discrepancies exist between thresholds obtained for increment detection and modulation detection (see Viemeister, 1979). Nevertheless, the data from Salvi et al. (1982) and Saunders et al. (1987) suggest that the chinchilla may

be more sensitive to intensity increments of broadband stimuli than for narrowband stimuli. However, comparisons of the DLs between these two studies must be made cautiously. The intensity discrimination data gathered by Saunders et al. for tones were obtained using gated conditions, while the data gathered for the amplitude modulation study by Salvi et al. were obtained with the noise carrier on continuously. In human subjects, thresholds are typically higher in gated conditions than in continuous conditions (for example, see Schacknow and Raab, 1976). An additional and perhaps more important consideration is that tones and noise have different statistical properties. In particular, tones are deterministic and periodic; there is no variability in the time domain waveform. On the other hand, broadband noise is random and does have variability in the waveform. Thus, a more systematic approach for comparing intensity discrimination performance of narrowband and broadband stimuli is to use bandlimited noises.

Many studies have addressed the effect of noise bandwidth on intensity discrimination in human subjects (Small et al., 1959; Green, 1960; Campbell, 1964; Bos and de Boer, 1966; Moore, 1975; Moore and Raab, 1975; Raab and Goldberg, 1975; Schacknow and Raab, 1976; Buus, 1990). These studies generally agree that intensity discrimination thresholds increase as the bandwidth of the noise decreases. As the bandwidth narrows, there is an increase in the temporal fluctuations of the instantaneous power in the noise waveform, and these fluctuations presumably interfere with a listener's ability to detect an increment in intensity.

Correspondence to: William P. Shofner, Parmlly Hearing Institute, Loyola University Chicago, 6525 N. Sheridan Avenue, Chicago IL 60626, USA. Fax: 312 508-2719.

Green (1960) derived an analytical model for intensity discrimination of noise for an ideal energy detector which measures the power in two noise samples and selects the waveform with the largest power. The ideal energy detector model is described as

$$d' = (WT)^{\frac{1}{2}} \frac{S}{N} \frac{1}{\left[1 + \frac{S}{N} + \frac{1}{2} \left(\frac{S}{N}\right)^2\right]^{\frac{1}{2}}} \quad (1)$$

where d' is the detectability, W is bandwidth, T is signal duration (or integration time), S is the signal power and N is the noise power. Note that S/N is equivalent to the Weber fraction $\Delta I/I$. This model is based on principles of signal detection theory and on the statistical properties of Gaussian noise. Thus, this model takes into account the increase in temporal fluctuations as the noise bandwidth narrows. One of the predictions of the ideal energy detector model is that for a given T and d' , intensity discrimination thresholds will decrease as the bandwidth of the noise increases. In terms of the effect of bandwidth on threshold, Equation 1 can be rearranged to give

$$10 \log \left(\frac{S}{N} \frac{1}{\left[1 + \left(\frac{S}{N}\right) + \frac{1}{2} \left(\frac{S}{N}\right)^2\right]^{\frac{1}{2}}} \right) \\ = 10 \log \frac{d'}{T^{\frac{1}{2}}} - 5 \log W \quad (2)$$

Equation 2 is now a linear equation where $10 \log(d'/T^{1/2})$ is the y-intercept and the slope is -5 . That is, as bandwidth increases, the threshold decreases at a rate of -5 dB/decade increase in bandwidth.

In this paper, we describe the intensity discrimination abilities of the chinchilla for noise signals based on the increment detection paradigm (i.e., with the standard continuously on). We first present data describing the effect of overall level on thresholds for wideband noise in order to compare to data obtained from modulation detection (Salvi et al., 1982). We then examine the effect of bandwidth on increment detection thresholds for noise in the chinchilla as described by the ideal energy detector model.

Methods

Subjects

Six (5 male and 1 female) binaural, adult chinchillas (*Chinchilla lanigera*) served as subjects. Three of these

chinchillas (chinchillas 3, 6 and 7) had served as subjects in a previous psychophysical study of frequency selectivity (Niemic et al., 1992). Animals were maintained at a body weight of around 400 g; daily body weights generally ranged between 85–95% of a 'normal' weight of 450 g. The diet for the animals consisted of Noyes chinchilla pellets (Formula N) which were given as food rewards during behavioral testing (see below); the amount of food received during testing was supplemented with Purina Chin Chow. In addition, animals received one raisin after each daily testing session, and once a week, animals were given a small piece of an alfalfa hay cube.

Apparatus

Noise stimuli were generated by a Wavetek VCG/noise generator (Model 132). The Wavetek noise generator was set such that the noise had a sequence length of $2^{20} - 1$ at a sampling rate of 160 kHz; these settings resulted in a noise with a bandwidth of 10 kHz which repeated itself once every 6.55 s. The output of the noise generator was divided into two channels; one channel was passed through a fixed attenuator (Leader LAT-45) and the second channel was passed through a programmable attenuator (Coulbourn S85-08 programmable attenuator). The second channel of noise was attenuated relative to the fixed attenuator using the programmable attenuator. The two channels of noise were then added in phase to generate an intensity increment. If both attenuators were set at -10 dB, then there was no difference in the attenuation between the two noises, and a level increment of 6 dB was produced. A one-shot timer and electronic switch (Coulbourn S84-04 Selectable Envelope Shaped Rise/Fall Gate) turned on the noise signal in the second channel for 1 s with a rise/fall time of 0 ms. The noise was bandpass filtered through a Krohn-Hite filter (Model 3550) so that the bandwidth of the signal increment and the noise masker were identical. The noise was then amplified by a Bryston power amplifier, and the overall level could be adjusted by another Leader LAT-45 attenuator. A loudspeaker (Realistic Minimus 3.5) faced towards the animal's head on the left side of the cage and was approximately 20 cm from the position of the animal's head. The transfer function of the acoustic system is shown in Fig. 1. Noise levels of the continuous standard were routinely calibrated for each animal before each test session by inserting an Ivie IE-1M condenser microphone in place of the animal's head and measuring the A-weighted sound pressure level with a sound level meter (Ivie Electronics IE-30A sound level meter). All SPL measurements expressed in this paper are dBA.

The effective passbands of the bandlimited noises are not equivalent to the passband settings (3 dB down points) of the filter, because the roll-off of the Krohn-

Hite filter is 24 dB/octave. The effective bandwidths of the noises used in this study were estimated by the following procedure. The calibration microphone was placed at the position of the animal's head, and the noise from the loudspeaker was adjusted to 72 dB SPL. The output of the microphone was sampled at a rate of 50 kHz by a MassComp 5400 computer system, and a 2048 point FFT of the sampled acoustic noise was then computed on-line. For each passband setting, a final spectrum was obtained by averaging a total of 1000 of these 2048 point FFTs. The linear amplitude coefficients were then normalized with respect to the maximum amplitude. Bandwidths were estimated by computing the equivalent rectangular bandwidths (ERBs) and the equivalent statistical bandwidths (ESBs) from the normalized spectra (see p. 278, Bendat and Piersol, 1971). The ERB is defined as

$$\text{ERB} = \int \frac{|H(f)|^2}{|H_m|^2} df \quad (3)$$

where $H(f)$ is the amplitude coefficient of frequency f from the spectrum and H_m is the maximum amplitude.

