

Frequency discrimination in the chinchilla

David A. Nelson and Thomas E. Kiester

University of Minnesota, Hearing Research Laboratory, 2630 University Avenue S.E., Minneapolis, Minnesota 55414

(Received 1 August 1977; revised 15 February 1978)

Chinchillas were trained with shock-avoidance procedures to discriminate or detect pure-tone frequency differences. Initial attempts at determining frequency-difference thresholds utilized a complex discrimination paradigm and a go-no-go response. Although discriminations of large frequency differences were obtained from chinchillas after considerable training, discriminations of small frequency differences could not be trained. Therefore, determinations of frequency-difference thresholds could not be made with the complex discrimination paradigm and the go-no-go response task. A simple detection paradigm, involving the detection of frequency alternation in an ongoing train of tone bursts proved to be a more successful technique. Frequency-alternation detection was quickly learned by six chinchillas, and frequency-difference thresholds were obtained with an adaptive sequential procedure. Psychometric functions were reconstructed from the threshold tracking data of chinchillas, and comparisons were made with differential frequency thresholds from cats and humans obtained by previous investigators. Differential frequency thresholds from chinchillas paralleled those from cats and were about twice as large. Differential frequency thresholds from humans were considerably smaller than from chinchillas, especially for low-frequency tones. When a constant detectability index was used to specify differential frequency sensitivity in chinchillas, chinchilla and human differential sensitivity functions paralleled one another. Human differential sensitivity was about ten times better than that of the chinchilla.

PACS numbers: 43.66.Fe, 43.66.Gf, 43.80.Lb

INTRODUCTION

Since the time when Miller (1964) first welcomed the chinchilla to investigations of the auditory sensory system, knowledge of the chinchilla's auditory capabilities has grown substantially. As an experimental "listener," highly devoted to animal psychophysics, the chinchilla has repeatedly demonstrated his cooperativeness by "sitting" for critical-ratio experiments (Miller, 1964), critical-bandwidth experiments (Seaton and Trahiotis, 1975), and temporal-summation experiments (Henderson, 1969). He has learned to recognize and discriminate among novel sounds of modern civilization (Luz, 1969). He has given us insight into the frequency-resolving capabilities of his auditory system by "jumping" reliably throughout tedious determinations of psychophysical "tuning curves" (McGee, Ryan, and Dallos, 1976). He has even taken on the challenge of decoding the sounds of human speech (Burdick and Miller, 1975; Kuhl, 1976), to hint to us that human speech is "not that special." As a friend to man, the chinchilla has begun to compete strongly with the cat in nearly all areas of auditory sensory investigation except one—frequency discrimination. The present report describes our attempts, both successful and unsuccessful, to enlist the chinchilla's participation in studies of frequency discrimination.

I. RECOGNITION OF FREQUENCY DIFFERENCES

A. Single dyads, go-no-go response

Our original goal was to develop psychophysical procedures that would allow efficient acquisition of frequency-discrimination behavior from the chinchilla. We wanted a procedure that could be used to obtain difference limens for frequency and could also be used to obtain discriminatory behavior for acoustic stimuli more complex than simple pure tones. Since other in-

vestigators were demonstrating success with psychophysical paradigms that utilized conditioned negative reinforcement to train chinchillas to make discriminations among complex sounds, such as bells, whistles, and even human speech (Luz, 1969; Luz and Burdick, 1972; Luz and Nugen, 1972; Miller and Luz, 1970; Burdick and Miller, 1975; Kuhl, 1976), we reasoned that the chinchilla should have little difficulty discriminating a pair of tones that had the same frequency from a pair of tones that had different frequencies.

We began our experiments with the paradigm shown in Fig. 1. It is similar to that used by Cornwell (1967) to study frequency discrimination in cats. Our paradigm involved frequency-difference recognition of two pure tones: one tone (*A*) was 1000 Hz and the other (*B*) was 2200 Hz, a frequency difference of 1200 Hz. Whenever a pair of tones was presented that differed in frequency by 1200 Hz (*AB* or *BA* dyads), the animals' task was to learn to jump over a center barrier from one side of the test cage to the other to avoid an electric shock. In addition, the animals had to learn to inhibit that avoidance response whenever a pair of tones was presented that were identical in frequency (*AA* or *BB* dyads). This type of dual response, avoidance and avoidance inhibition, is commonly referred to as a go-no-go response (Trahiotis and Elliott, 1970). Each of the sessions consisted of 40 trials. The *a priori* probability of occurrence of *AB* or *BA* trials was 0.70. During any single session only discriminations between *AB* and *AA* (or *BA* and *BB*) were tested. Habituation trials, consisting only of *AA* (or *BB*) trials, were employed with some of the animals to minimize response acquisition time. All chinchillas were binaural animals.

Figure 2 presents the performance data of one of the six chinchillas trained with the single dyad paradigm for the first ten sessions. The graph shows hit rates (solid