The ESB is defined as

$$\text{ESB} = \frac{\left[\int |H(f)|^2 df \right]^2}{\int |H(f)|^4 df} \quad (4)$$

which can be arranged to yield

$$\text{ESB} = \frac{(\text{ERB})^2}{\int \frac{|H(f)|^4}{|H_m|^4} df} \quad (5)$$

The ERB is the bandwidth of a perfectly rectangular filter that passes the same mean square value as the actual filter. The ESB is the bandwidth of a perfectly rectangular filter that passes the same mean square statistical error as the actual filter; that is, the bandwidth of a rectangular filter in which the output would have the same statistical properties as the actual filter if the input is Gaussian noise. Noise bandwidths used in this study are shown in Table I. Note that because

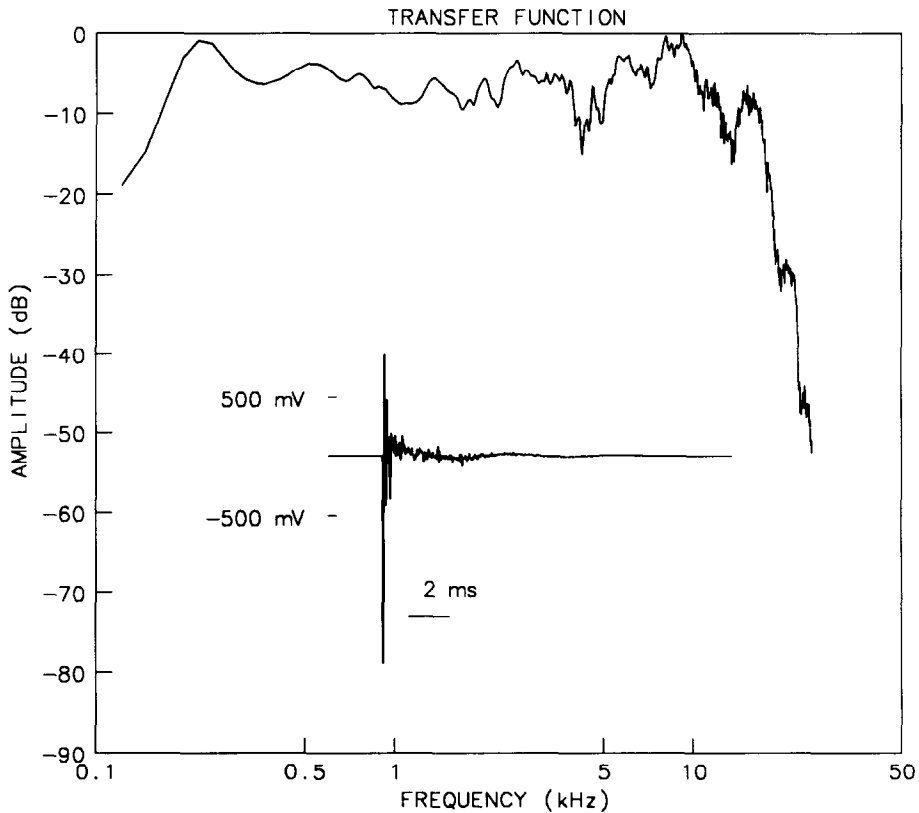


Fig. 1. Transfer function of the acoustic system. A 40 μ s click was presented through the loudspeaker and was measured with the calibration microphone. A total of 1000 clicks were averaged to generate the impulse response of the system (inset). A 2048 point FFT was carried out on the averaged impulse response to obtain the transfer function. The overall frequency response from 0.146–11.7 kHz is ± 7.6 dB. The frequency responses over specific regions are ± 7 dB from 0.146–1.46 kHz; ± 3 dB from 1.46–2.92 kHz; ± 6.2 dB from 2.92–5.86 kHz; ± 4.8 kHz from 5.86–11.7 kHz.

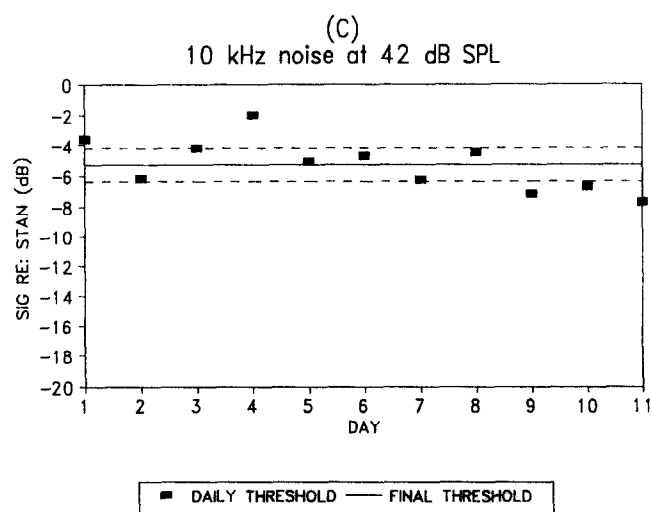
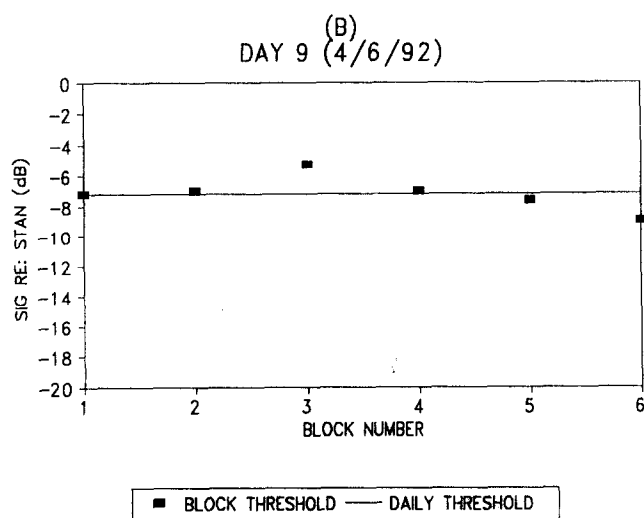
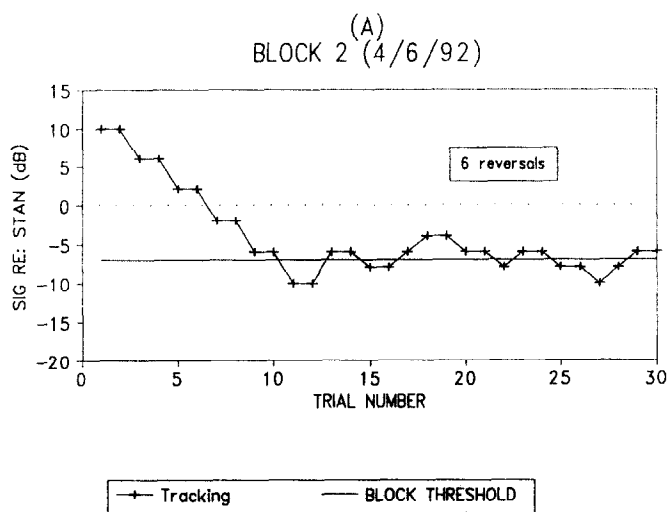


TABLE I

Noise bandwidths used in the study

Passband Settings (Hz)	ERB (Hz)	ESB (Hz)	Frequency at H_m
400- 600	272	431	562
200- 800	461	704	562
100- 1200	790	1299	757
900- 1100	684	946	1123
800- 1200	745	1030	1294
500- 1500	836	1398	1343
1100- 1900	809	1500	1367
100- 5000	2239	4202	2417
20-10000	4765	8461	3296

the roll-off of the filter is 24 dB/octave, the narrowest bandwidths that could be produced have the lowest center frequencies.

Behavioral procedure

The experimental procedure was under the control of an IBM compatible computer system and is similar to the behavioral procedure described by Clark et al. (1974). Animals were placed inside of a cage in a single-walled sound attenuating chamber (Industrial Acoustics, Inc.). Animals were not restrained in any manner, but were free to roam around inside of the test cage (16" $l \times 12$ " $h \times 10$ " w). At one end of the cage was a pellet dispenser with a reward chute attached to a response lever. Chinchillas were trained in an increment detection paradigm; that is, the animal's task was to detect the presence of a 1 s signal (intensity increment) against a continuous standard. During the initial phase of training, chinchillas pressed the response lever to receive a food pellet reward (Noyes Precision Pellets; 20 mg/pellet). After the animals learned consistently to press the lever to receive food, the animals were trained to hold the lever down for 1 s, after which the signal came on. If the animal released the lever during the signal, it was rewarded with a food pellet. During this phase of training, hold times were gradually increased up to 8 s.

Fig. 2. (A). Example of the tracking for a representative block (Block #2 on 4/6/92) of 30 trials for chinchilla #8. This block contained a total of 8 reversals; the first two reversals are discarded, and the block threshold is computed for the remaining 6 reversals. The solid line indicates the threshold for this block. (B). Scatter plot showing the block thresholds obtained for chinchilla #8 on day 9 (4/6/92). The solid line shows the threshold computed for day 9. (C). Scatter plot showing the daily thresholds obtained for chinchilla #8 for the wideband noise at 42 dB SPL. The solid line shows the final mean threshold computed across 11 days. The dashed lines indicate the 95% confidence interval.

After this initial training, animals were tested in a positive reinforcement, adaptive tracking procedure. In this procedure, the standard noise was present continuously, and the chinchilla pressed the response lever to initiate a trial. There was a hold time which varied from trial to trial. The hold time varied from 1–8 s for chinchillas 3, 6, 7, and 8, but varied from 1–6 s for chinchillas 9 and 10. The hold time was determined using a rectangular probability function. If the animal released the lever before the minimum hold time was up, the trial was aborted and the trial began again with the next lever press. If the animal held the lever down for the duration of the hold time, the signal (i.e. the intensity increment of 1 s duration) was presented through the loudspeaker. The response interval coincided with the duration of the intensity increment. The animal reported that it detected the intensity increment if the animal released the response lever during the 1 s interval. The animal reported that it did not detect the intensity increment by continuing to hold the response lever down through the 1 s interval. For a signal trial, if the animal reported detecting the signal by releasing the response lever, the response was classified as a hit. For a blank trial, if the animal reported the absence of a signal by continuing to hold the lever down, the response was classified as a correct rejection. Chinchillas received food pellet rewards for correct responses, that is for both hits and correct rejections. If the animal released the lever during a blank trial, it was an incorrect response and classified as a false alarm. If the animal continued to hold the lever down during a signal trial, it was classified as a miss. False alarms and misses were not rewarded with food pellets, and there was no time-out following incorrect responses. Animals were initially trained in the tracking procedure using 100% probability of a signal during a trial, and then again trained at 90% signal probability. Data obtained at the 90% and 100% probabilities were not used to compute thresholds. During the actual testing procedure, the probability of a signal was 75% with the probability of a blank or 'catch' trial being 25%.

Thresholds were obtained using a two-down, one-up tracking rule (Levitt, 1971) on the programmable attenuator value. In the experiment, the attenuator value was increased after two consecutive correct responses and was decreased following one incorrect response. This rule tracks on the threshold corresponding to 70.7% correct (Levitt, 1971). Animals ran in blocks of 30 fixed trials. The attenuator initially changed in 4 dB steps until two attenuation reversals occurred. After these first two reversals, the attenuation was then changed in 2 dB steps. The first two reversals were ignored, and the threshold for a given block was computed from the remaining reversals of the attenuator (Fig. 2a). This threshold is the attenuator value corre-

sponding to the intensity increment in terms of the signal re: standard ratio in dB for in phase addition. A minimum of 4 reversals was required to accept the threshold for a given block, although typically more than 4 reversals occurred. Animals were tested for approximately 1 hour per day and generally completed 6–8 blocks for the day. If a block contained fewer than 4 reversals, that block was not included in the computation of the daily threshold. A minimum of 4 usable blocks was required to compute a daily threshold which was the average threshold across the usable blocks (Fig. 2b). In addition, false alarm rates were computed across all blocks (usable and unusable) for each day. If the animal responded with a false alarm rate greater than 20% for the day, the data for the whole day were eliminated and not used to compute a final threshold. When false alarm rates were greater than 20%, it was interpreted that the behavior of the animal was not under proper stimulus control during the session. False alarm rates were generally easily maintained below 20% by adjusting the ratio of the number of food pellets rewarded for hits and correct rejections for each animal. Typical ratios of the number of pellets given for hits:correct rejections were 2:1 for chinchillas 3, 7, and 8; 1:2 for chinchillas 6, 9, and 10. Thresholds were typically determined over a period of 10–15 days to insure stable estimates. The final threshold for a given stimulus condition was an average of all daily threshold values (Fig. 2c). A statistical test was carried out to determine if the highest daily threshold value was an outlier (see p. 460, Davies and Goldsmith, 1984). If a daily threshold value was determined to be an outlier, it was eliminated from the data set. Out of 1116 daily threshold values across the 6 chinchillas, 13 (1.16%) were determined to be outliers.

Data analysis

There is no standard terminology for expressing thresholds in the intensity discrimination literature (see Grantham and Yost, 1982; Green, 1988), and the lack of a standard measure generally makes direct comparisons across studies difficult. Because intensity discrimination was estimated using an increment detection paradigm, we will refer to thresholds as increment detection thresholds for the remainder of the paper. The raw increment detection thresholds were obtained in terms of the signal re: standard ratio expressed in dB attenuation. The reader is referred to Appendix Tables AI and AII for thresholds and standard deviations for individual animals in terms of the signal re: standard ratio in dB for in phase addition. Other measures of intensity discrimination can be computed from these values (see Grantham and Yost, 1982; Green, 1988). The value $\Delta I/I$ is the Weber fraction and is computed in the present study, because it is equal to S/N in the ideal energy detector model (see

Equation 1). The DL is the difference in level at threshold between the signal and masker and is presented in this paper, because it was the measure reported in previous chinchilla studies (Salvi et al., 1982; Saunders et al., 1987). DLs are reported to 3 decimal places as suggested by Green (1988). Average values of DL or $\Delta I/I$ (i.e. S/N) presented in this paper for a given stimulus condition were not generated by computing an average across individual DL or $\Delta I/I$ values, but were generated by first computing an average signal re: standard threshold and then converting that average signal re: standard value into a DL or $\Delta I/I$ value.

In order to evaluate the data in terms of the ideal energy detector model, increment detection thresholds are expressed according to Equation 2 as $10 \log(S/N \cdot 1/P)$ where

$$\frac{1}{P} = \frac{1}{\left[1 + \frac{S}{N} + \frac{1}{2} \left(\frac{S}{N}\right)^2\right]^{\frac{1}{2}}} \quad (6)$$

is used for convenience. Previous studies using human subjects (i.e., Green, 1960; Raab and Goldberg, 1975; Schacknow and Raab, 1976) have generally assumed $S/N \ll 1$ and thus, approximated Equation 2 by expressing thresholds as $10 \log(S/N)$ rather than $10 \log(S/N \cdot 1/P)$. This approximation holds for signal re: standard ratios less than about -20 dB, but above -20 dB there is an increase in the difference between $10 \log(S/N)$ and $10 \log(S/N \cdot 1/P)$. The increment detection thresholds in this paper are expressed as $10 \log(S/N \cdot 1/P)$, because the signal re: standard ratios obtained from the chinchillas for many of the bandwidth conditions studied are higher than -20 dB (see Tables AI and AII).