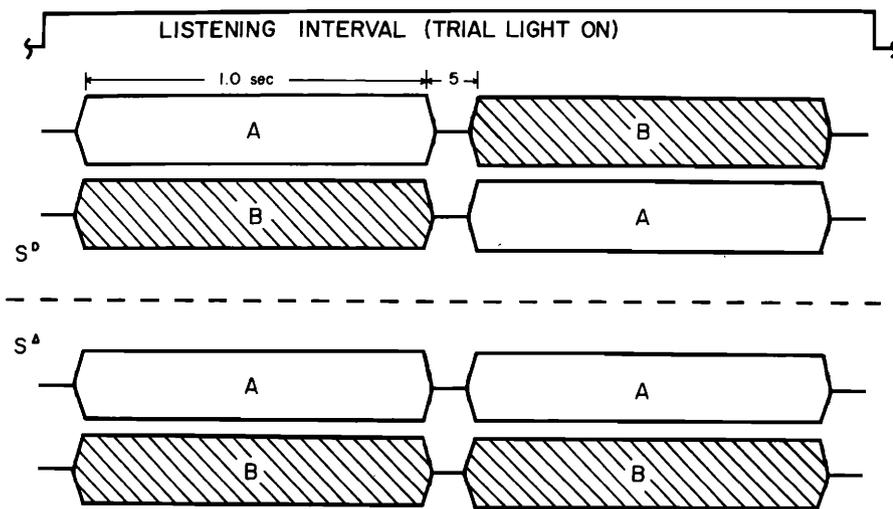


FIG. 1. "Single-dyad" stimulus paradigm used to train chinchillas to discriminate frequency differences. An animal's task was to make an avoidance response during an S^D trial (AB or BA) and to inhibit an avoidance response during an S^A trial (AA or BB). Initially, tone bursts labeled A were 1000 Hz and tone bursts labeled B were 2200 Hz, a 1200-Hz frequency difference.

circles) and false-alarm rates (open circles) obtained during consecutive training sessions. This chinchilla's performance is typical of the performance obtained from the other five animals; he could not learn the task. In fact, none of the six chinchillas demonstrated good discriminative performance (hit rates greater than 0.70 and false-alarm rates less than 0.30) within the ten sessions (see Table I) that we considered to be a reasonable number of training sessions for our purposes. Admittedly our criteria were strict, but we did not wish to require more than ten training sessions just to develop the discriminative response. Our goal was to shape discriminative behavior to its limit, at the difference limen for frequency, and to accomplish this at many different frequency regions.

B. Multiple dyads, go-no-go response

We then reasoned that the chinchilla may require more "looks" at the dyadic stimuli than we were giving them in the single dyad paradigm. Therefore, we initiated a multiple dyad paradigm similar to that used by Thompson (1960) to study frequency discrimination in cats. The duration of our tones was decreased from 1.0 to 0.25 s, silent intervals between tones were reduced from 0.5 to 0.15 s, and five dyads were presented during each trial instead of just one dyad per trial. Nineteen chinchillas were trained on multiple dyad frequency-difference recognition tasks, utilizing frequency differences from 1200 to 200 Hz.

Again we were mistaken. None of the chinchillas trained with the multiple dyad paradigm could learn the discrimination task in the ten sessions required to meet our criteria of training efficiency.

Table I summarizes our attempts to train chinchillas to perform adequately in frequency-difference recognition tasks. We approached success in obtaining performance that met our criteria for good discrimination in several animals, but only after training had proceeded for more than 30 sessions. Part of the reason for the difficulty our chinchillas displayed in quickly learning the frequency-difference recognition task may have been response incompatibility. Development of the avoidance

response that was appropriate for the S^D stimuli may have been incompatible with acquisition of response inhibition that was appropriate for the S^A stimuli.

To elaborate, consider the following argument. During the recognition tasks, a trial light was illuminated to define a "listening" interval for the chinchilla. Pairing the trial light with the eventual threat of shock results in the trial light acquiring some secondary negative reinforcing properties, which we assume would tend to elicit an avoidance response by itself, or at least contribute to the probability of occurrence of an avoidance response elicited by the S^D stimulus that follows the trial light. The S^D trial includes two stimuli. Both stimuli elicit physiologic responses that lead to avoidance behavior. In that sense, we consider the response to the trial light and the response to the S^D stimulus to be compatible responses. The S^A trial, on the other hand, includes two stimuli which lead to responses that are incompatible with one another. The trial light, we assume, elicits physiologic responses consistent with an avoidance response. Then the S^A stimulus that fol-

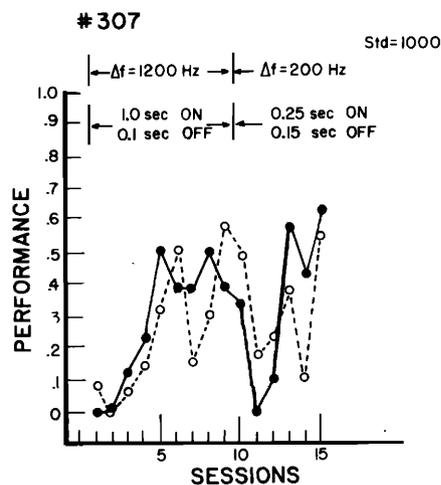


FIG. 2. Performance history on frequency-difference recognition tasks for chinchilla No. 307. Hit rates are shown by filled circles and false-alarm rates are shown by open circles.

TABLE I. Performance of chinchillas on frequency-difference recognition tasks that involved go-no-go responses. S^D is a positive or discriminative stimulus that required a response, S^A is a negative stimulus that required response inhibition, A is a lower-frequency tone, and B is a higher-frequency tone.

	Number of animals	Frequency difference (Hz)	Average number sessions	Average hit rate	Average false-alarm rate
Single dyads	4	1200	10.2	0.21	0.16
$S^A = AA$ or BB , $S^D = AB$ or BA	2	100	7.0	0.54	0.57
Multiple dyads	10	1200	30.4	0.62	0.31
$S^A = AAAAAAAAAA$ or $BBBBBBBBBB$	3	300	25.7	0.65	0.24
$S^D = ABABABAB$ or $BABABABA$	4	200	7.0	0.41	0.27
	2	200	34.6	0.64	0.33

lows the trial light requires the inhibition of those physiologic responses, because the correct response following the S^A stimulus is the lack of an avoidance response. The arousal of physiologic responses leading to avoidance behavior, followed immediately by the requirement of inhibition of those responses, is a situation in which we consider the responses to be incompatible with efficient acquisition of discrimination learning.

In addition, the fact that other chinchillas have been trained to make avoidance responses to complex stimuli—and ours demonstrated difficulty learning to discriminate among two simple pure tones widely separated in frequency—may be partially explained by the concept of acoustic redundancy. Complex sounds, like speech sounds, differ from one another on several acoustic dimensions at the same time; they are acoustically redundant. Simple pure tones usually differ from one another only on one dimension, frequency. It may be an easier task for chinchillas to learn to discriminate between two sounds when differences exist in more than one dimension of sound at the same time.