Results and Discussion

Increment detection of wideband noise

The DLs computed from the signal re: standard ratios are shown in Fig. 3a for individual chinchillas and in Fig. 3b for the average chinchilla as a function of the overall level of the continuous noise masker with the widest bandwidth studied (ERB = 4765 Hz; see Table I). The range of levels tested was limited to 42–82 dB SPL. The lowest level at 42 dB SPL approaches the noise floor of the sound attenuating chamber which was 39 dB SPL (ERB = 534 Hz; ESF = 2881 Hz; frequency at $H_m = 195$ Hz). Table II shows the thresholds for detection of the wideband noise in quiet, i.e., against the noise floor background. Levels above 82 dB SPL were not presented in order to avoid causing any temporary threshold shifts and possible

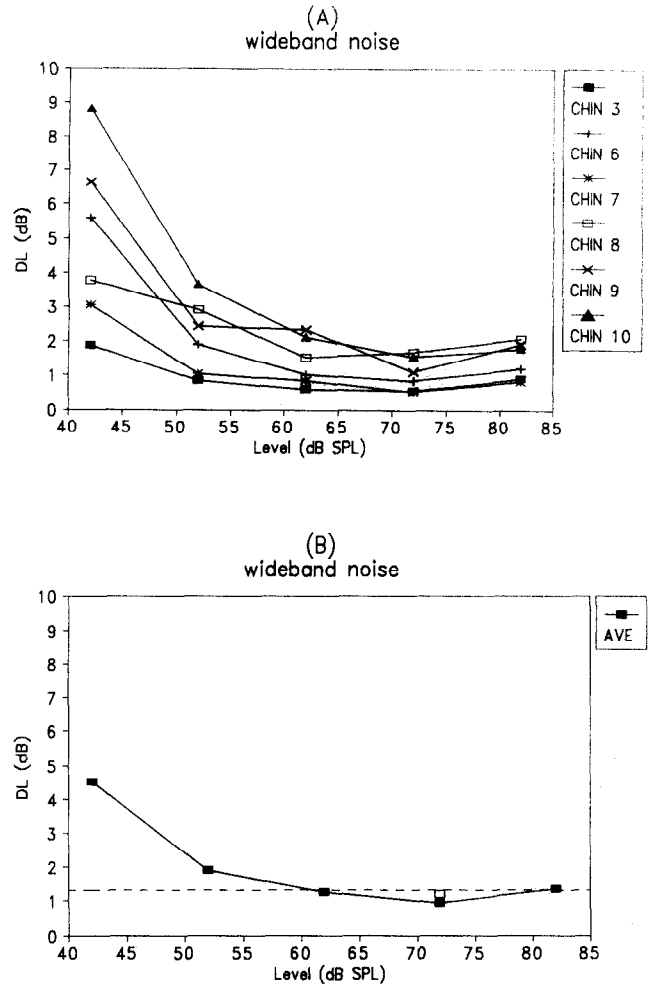


Fig. 3. (A). Difference limens (DLs) as a function of overall level of the continuous masker for the wideband noise for individual animals. (B). DLs as a function of level for the average chinchilla (filled squares). The dashed line indicates the asymptotic DL of 1.334 dB. The open square at 72 dB SPL is the average DL obtained 8 months after the original DL at 72 dB SPL.

cochlear damage to the animals (see Carder and Miller, 1972; Henderson et al., 1984). In the averaged data, there is a decrease in threshold from 4.520 dB at 42 dB SPL to a relatively constant value between 52–82 dB SPL. The average values of DL range from 0.949 dB at 72 dB SPL to 1.907 dB at 52 dB SPL, and the average

TABLE II

Detection thresholds for the 20–10 kHz wideband noise condition in a quiet background

Chinchilla	N (days)	Threshold (dB SPL) + SD
3	11	29.3 ± 0.99
6	11	41.7 ± 2.77
7	10	26.6 ± 2.87
8	11	44.5 ± 4.09
9	10	41.6 ± 1.79
10	10	42.0 ± 1.31

DL over the range of 52–82 dB SPL is 1.334 dB (Fig. 3b). An analysis of variance (ANOVA) was carried out on the averaged thresholds for the levels between 52–82 dB SPL. The ANOVA confirmed that the average increment detection thresholds are not significantly different at standard levels of 52, 62, 72 and 82 dB SPL ($F = 1.887$; $F < F_{0.05(1),3,20}$). Thus, Weber's Law appears to be followed over the range of levels from 52–82 dB SPL for the largest noise bandwidth studied.

Thresholds for the wideband noise at 72 dB SPL were repeated over a 5 day period 8 months after the original thresholds for this condition were obtained (open square in Fig. 3b). The averages of the original threshold and the threshold obtained 8 months later are not significantly different ($t = 1.279$; $t < t_{0.05(2),10}$). Thus, there appears to be no significant changes in increment detection ability over this period of time.

The asymptotic DL of 1.334 dB for the average chinchilla for the broadband noise computed from the continuous masker, increment detection paradigm is similar to the DL of 1.3–1.5 dB computed from the detection of sinusoidal amplitude modulation of continuous broadband noise (Salvi et al., 1982). The bandwidth of the noise at the input to the loudspeaker was similar between the present study and that of Salvi et al., and the duration of the signal interval was also similar between the present study (1 s) and that of Salvi et al. (2 s). Over a similar range of overall levels, the DLs from the amplitude modulation paradigm also remain constant (Salvi et al., 1982). The DLs of the present study and those found by Salvi et al. for continuous, broadband noise are lower than the DLs of chinchillas for pulsed tones, which are around 3.5–4.0 dB (Saunders et al., 1987). It is unclear if the difference between the intensity discrimination abilities of chinchillas for broadband noise and tones are due to procedural differences (continuous vs. pulsed) or are due to differences in auditory processing of noise and tones.

Miller (1947) studied intensity discrimination in humans using a continuous noise masker with a 1.5 s signal interval and obtained DLs around 0.5 dB. While the average DL for noise increment detection for chinchillas is 1.334 dB, the DLs obtained for some individual animals are as low as values generally reported for human subjects (0.531 dB for chinchilla #7 and 0.543 for chinchilla #3 at 72 dB SPL). Noise increment detection has been studied in relatively few other animal models. The data from these studies show that DLs are highest for the goldfish (2.1 dB; Fay, 1985) followed by the chinchilla (1.334 dB; present study) and the rhesus monkey (~ 1.3 dB; Clopton, 1972).

Increment detection of bandlimited noise

Tables AI and AII indicate that increment detection thresholds expressed as the signal re: standard ratios

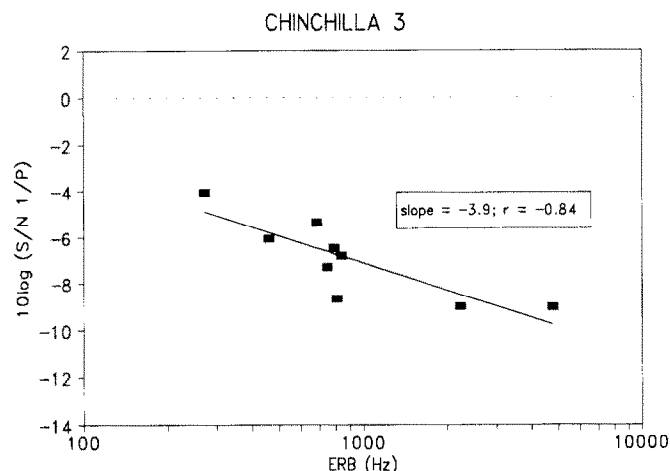


Fig. 4. Scatter plot showing increment detection thresholds (solid squares) as a function of bandwidth for chinchilla #3. Thresholds are expressed as $10 \log(S/N 1/P)$ as described by the ideal energy detector model (see Equation 2) and bandwidth is expressed as ERB. The solid line is the linear regression through the data points: $y = 4.6 - 3.9 \log(\text{ERB})$; $r = -0.84$.

for the chinchillas decrease as the bandwidth of the noise increases. Fig. 4 shows increment detection thresholds expressed as $10 \log(S/N 1/P)$ as a function of ERB for a representative chinchilla for a continuous masker noise having a total noise power of 72 dB SPL. Thus, the noise power density or spectrum level is not constant (see Bos and de Boer, 1966; Buus, 1990), but varies with bandwidth over a 13 dB range. Note that the bandwidth function is expressed in the form of Equation 2, which is a linear equation. The solid line in Fig. 4 is the linear regression through the data points. For all 6 of the chinchillas tested, there is a decrease in threshold as bandwidth increases. The slopes of the individual regression lines are all less than the predicted slope from Equation 2 of -5 dB/decade increase in bandwidth (Table III). Individual slopes range from -2.6 to -4.4 dB/decade increase in bandwidth, and the mean of this sample of slopes is significantly less negative than the predicted slope of -5 ($t = 6.124$; $t > t_{0.001(1),5}$).

Fig. 5 shows the increment detection thresholds for the average chinchilla. Each point is the increment detection threshold expressed as $10 \log(S/N 1/P)$

TABLE III

Linear regression analysis for individual chinchillas

Chinchilla	Linear regression	correlation coefficient (r)
3	$y = 4.6 - 3.9 \log(\text{ERB})$	-0.84
6	$y = 4.1 - 3.3 \log(\text{ERB})$	-0.81
7	$y = 6.5 - 4.4 \log(\text{ERB})$	-0.91
8	$y = 7.4 - 3.4 \log(\text{ERB})$	-0.83
9	$y = 7.5 - 3.8 \log(\text{ERB})$	-0.93
10	$y = 3.7 - 2.6 \log(\text{ERB})$	-0.66

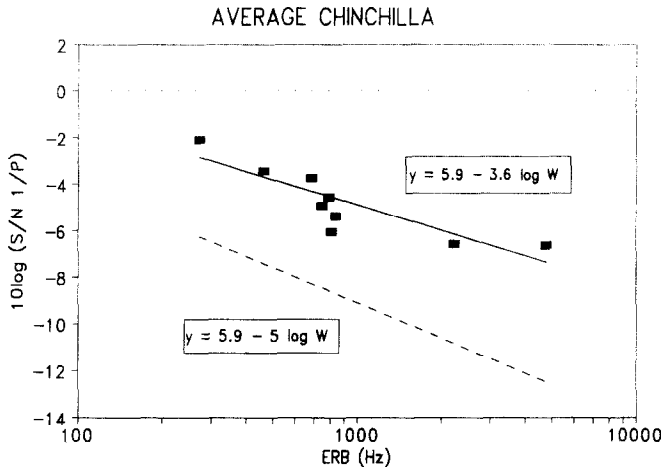


Fig. 5. Scatter plot showing increment detection thresholds (solid squares) as a function of bandwidth for the average chinchilla. Bandwidth is expressed as ERB. The solid line is the linear regression through the data points: $y = 5.9 - 3.6 \log(\text{ERB})$; $r = -0.87$. The dashed line shows the predicted thresholds from the ideal energy detector model.

across animals computed from the average signal re: standard ratio for each condition. The solid line is the linear regression through these data and has a slope of -3.6 dB/decade increase in bandwidth. The Y-intercept of this regression line is 5.9 and is equal to $10 \log(d'/T^{1/2})$ in Equation 2. The dashed line in Fig. 5 is the prediction of the ideal energy detector model (see Equation 2) having a slope of -5 and a Y-intercept of 5.9; that is, the dashed line shows the predicted thresholds for the same d' and T that the average chinchilla uses. The empirical thresholds for the average chinchilla fall above those predicted by the ideal energy detector model. Fig. 6 shows the empirical thresholds for the average chinchilla and the predicted thresholds of the model as a function of ESB. The slope of the linear regression line through the average data is -2.6 dB/decade increase in bandwidth, and this function again lies well above the predicted thresholds.

In order to investigate whether the slope of the bandwidth function is dependent on overall level, increment detection thresholds for the narrowband noise (ERB = 272 Hz) were obtained at 52–82 dB SPL. Fig. 7 compares increment detection thresholds expressed as $10 \log(S/N 1/P)$ for both this narrowband noise and the wideband noise for the average chinchilla as a function of level. Increment detection thresholds for the narrowband noise are consistently higher than thresholds for the wideband noise for the average chinchilla; this relation is also observed for each of the individual animals (see Table AI). The difference in thresholds between the wideband and narrowband conditions reflects the slope of the bandwidth function at each of the levels. Relative to the wideband noise

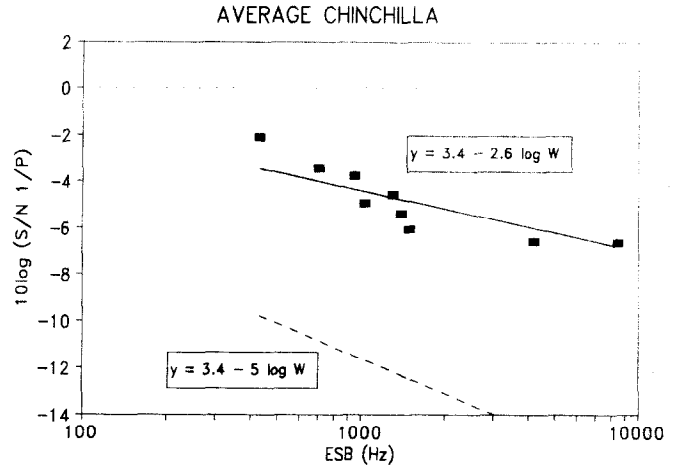


Fig. 6. Scatter plot showing increment detection thresholds (solid squares) as a function of bandwidth for the average chinchilla. Bandwidth is expressed as ESB. The solid line is the linear regression through the data points: $y = 3.4 - 2.6 \log(\text{ESB})$; $r = -0.77$. The dashed line shows the predicted thresholds from the ideal energy detector model.

thresholds, the observed thresholds for the narrowband noise are below those expected if the slope of the bandwidth function is -5 dB/decade (Fig. 7). The fact that the empirical thresholds for narrowband noise are below the expected thresholds indicates that the slope of the bandwidth function is shallower than -5 dB/decade. The slopes of the bandwidth functions corresponding to the difference between empirical thresholds for the narrowband and wideband noises are -2.5 at 52 dB SPL, -2.8 at 62 dB SPL, -3.6 at 72