II. DETECTION OF FREQUENCY ALTERNATION

A. Methods and procedures

1. Single response training procedures

To accomplish our goals, we finally resorted to the familiar detection paradigm used by Butler, Diamond, and Neff (1957), Goldberg and Neff (1961), and Thompson (1960) to study frequency discrimination in cortically ablated cats. The procedures are similar to those employed by Miller (1970) and by Nelson *et al.* (1976) to measure sensitivity thresholds in the chinchilla, except that the acoustic background between trials is not “quiet,” but rather filled with tone bursts, all at the same frequency.

A graphic representation of the stimulus time line of the “filled background” frequency-difference detection paradigm is shown in Fig. 3. At the beginning of a test session, tone bursts with frequency A are repeatedly presented to a chinchilla. Tone bursts are on for 250 ms, off for 150 ms, and are gated on and off with 25-ms

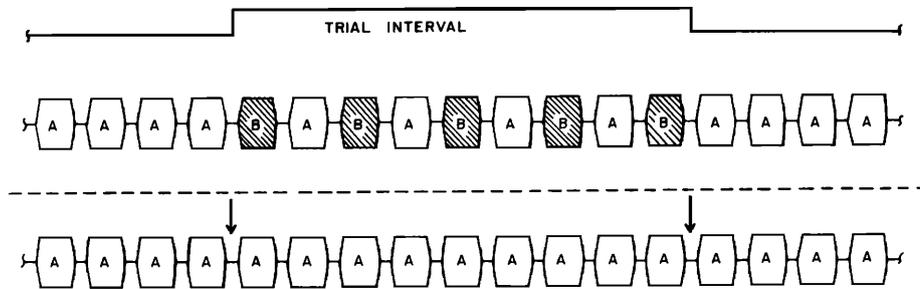


FIG. 3. “Filled-background” stimulus paradigm used to obtain frequency-difference detection thresholds from chinchillas. The solid line at the top of the figure defines the duration of a trial for the purposes of this graph only. Tone bursts, labeled A , continue repeatedly throughout a test session. A “signal trial” consists of the interjection of tone bursts with frequency B amongst the ongoing tone bursts of frequency A . A “catch trial” is delineated here by the vertical arrows. No indication is given an animal of the occurrence of a catch trial. A catch trial is essentially a probabilistic sample of an animal’s spontaneous jumping behavior taken during a period of time equal to a signal trial.

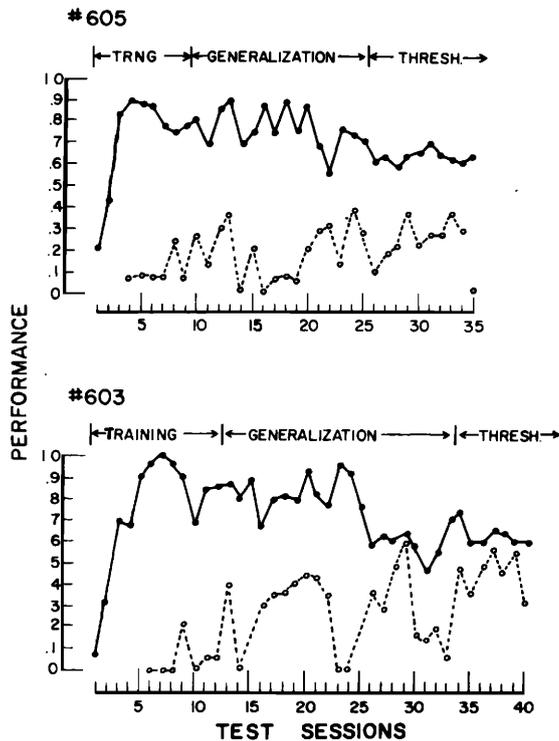


FIG. 4. Performance data obtained from two chinchillas (Nos. 605 and 603) for three portions of training: initial frequency-difference training, generalization training to small frequency differences at frequency regions of 500, 1000, 2000 and 4000 Hz, and threshold training for differential frequency thresholds. Hit rates are indicated by solid circles and false-alarm rates by open circles.

rise and decay times. At irregular intervals (10–30 s), determined randomly from trial to trial, a signal trial is introduced that consists of five tone bursts with frequency *B* in place of every other *A* tone burst. A trial begins at the onset of the first *B* tone burst and ends at the offset of the fifth *B* tone burst. No indication is given the chinchilla that a trial has begun; the only trial cue for the chinchilla is the occurrence of acoustic differences between alternating tone bursts. In this case the acoustic difference is the frequency of every other tone burst. An animal is required to jump over a barrier, from one side of the test cage to the other, to avoid the sounding of a buzzer and the presentation of electric shocks at the end of a signal trial. When an animal makes an avoidance response during the duration of a signal trial, that event is scored as a correct avoidance response (hit). When an animal fails to make an avoidance response during a signal trial, that event is scored as an incorrect response (miss).

Since no visual cues are used to define an observation interval for the chinchilla, definition of a chinchilla's "response criterion" is not as straightforward as with discrete-trial signal detection experiments. The problem is similar to that involved in vigilance experiments (Egan, Greenberg, and Schulman, 1961; Watson and Nichols, 1976). In order to specify whether a specific avoidance response is indeed related to the occurrence of frequency differences between alternating tone bursts

or is just a sample of the chinchilla's operant level of spontaneous jumping, catch trials are introduced during intertrial intervals to estimate the probability of an incorrect response. A catch trial consists of a time sample of a chinchilla's spontaneous jumping behavior. No change in the frequency of alternating tone bursts is made during a catch trial. A random 3-s extension of the intertrial interval results. The duration of catch trials, indicated by arrows in Fig. 3, is identical to the duration of signal trials. When an animal makes a response during a catch trial, that event is scored as an incorrect response (false alarm). When an animal does not make a response during a catch trial, that event is scored as a correct response (correct rejection). During threshold training and threshold testing, 30% of the trials included catch trials.

During the first five sessions of training, performance exceeded our criteria; hit rates were greater than 0.70, and false-alarm rates less than 0.30. The performance data of the two chinchillas shown in Fig. 4 are representative. Criterion hit rates were reached in only three sessions. When catch trials were introduced, about the fourth or fifth session, performance more than satisfied the false-alarm-rate criterion.

Frequency differences between tones *A* and *B* were varied during training, starting at the very first training session. Tone *A* was 1000 Hz and tone *B* varied in frequency during training from 2024 Hz at the beginning of each training session to about 1016 Hz at the end of a session, depending upon an animal's performance throughout each training session. Every time a hit response was made, the frequency difference for the succeeding signal trial was reduced. Every time a miss response was made, the frequency difference for the succeeding signal trial was increased. Training sessions continued until 40 trials, either signal trials or catch trials, had been presented.

The changes in frequency difference between tones *A* and *B*, introduced from one trial to the next, were somewhat unusual for frequency discrimination experiments. Instead of a constant interval change in frequency difference each time a hit or a miss was made, we employed a constant ratio change in frequency difference. Our reasons were both practical and theoretical. To maintain performance in our chinchillas we found it necessary to begin each session with a large frequency difference. Then, with each successive correct response, an animal's behavior was gradually generalized to progressively smaller frequency differences. If we had used constant interval changes in frequency difference, the length of the training sessions would have been impractical. From a theoretical point of view, the appropriate changes in frequency that correspond to equally perceptible changes in pitch magnitude are closer to equal-ratio changes than to equal-interval changes. The ratio scale we chose was logarithmic to the base two (2^x). For example, at the beginning of a training session Δf might be set to $2^{10} = 1024$ Hz. After a correct response, the next Δf would be set to $2^9 = 512$ Hz. Following each hit or miss, a constant was subtracted or added from the previous exponent.

TABLE II. Number of sessions required to train and test frequency-detection in chinchillas. Each session required from 30 to 40 min to complete. During tone training (TNTN) and discrimination training (DSTN), 40 trials were presented in a single session. During threshold training (THTN) and threshold testing (THTS), the number of trials presented an animal depended upon that animal's performance during each session.

Session	Animal number					Mean
	515	603	605	612	613	
TNTN: 1024-16 Hz Δf	7	4	3	6	5	5.0
DSTN: 1024-16 Hz Δf	9	6	7	6	6	6.8
THTN: 0.25-8 kHz	75	34	38	41	34	44.4
THTS: 0.25-8 kHz	39	38	35	19	27	31.6
Total sessions	130	82	83	72	72	87.8

Table II summarizes the training history for the six chinchillas involved in this detection experiment. The initial training sessions included tone training (TNTN) sessions during which no catch trials were presented, and discrimination training (DSTN) sessions during which the chinchillas learned to respond correctly for frequency differences as small as 16 Hz. Discriminations learned for tones at 1000 Hz were then generalized to other frequency regions during threshold training (THTN). Finally, after an average of 56 training sessions, threshold testing (THTS) was accomplished. Timing parameters, stimulus response chains, and conditional probabilities for parameters employed in different stages of training were similar to those used to obtain sensitivity thresholds and are described elsewhere in considerable detail (Nelson *et al.*, 1976).

2. Threshold estimation procedures

Thresholds for detection of frequency difference (Δf) between alternating tone bursts were obtained with a modified version of the classic staircase method (Cornsweet, 1962). Graphic representations of the results of the threshold tracking procedure are shown in Fig. 5. When an animal scored a hit, Δf for the next trial was decreased by a constant ratio. When an animal scored a miss, Δf for the next trial was increased by a constant ratio. No changes in Δf were made when an animal scored either a false alarm or a correct rejection. Threshold testing at a particular frequency continued until an animal scored two hits at one Δf and two misses at the next smaller Δf . Threshold was defined halfway between those two Δf 's.

Decrements and increments in Δf between tones *A* and *B* were specified as constant integer changes in the logarithm to the base two. Frequency differences were essentially treated as exponents during the entire experiment—during threshold tracking, during threshold calculation of the raw tracking data, and during calculation of average frequency-difference thresholds. Transformations from exponents to Δf in Hertz were not made until the end of the experiments. Therefore, all averages of frequency-difference thresholds are geometric averages and not arithmetic averages.

3. Apparatus

A PDP-8 minicomputer and associated peripheral-interface electronics controlled the timing of the experiment by means of an electronic switch, monitored the animals' avoidance responses with the aid of photo cells inside the test cage, controlled the frequency of tones *A* and *B* generated by a programmable oscillator, and displayed the performance of each animal on a graphic recorder and on a teletype terminal. Tone bursts were delivered through a speaker mounted in a sound-treated booth. Further details of the apparatus and sound-field calibrations are reported elsewhere (Nelson *et al.*, 1976).

4. Signal-intensity cues

Tones of different frequency were presented to the chinchillas in a sound field. The resulting sound pressures within the test cage varied from about 50 to 75 dB SPL, depending upon frequency. On the average, the tones were about 66-73 dB above normal chinchilla threshold for the frequency range between 500 and 4000 Hz, about 54 dB above threshold around 250 Hz, and about 62 dB above threshold around 8000 Hz.