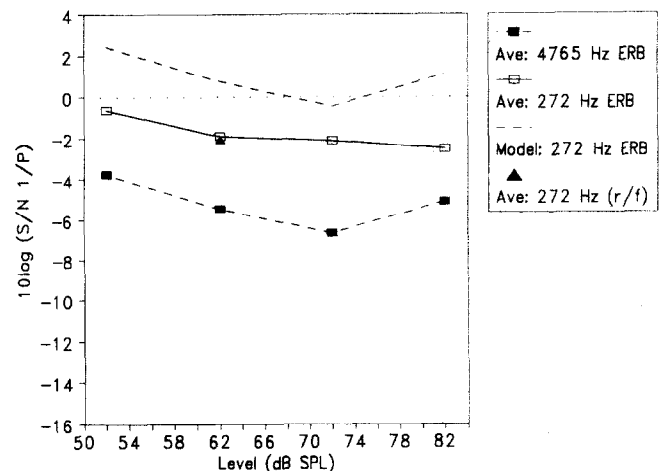


Fig. 7. Increment detection thresholds for the average chinchilla as a function of overall level of the continuous masker for a wideband noise (filled squares and dashed line) and a narrowband noise (open squares and solid line). The ERBs are 4765 Hz for the wideband noise and 272 Hz for the narrowband noise. The filled triangle at 62 dB SPL shows the increment detection threshold for the average chinchilla in which the signal interval is gated with a rise/fall time of 100 ms. The dashed line without symbols shows the predicted thresholds for the narrowband noise relative to those for wideband noise if the slope of the bandwidth function were -5 dB/decade.

dB SPL, and -2.1 at 82 dB SPL. The average slope across levels is -2.8 dB/decade.

The signal interval in the intensity increment paradigm was gated using a rise time of 0 ms (see Methods). The energy distribution for the signal with a 0 -ms rise time may differ from that of a signal with a long rise time, particularly for narrowband signals. This 'spectral splatter' could potentially be used as a cue for 'off-frequency listening' (see Leshowitz and Wightman, 1971), thus improving performance. The effect of rise time was investigated at 62 dB SPL for the narrowest noise bandwidth (ERB = 272 Hz) by adding a rise/fall time of 100 ms to the signal interval. Fig. 7 shows that the average increment detection threshold obtained for the signal interval with a 100 -ms rise time is similar to that obtained with a 0 -ms rise time. The average signal re: standard ratios at 62 dB SPL are -7.4 dB for the signal having a 0 ms rise time and -7.9 dB for the signal having a 100 -ms rise time; these values are not significantly different ($t = 0.198$; $t < t_{0.05(2),10}$) suggesting that 'off-frequency' listening is not having a large effect.

The present results for chinchillas demonstrate that for conditions of a continuous masker and where the masker and signal have the same bandwidth, there is a decrease in increment detection threshold as bandwidth increases. Green (1960) derived a model for intensity discrimination in which an ideal energy detector measures the power in two noise samples and selects the waveform with the largest power. The ideal energy detector model predicts a 5 dB decrease in threshold for a 10 -fold increase in bandwidth (see Equation 2). The measured slopes for each chinchilla in the present study are shallower than those predicted by the model; that is, the values of individual slopes are consistently less negative than the predicted value of -5 from the ideal energy detector model. The slope of the bandwidth function appears to be independent of overall level, as predicted by the ideal energy detector model. The slopes of the bandwidth functions obtained for the chinchillas are similar to those generally reported for human subjects under similar conditions (see Schacknow and Raab, 1976 for review). Schacknow and Raab (1976) found that the slopes of the bandwidth functions were less than the -5 dB/decade prediction if the signal and masker noises both have the same bandwidth, but that steeper bandwidth functions were obtained when the signal bandwidth was less than the masker noise bandwidth. There was no difference in the slopes of the bandwidth functions obtained under continuous and gated conditions for human subjects (Schacknow and Raab, 1976).

One prediction of the ideal energy detector model is that intensity discrimination thresholds for a given bandwidth are independent of the center frequency of the bandlimited noise (Green, 1960). Green (1960) did

show that in human subjects, the threshold for intensity discrimination does not vary with the center frequency of the noise signal. We were unable to test this prediction in the present study, because noise signals were generated by a bandpass filter having relatively shallow skirts (24 dB/octave). Consequently, the narrowest noise bandwidths that could be generated had the lower center frequencies (i.e. frequency at H_m ; see Methods); narrow bandwidths at higher center frequencies could not be generated with the equipment available. However, this limitation should have little consequence on the interpretation of the present results. Green (1960) states that the ideal energy detector model does not apply if the signal bandwidth is less than a critical band. The bandwidths of the noises used in the present study are all greater than the bandwidths of the corresponding auditory filters having center frequencies equal to the frequency at H_m (see Niemiec et al., 1992). Thus, all of the signals used in the present study meet the assumptions of the ideal energy detector model. It should also be noted, that intensity discrimination thresholds for gated tones in chinchillas are independent of frequency (Saunders et al., 1987). If intensity discrimination is independent of tonal frequency, it seems likely that intensity discrimination is also independent of the center frequency of a narrowband noise.

General Discussion

The difference between the empirical thresholds for the chinchilla and the predicted thresholds of the energy detector model can be accounted for by the addition of internal noise. Note from Figs. 5 and 6, that as the bandwidth increases, the *difference* between empirical and predicted thresholds also increases. If this difference represents the amount of internal noise, then it would appear that the internal noise increases as the bandwidth increases. The linear regression equation for the average chinchilla thresholds is

$$10 \log \left(\frac{S}{N} \frac{1}{P} \right) = 10 \log \left(\frac{d'}{T_i} \right) - 3.6 \log W \quad (7)$$

where -3.6 is the slope for the average chinchilla data (Fig. 5). The slope of -3.6 represents the slope of the ideal energy detector of -5 added to an internal noise term. Thus, Equation 7 can be rewritten as

$$10 \log \left(\frac{S}{N} \frac{1}{P} \right) = 10 \log \left(\frac{d'}{T_i} \right) - 5 \log W + K \log W \quad (8)$$

where $K \log W$ is the internal noise. For example, K is 1.4 for the average chinchilla bandwidth functions

based on ERB (Fig. 5). Solving Equation 8 for d' gives

$$d' = (WT)^{\frac{1}{2}} \frac{1}{W^{\frac{K}{10}}} \frac{S}{N} \frac{1}{\left[1 + \frac{S}{N} + \frac{1}{2} \left(\frac{S}{N}\right)^2\right]^{\frac{1}{2}}} \quad (9)$$

Note that Equation 9 is similar to the ideal energy detector model, but with the additional term $1/W^{K/10}$. Green (1960) added an attenuation factor to account for the difference between empirical and theoretical psychometric functions. The term $1/W^{K/10}$ is similar to the attenuation factor that Green originally included, but is a compressive power function of bandwidth rather than a constant. Equation 9 is largely a mathematical expression that can be used to predict the threshold (for a given W , T , and d') or detectability (for a given W , T , and S/N) for chinchillas as well as for human subjects with the appropriate value of K . However, the nature of the internal noise is not clear from Equation 9.