In frequency-discrimination experiments, the only significant cue for performing the discrimination between the standard tone *A* and the comparison tone *B* should be the frequency difference between tones. Intensity cues or spectral density cues must either be eliminated or rendered irrelevant. Otherwise, it could be argued that the obtained frequency-difference thresholds were the result of detecting intensity differences (Henning, 1966)

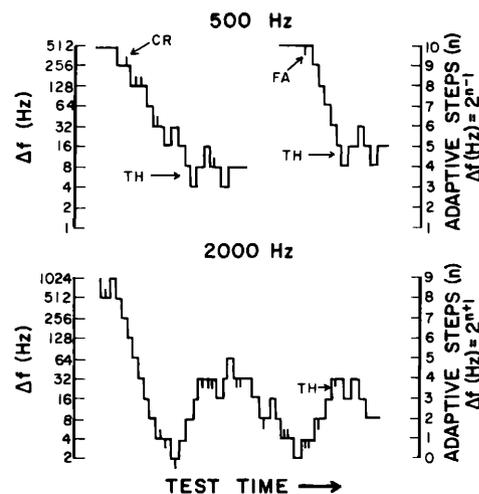


FIG. 5. Sample graphic recordings of frequency-difference-threshold tracking by a chinchilla for test frequencies of 500 and 2000 Hz. Frequency differences between alternating tone bursts are shown on the left-hand ordinate in units of Δf (in Hz) on a linear scale. On the right-hand ordinate the adaptive step numbers for a ratio scale is shown (see text). A downward change in the time line indicates a "hit," an upward change indicates a "miss," a momentary upward deflection indicates a "correct rejection," and a momentary downward deflection indicates a "false-alarm" response. Frequency-difference thresholds, determined with the criteria described in the text, are indicated with the letters TH and by a horizontal arrow.

TABLE III. Average frequency-difference thresholds for each chinchilla, expressed as the logarithm to the base two of frequency ($df = 2^n$). Numbers in parentheses indicate the number of threshold determinations upon which each average is based.

Chinchilla number	Test frequency (f)					
	250	500	1000	2000	4000	8000
CHN515	3.22 (18)	3.32 (17)	3.55 (20)	4.60 (21)	5.82(22)	8.50 (09)
CHN603	2.82 (28)	3.70 (20)	3.91 (22)	5.22 (25)	6.22 (25)	7.11 (28)
CHN605	3.42 (25)	3.92 (26)	3.88 (21)	5.37 (23)	6.69 (21)	8.70 (15)
CHN612	3.93 (07)	5.13 (08)	5.00 (08)	6.28 (09)	6.50 (09)	8.38 (16)
CHN613	4.21 (07)	3.63 (15)	4.13 (24)	4.92 (12)	5.50 (12)	8.50 (07)
Mean (2^n)	3.52	3.94	4.09	5.28	6.15	8.24
Std Dev (2^n)	0.56	0.70	0.55	0.63	0.49	0.64
Median (Hz)	10.7	13.0	15.0	37.3	74.5	362.0
Mean (Hz)	11.5	15.4	17.1	38.8	70.8	302.0
Mean df/f	0.0459	0.0307	0.0171	0.0194	0.0177	0.0377

or spectral density differences between tones *A* and *B*. To eliminate spectral density cues, we produced both tones *A* and *B* with the same programmable oscillator (Krohn-Hite 4141R). Its harmonic distortion was less than 0.02% (-74 dB) at all test frequencies employed in the experiment.

To render any consistent intensity differences between tones irrelevant to the discrimination task, randomization of signal intensity from trial to trial was considered. We reasoned, however, that such trial by trial variations in intensity were unnecessary in this particular sound environment and with this particular threshold tracking task. The sound field existing in the test booth was calibrated at 90 different positions within the test cage, 45 positions along two horizontal planes. The standard deviations of sound pressure among those 90 positions ranged from 1.5 to 4.5 dB at different frequencies. Since an animal is not restricted to any particular portion of the sound field, and since he varies his position within the sound field from trial to trial and sometimes from tone burst to tone burst, we considered the confusion of sound-field intensity and animal position to be sufficient to prevent an animal from reliably detecting intensity-difference cues.

Furthermore, during threshold tracking procedures, an animal was never allowed to listen to the same Δf on two consecutive trials. Frequency difference was varied after each trial, dependent upon a hit or miss response. Variations in sound-field intensity and in animal position, along with constantly changing Δf from trial to trial, present a significantly more difficult intensity-discrimination task to chinchillas than that which exists for highly trained human listeners presented with a constant-stimulus psychophysical paradigm and listening under earphones.

B. Results and discussion

1. Differential thresholds

Average frequency-difference thresholds obtained from six chinchillas are listed in Table III for octave test frequencies 250, 500, 1000, 2000, 4000, and 8000 Hz. Notice that an average threshold for an individual chinchilla is expressed as the logarithm to the base two of frequency difference between tones, since those were the units employed during threshold tracking. Group means and standard deviations were calculated on the logarithms and are shown in Table III along with the more conventional parameters which express Δf in Hertz.

Variability among repeated threshold estimates for individual chinchillas cannot be meaningfully expressed as Δf in Hertz, because the step size during threshold tracking was logarithmic. However, in terms of step size, the standard deviations were reasonable. None of the chinchillas obtained a standard deviation larger than 2.0, and on the average, the standard deviation among repeated threshold estimates was 1.4. Average standard deviations among chinchillas for different test frequencies varied from 1.3 to 1.5. Variability in the averaged thresholds among animals was also reasonable. In terms of step size, the standard deviation at any of the six test frequencies did not exceed 0.70 (Table III). Mean and median frequency-difference thresholds for the group are included in Table III. They correspond closely at all test frequencies.

Comparisons of Δf thresholds from the chinchilla with Δf thresholds from two other species, cat and human, are shown in Fig. 6. Test frequency is represented on the abscissa using a scale that depicts equal units of the square root of frequency (Wier, Jesteadt, and Green, 1977) as equal spatial distances on the graph. This

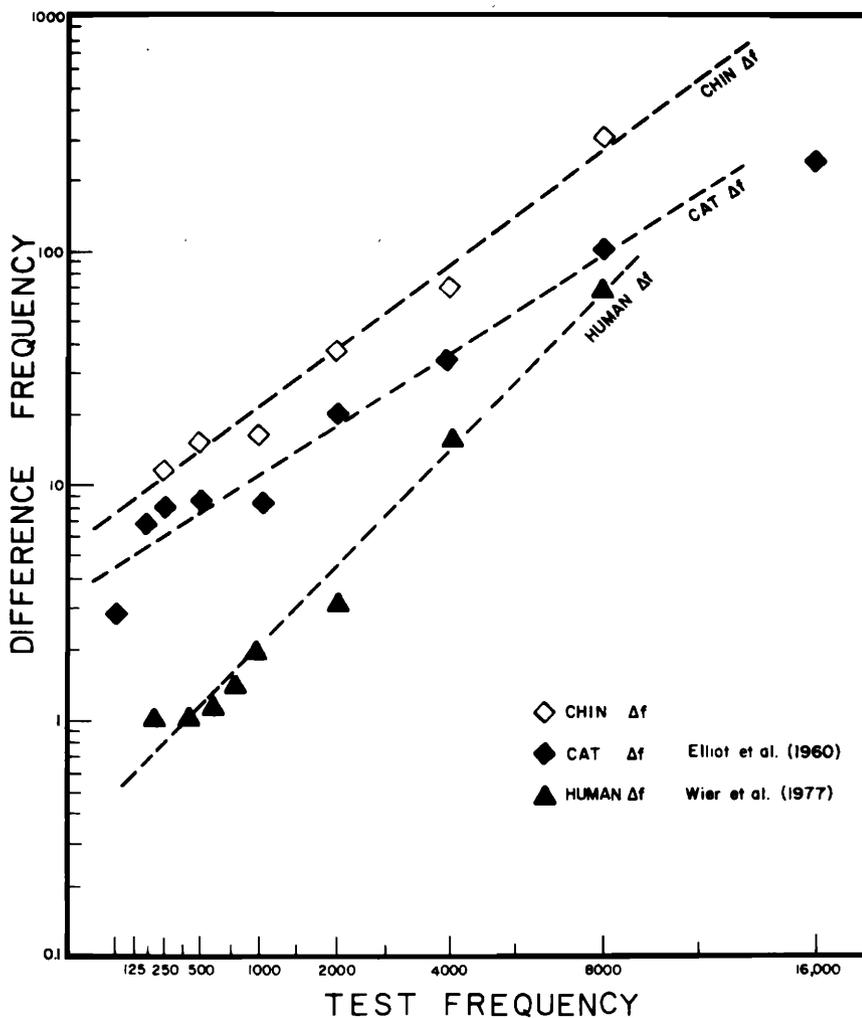


FIG. 6. Differential threshold for frequency from chinchillas, cats, and humans. The dashed lines are linear-regression least squares fits of $\log_{10} \Delta f$ as a function of $f^{1/2}$.

square-root scale is used here simply because it allows one to obtain a better linear fit to chinchilla Δf data ($r = 0.999$) than is obtained with the conventional logarithmic frequency scale ($r = 0.945$). The square-root scale essentially deemphasizes "frequency distance" for the low test frequencies, a process that appears to have some neurophysiological significance (Evans, 1972). Frequency-difference thresholds are shown along the ordinate on a conventional logarithmic frequency scale.

The human frequency-difference thresholds, shown in Fig. 6 by filled triangles, are averages from four listeners (Wier, Jesteadt, and Green, 1977). A two-interval forced-choice adaptive procedure was used to estimate 71%-correct detection of frequency differences between pairs of gated tone bursts. Frequency-difference thresholds for the cat, shown in Fig. 6 by filled diamonds, were obtained by Elliott, Stein, and Harrison (1960) using a conditioned avoidance procedure similar to that used here with chinchillas, except that the trials were discrete instead of continuous. A method of limits, with descending series only, was used to determine differential thresholds in cat. Two correct responses in three trials were required before the next lower frequency difference was presented. Threshold was defined as "the difference in frequency between the standard tone [A] and a tone lying midway between the last comparison tone [B] to which the animal had responded

satisfactorily and the next lower comparison tone." Standard tones and comparison tones were presented to the eight cats at about 40 dB SL. Differential thresholds for frequency difference between alternating tone bursts, averaged across five chinchillas for each test frequency, are shown in Fig. 6 by open diamonds.

Differential thresholds from each species were subjected to linear regression analyses to describe the Δf functions shown in Fig. 6 with least squares "best fit" straight lines. The results of those analyses are listed in Table IV. The Δf functions for cat and chinchilla have comparable slopes, 0.0167 and 0.0191, respectively, while the intercepts vary by a factor of about 2:1. At 250 Hz the ratio of the differential threshold predicted by the regression equation for the chinchilla to the differential threshold predicted for the cat is 1.7, at 1000 Hz the ratio is 2.0, and at 8000 Hz the ratio is 2.8. For example, at 1000 Hz the Δf predicted by the linear regression equation is 20 Hz for the chinchilla and 10 Hz for the cat. At differential threshold chinchillas require frequency differences that are about twice as large as those required by cats.

Comparisons of differential thresholds from chinchillas or cats with differential thresholds from humans are not quite as straightforward. There are both slope dif-

TABLE IV. Least squares linear regression analysis for frequency-difference thresholds ($\log_{10}\Delta f$) as a function of test frequency ($f^{1/2}$): $\Delta f = 10^{**}(a + b * f^{1/2})$, where b = slope and a = intercept.