Frozen or pseudorandom noise has been used in human studies of noise intensity discrimination in an attempt to describe the internal noise (Raab and Goldberg, 1975; Buus, 1990). Because the same waveform is repeated, pseudorandom noise does not possess variability in the stimulus domain; that is, pseudorandom noise is deterministic much like a tone. Theoretically, the only source of variability that exists for intensity discrimination of pseudorandom noise is the internal noise. The intensity discrimination thresholds obtained using pseudorandom bandlimited noise should, therefore, reflect whether or not internal noise varies as a function of bandwidth. Raab and Goldberg (1975) found that with frozen noise, the intensity discrimination thresholds do not vary with bandwidth. In contrast, Buus (1990) found that bandwidth effects on intensity discrimination thresholds obtained with pseudorandom bandlimited noise are level dependent. At high levels (90 dB SPL), thresholds do not vary as a function of bandwidth, while at low and moderate levels (30 and 60 dB SPL), thresholds decrease as bandwidth increases (Buus, 1990). Raab and Goldberg (1975) show that additive internal noise similar to that described by de Boer (1966) results in a bandwidth function having a slope less than the predicted -5 dB/decade. This additive internal noise is independent of bandwidth. Establishing the performance of intensity discrimination of pseudorandom noise in the chinchilla would be an important comparison with respect to previous studies using human subjects. However, while pseudorandom bandlimited noise may be useful in describing how internal noise may vary as a function of bandwidth, the models of intensity discrimination that incorporate internal noise are ambiguous as to what is the physiological correlate of internal noise

(see de Boer, 1966; Raab and Goldberg, 1975). Schacknow and Raab (1976) show that prewhitening of the noise alters the ESB which results in a bandwidth function having a slope less than -5 dB/decade. These authors attribute at least part of the prewhitening (or internal noise) to neural compression.

At least part of the internal noise must result from the stochastic nature of discharge of auditory neurons. Several physiological studies have examined the effect of bandwidth on the responses of auditory neurons (Greenwood and Maruyama, 1965; Goldberg and Greenwood, 1966; Greenwood and Goldberg, 1970; Ruggero, 1973; Young and Brownell, 1976; Schalk and Sachs, 1980). These studies have generally shown that for a constant spectrum level, there is an increase in discharge rate as bandwidth increases, followed by a subsequent decrease in discharge rate as bandwidth continues to widen. However, only one study has been concerned with the stochastic properties of neuronal discharge. Goldberg and Greenwood (1966) studied the responses of single units in the dorsal and posteroventral cochlear nuclei in the cat to narrowband noise. Although the physiological response types of units were not described, these authors found that the coefficient of variation of neural discharge for some units decreases as noise bandwidth increases, while other units show little change in discharge variability with bandwidth (see Fig. 9 of Goldberg and Greenwood, 1966, for example). One important advantage in establishing intensity discrimination performance for bandlimited noise in chinchillas is that physiological experiments can be carried out using stimulus conditions similar to those that have been used psychophysically. Future neurophysiological experiments in the chinchilla auditory system should provide important insights into the underlying neural correlates of intensity discrimination of bandlimited noise.

Appendix

Increment detection thresholds expressed as signal re: standard ratios for in phase addition are presented in Appendix Tables AI and AII for individual animals. These signal re: standard ratios are the final mean thresholds computed over a period of N days. The standard deviations are generally small (78/96 (81%) of the standard deviations in Tables AI and AII are less than 2 dB) and argue that the thresholds values obtained by the specific behavioral procedures used in the present study generate reliable estimates of threshold.

The most important underlying assumption made when applying adaptive tracking procedures is that the psychometric function is monotonic with stimulus level (see Levitt, 1971). In order to verify this assumption for

ERB = 272 Hz at 62 dB SPL

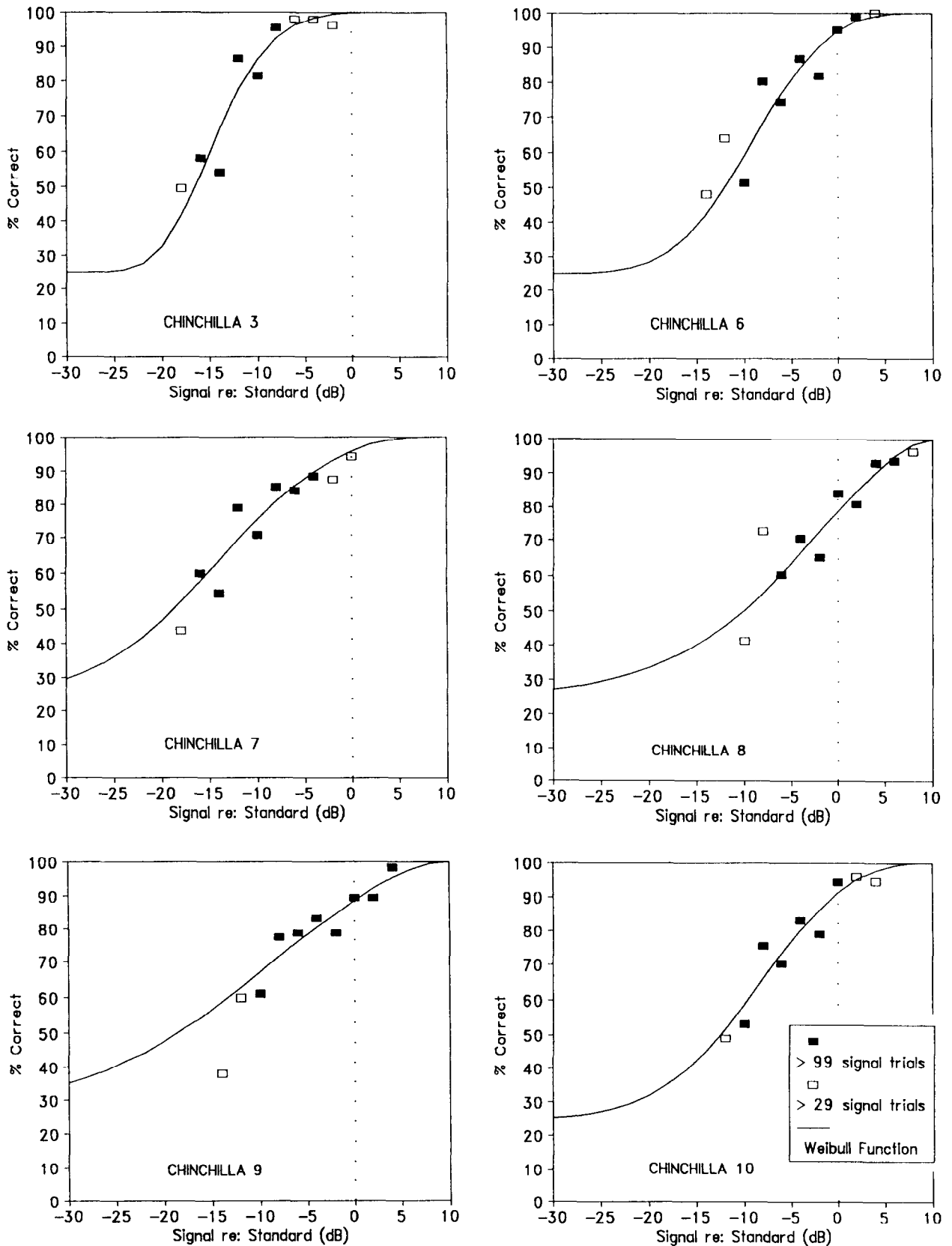


Fig. A1. Psychometric functions reconstructed from the tracking data for the increment detection of narrowband noise (ERB = 272 Hz) at 62 dB SPL. Filled squares are data points from stimulus levels having a total of at least 100 signal trials; open squares are data points from levels having at least 30 signal trials, but less than 100 signal trials. The solid line is the best fitting Weibull function to the data points having at least 100 signal trials (filled squares).