	Slope	Intercept	r^2	r
Human (Wier <i>et al.</i> , 1977)	0.0262	-0.5333	0.9801	0.990
Cat (Elliott <i>et al.</i> , 1960)	0.0167	0.4858	0.9740	0.987
Chinchilla (average thresholds)	0.0191	0.7145	0.9929	0.996
Chinchilla ($d_p = 1.0$)	0.0266	0.9939	0.9979	0.999
Chinchilla ($d_p = 0.325$)	0.0258	0.5129	0.9969	0.998

ferences and intercept differences to contend with (see Table IV). At 250 Hz the ratio of predicted Δf for chinchillas and humans is 13.6, at 1000 Hz the ratio is 10.6, and at 8000 Hz the ratio drops to only 4.0. However, this does not necessarily mean that at low frequencies humans are 13.6 times more sensitive to frequency changes than chinchillas, and only 4.0 times more sensitive at high frequencies. There are procedural differences in the psychophysical paradigms used to obtain chinchilla and human differential thresholds. More specifically, the procedures used with humans involved a criterion-free index of detection (two-interval forced choice), while the procedures used with chinchillas did not. The simple method of estimating frequency-difference thresholds for chinchillas (and perhaps cats also) did not allow for changes in an animal's operant response level, or false-alarm rate. If false-alarm rates were not the same for large Δf 's and small Δf 's, or if false-alarm rates were not constant from one test frequency to the next, then estimates of differential thresholds would be biased by changes in operant response levels (spontaneous jumping rates).

2. Reconstruction of psychometric functions

To explore the nature of operant response levels during the testing of differential thresholds in the chinchilla, hit rates and false-alarm rates were collected for each frequency difference presented at each test frequency. For example, for all trials in which tone A was 1000 Hz and the frequency difference between tones A and B was 512 Hz, hits were accumulated across all animals and all retests. The false-alarms associated with catch trials just preceding 512-Hz Δf trials were also accumulated across all animals and all retests. Then, hit rates (or false-alarm rates) were calculated by dividing the accumulated number of hits (or false alarms) by the accumulated number of signal trials (or catch trials) associated with a Δf of 512 Hz. This process was repeated for each frequency difference that was tested, in order to yield the "group" psychometric functions shown in Fig. 7. Performance rate is represented on the ordinate as a function of frequency difference between tones A and B on the abscissa.

Consistent decreases in hit rates are seen for progressively smaller frequency differences, until hit rates are about the same as false-alarm rates (the spontaneous jumping rates or operant levels). The averaged dif-

ferential thresholds, obtained with the threshold tracking procedure described earlier, are shown by arrows pointing to the abscissa in Fig. 7. Differential thresholds correspond approximately to the region of 50% hit rate. If false-alarm rates were constant at all frequency differences and for all test frequencies, one could claim that those averaged differential thresholds, obtained with our threshold criteria, are valid estimates of chinchilla differential threshold; they would be valid as long as differential threshold is defined only as the frequency difference at which chinchillas perform at a 50% hit rate. The false-alarm rates, however, are not constant among test frequencies. Neither are they constant for different frequency differences.

In Fig. 7, for example, false-alarm rates at 1000 Hz increase progressively as the threshold testing session progresses. False-alarm rates are low at the beginning of a test session when large frequency differences are tested. False-alarm rates become progressively larger as the test session continues and smaller frequency differences are introduced. At 8000 Hz, false-alarm rates are relatively constant throughout the test session and therefore throughout the range of frequency differences tested. It appears that chinchilla operant levels change over time during a threshold test, or they change from one frequency difference to another, or both.

Because false-alarm rates from the chinchillas in these experiments are not constant, and because our goal at this point is to compare differential thresholds from chinchillas with differential thresholds from humans (the latter obtained with criterion-free detectability indices), the performance data from chinchilla were transformed into a detectability index using d' tables for a yes-no decision task (Swets, 1964). The assumptions underlying the use of d' as a detectability index do not strictly apply to the vigilance type of detection task used with these chinchillas. Therefore, we will refer to this detectability index as d_p . Each pair of hit rates and false-alarm rates shown in Fig. 7 were converted to $\log_{10}d_p$, plotted against $\log_2\Delta f$, and were subjected to linear regression analysis to obtain best fit straight lines through the transformed psychometric functions.

The results of the linear regression analysis are given in Table V. As indicated in the table, there are no consistent changes in the slopes of those transformed psychometric functions from one test frequency to another. The intercepts increase progressively with test frequency, reflecting decreasing absolute sensitivity to frequency changes with test frequency.

Psychometric functions taken from three human subjects performing in a same-different frequency-discrimination experiment (Jesteadt and Sims, 1975) are shown in Fig. 8 together with chinchilla psychometric functions. The most obvious differences between human and chinchilla functions are that the chinchilla functions are displaced to the right of human functions, indicating decreased differential frequency sensitivity in chinchillas relative to humans. The contrast we find most interesting in the results of the regression analysis involves the differences among the slopes of the chinchilla and