Appendix TABLE AI

Thresholds for increment detection as a function of overall level of the continuous masker noise for a wideband noise (WBN; ERB = 4765 Hz) and a narrowband noise (NBN; ERB = 272 Hz)

Chinchilla	Level (dB SPL)	N (days)		Signal re: Standard Ratio (dB) + sd	
		WBN	NBN	WBN	NBN
3	42	11	-	-12.3 ± 2.20	-
	52	12	7	-19.8 ± 1.77	-10.7 ± 1.85
	62	11	10	-23.2 ± 1.15	-12.9 ± 1.20
	72	14	9	-23.8 ± 0.61	-13.0 ± 1.40
	82	11	10	-19.2 ± 1.87	-10.3 ± 2.97
6	42	11	-	-0.9 ± 1.67	-
	52	12	8	-12.2 ± 1.62	-1.7 ± 1.55
	62	10	10	-18.0 ± 0.94	-6.7 ± 1.14
	72	13	9	-19.7 ± 1.61	-9.7 ± 1.25
	82	11	12	-16.5 ± 1.17	-11.4 ± 0.66
7	42	10	-	-7.5 ± 2.37	-
	52	12	8	-17.8 ± 2.52	-5.8 ± 1.29
	62	11	10	-19.7 ± 2.35	-10.6 ± 2.27
	72	12	9	-24.0 ± 1.27	-12.6 ± 1.60
	82	10	10	-20.1 ± 1.21	-14.1 ± 1.52
8	42	11	-	-5.3 ± 1.63	-
	52	13	8	-8.0 ± 1.89	+1.1 ± 2.80
	62	11	10	-14.3 ± 1.55	-2.0 ± 1.35
	72	15	9	-13.4 ± 2.15	-0.7 ± 1.50
	82	11	11	-11.3 ± 1.25	-1.6 ± 2.29
9	42	11	-	+1.2 ± 3.08	-
	52	10	8	-9.8 ± 1.83	-1.8 ± 0.60
	62	11	9	-10.2 ± 1.27	-5.9 ± 1.99
	72	13	6	-17.4 ± 1.48	-6.9 ± 1.18
	82	11	11	-12.1 ± 3.47	-7.4 ± 1.52
10	42	10	-	+4.9 ± 1.36	-
	52	12	7	-5.6 ± 1.59	-0.4 ± 0.64
	62	8	10	-11.2 ± 0.80	-6.0 ± 1.18
	72	12	9	-14.2 ± 1.52	-5.0 ± 1.02
	82	11	11	-12.9 ± 0.96	-9.7 ± 1.13

the specific behavioral procedures used in the present study, psychometric functions were reconstructed from tracking data in the following manner. The number of signal trials, the number of blank trials, the number of hits, and the number of correct rejections for each stimulus level were first tallied across every block (including blocks that were not used for computing tracking thresholds). Percent correct then equals the sum of the number of hits and correct rejections divided by the sum of the number of signal trials and blank trials, multiplied by 100. It is clear from data like that illustrated in Fig. 2a that most trials will be around threshold, with fewer trials at levels well above threshold, and essentially no trials well below threshold. Thus, a psychometric function obtained from the tracking data will not reflect the entire psychometric function, nor will

Appendix TABLE AII

Thresholds for increment detection as a function of bandwidth for a continuous masker noise of identical bandwidth at 72 dB SPL

Chinchilla	N (days)	ERB (Hz)	Signal re: Standard Ratio (dB) + sd	
3	9	272	-13.0 ± 1.40	
	9	461	-17.5 ± 0.75	
	10	684	-16.0 ± 1.10	
	9	745	-20.1 ± 0.99	
	13	790	-18.4 ± 1.44	
	10	809	-23.0 ± 1.20	
	10	836	-19.1 ± 1.51	
	10	2239	-23.7 ± 1.35	
	14	4765	-23.8 ± 0.61	
	6	9	272	-9.7 ± 1.25
		10	461	-12.7 ± 0.93
		10	684	-14.2 ± 2.31
		10	745	-17.2 ± 1.02
		13	790	-17.4 ± 0.94
10		809	-18.3 ± 1.68	
10		836	-18.7 ± 1.03	
10		2239	-19.0 ± 0.95	
13		4765	-19.7 ± 1.61	
7		9	272	-12.6 ± 1.60
		8	461	-14.9 ± 0.69
		10	684	-15.5 ± 2.02
		9	745	-17.2 ± 1.82
	12	790	-18.1 ± 1.62	
	11	809	-21.6 ± 1.48	
	8	836	-19.4 ± 1.29	
	10	2239	-23.0 ± 1.12	
	12	4765	-24.0 ± 1.27	
	8	9	272	-0.7 ± 1.50
		10	461	-7.8 ± 1.60
		9	684	-7.6 ± 2.38
8		745	-9.6 ± 0.88	
13		790	-6.9 ± 2.26	
11		809	-12.0 ± 0.92	
10		836	-12.1 ± 0.94	
10		2239	-15.0 ± 1.82	
15		4765	-13.4 ± 2.15	
9		6	272	-6.9 ± 1.18
		10	461	-7.1 ± 1.46
		10	684	-9.4 ± 2.16
		10	745	-11.8 ± 2.70
		10	790	-12.5 ± 1.90
		9	809	-14.0 ± 2.26
	8	836	-12.2 ± 1.33	
	10	2239	-16.1 ± 1.13	
	13	4765	-17.4 ± 1.48	
	10	9	272	-5.0 ± 1.02
		9	461	-8.9 ± 0.41
		8	684	-10.7 ± 1.58
		8	745	-14.3 ± 0.68
11		790	-11.9 ± 0.61	
10		809	-16.3 ± 1.18	
9		836	-14.8 ± 0.92	
10		2239	-15.0 ± 0.85	
12		4765	-14.2 ± 1.52	

there be equal number of trials at each level. Nevertheless, the reconstructed psychometric function should reflect whether the percent correct increases monotonically with stimulus level.

Fig. A1 shows the psychometric functions for each individual chinchilla for increment detection of narrowband noise (ERB = 272 Hz) at 62 dB SPL. The data points shown in Fig. A1 were fitted with a Weibull function (see Macmillan and Creelman, 1991; Green and Luce, 1975). The Weibull functions in Fig. A1 have the form of

$$P(C) = 100 \left[g + (1 - g) \exp(- (I_s/I_t)^\beta) \right] \quad (A1)$$

where $P(C)$ is the percent correct, I_s is the signal re: standard ratio, I_t is a threshold parameter, g is the lower asymptote, and β is the slope. For the data points having at least a total of 100 signal trials (filled squares in Fig. A1), a Weibull function was obtained through an iterative algorithm which found values of β and I_t that gave the minimum sum squared deviation between the data points and the Weibull function. The value of g was fixed at 0.25, because the a priori signal probability is 75%. Consequently, at signal levels well below threshold where the animal cannot detect the signal (i.e. hit rate is 0/75), it would be expected that the animal continue to press on the response lever, thus having a 100% correct rejection rate (i.e. 25/25). Hence, the expected percent correct at levels well below threshold would be 25%. It can be observed in Fig. A1 that percent correct increases with the signal re: standard ratio. These monotonic psychometric functions satisfy the underlying assumption required for tracking procedures and argue that the specific behavioral procedures used in the present study are valid.

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