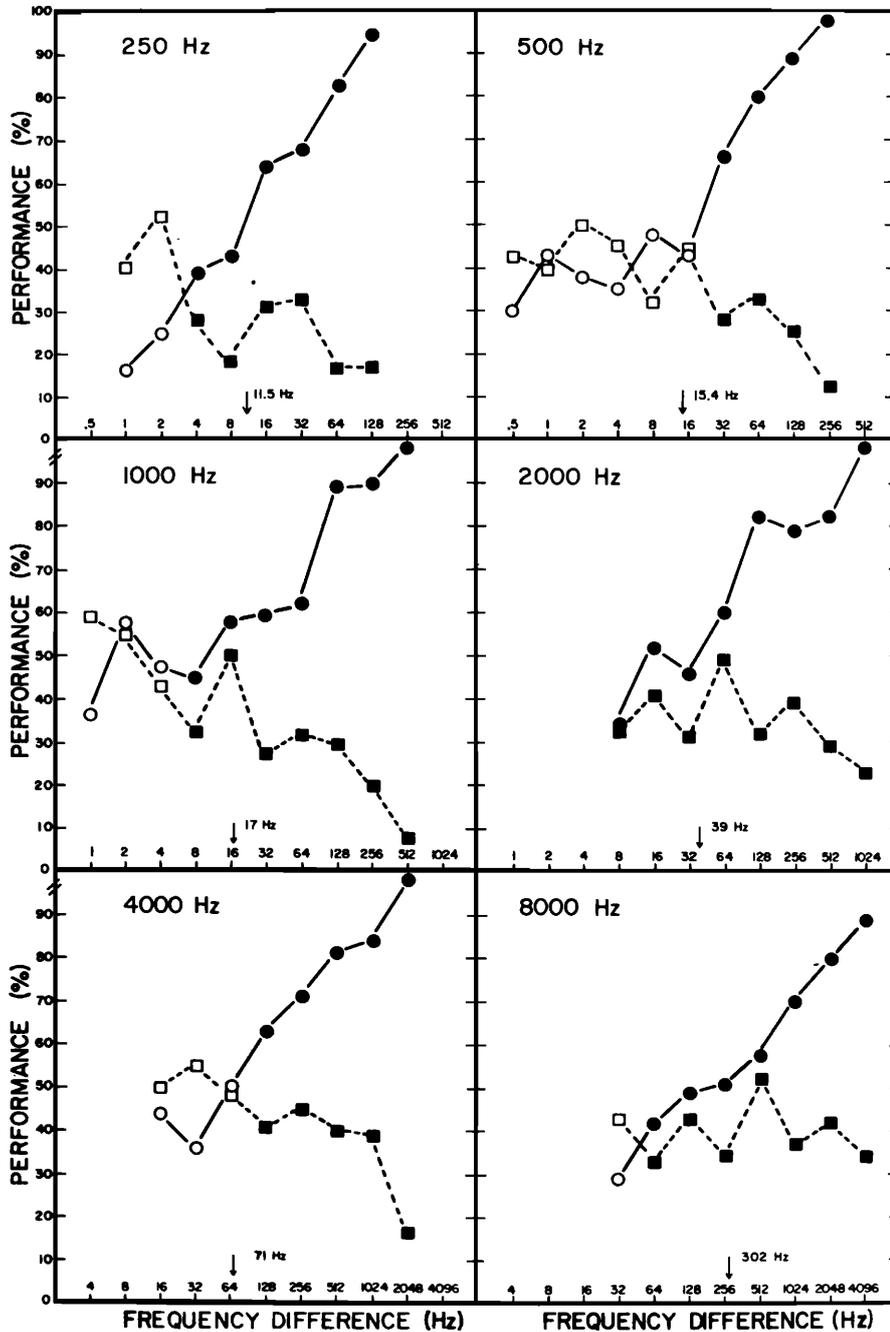


FIG. 7. Performance functions accumulated from five chinchillas. Hit rates (%) are plotted as circles, and false alarm rates (%) are plotted as squares, both as a function of frequency difference (Hz). Filled symbols indicate the data points that were included in a linear-regression analysis of d_p , which was performed in order to estimate the slopes of psychometric functions from chinchillas. Frequency-difference thresholds, obtained with the threshold-tracking procedure described in the text, are indicated by vertical arrows.

human psychometric functions. The slopes of chinchilla functions are about half those of human functions.

Since the slopes of psychometric functions are so drastically different for chinchillas and humans, questions arose about the appropriate detectability index to use when comparing differential sensitivity between these two species. What point on the psychometric function will allow a valid interspecies comparison? We were unable to resolve that issue, and alternatively chose to compare chinchilla and human differential sensitivity at several detectability indices.

3. Equal detectability Δf functions

From the linear regression equations in Table V for chinchilla psychometric functions, the frequency differ-

ences corresponding to a $d_p = 1.0, 0.75, 0.50,$ and 0.325 were calculated for all six test frequencies. Then linear regression equations were calculated for $\log_{10} \Delta f$ as a function of $f^{1/2}$. This was done for each detectability index listed above. The predicted Δf 's for $d_p = 0.325$ and the best fit straight line through those Δf 's are shown in Fig. 9. The best fit straight lines describing predicted $\log_{10} \Delta f$ as a function of $f^{1/2}$ for detectability indices of $d_p = 1.0, 0.75,$ and 0.50 are also shown in Fig. 9. For comparison, the Δf function obtained by Wier, Jesteadt, and Green (1977) for humans is included. Linear regression equations for chinchilla ($d_p = 1.0$ and 0.325) and for human ($d_p = 1.11$) Δf functions are listed in Table IV.

When chinchilla frequency-discrimination data are transformed into equally detectable Δf functions, as rep-

TABLE V. Least squares linear regression analysis for $\log_{10}d_p$ by $\log_2\Delta f$. Chinchilla results are from the present experiments; Human results are from Jesteadt and Sims (1975).

	Slope	Intercept	r^2	r
Chinchilla (Hz)				
250	0.1696	-0.77	0.9243	0.96
500	0.1852	-0.97	0.9792	0.99
1000	0.1961	-1.20	0.8850	0.94
2000	0.1821	-1.38	0.8168	0.90
4000	0.1801	-1.57	0.9119	0.95
8000	0.1592	-1.78	0.6715	0.82
Human (Hz)				
250	0.2903	0.0419	0.8657	0.93
1000	0.3925	-0.5834	0.8348	0.91

resented in Fig. 9, the large slope difference between the chinchilla Δf function and the human Δf function, seen earlier in Fig. 6, is minimized. Now the comparison of differential sensitivity between species is reduced to a simple comparison of intercept constants for the various detectability indices. The human Δf function, based upon the 71%-correct point on the human psychofunction, was obtained with a two-interval forced-choice procedure; a $d_p = 1.11$ would be the value of the corresponding detectability index for 71% correct. The comparable Δf function from chinchilla, at $d_p = 1.0$, has an intercept that is approximately 34 times larger than the corresponding intercept for the human Δf function. From this comparison, it appears that the chinchilla requires a frequency difference that is 34 times larger than required by humans to reach the same performance criterion as humans. We hesitate, however, to con-

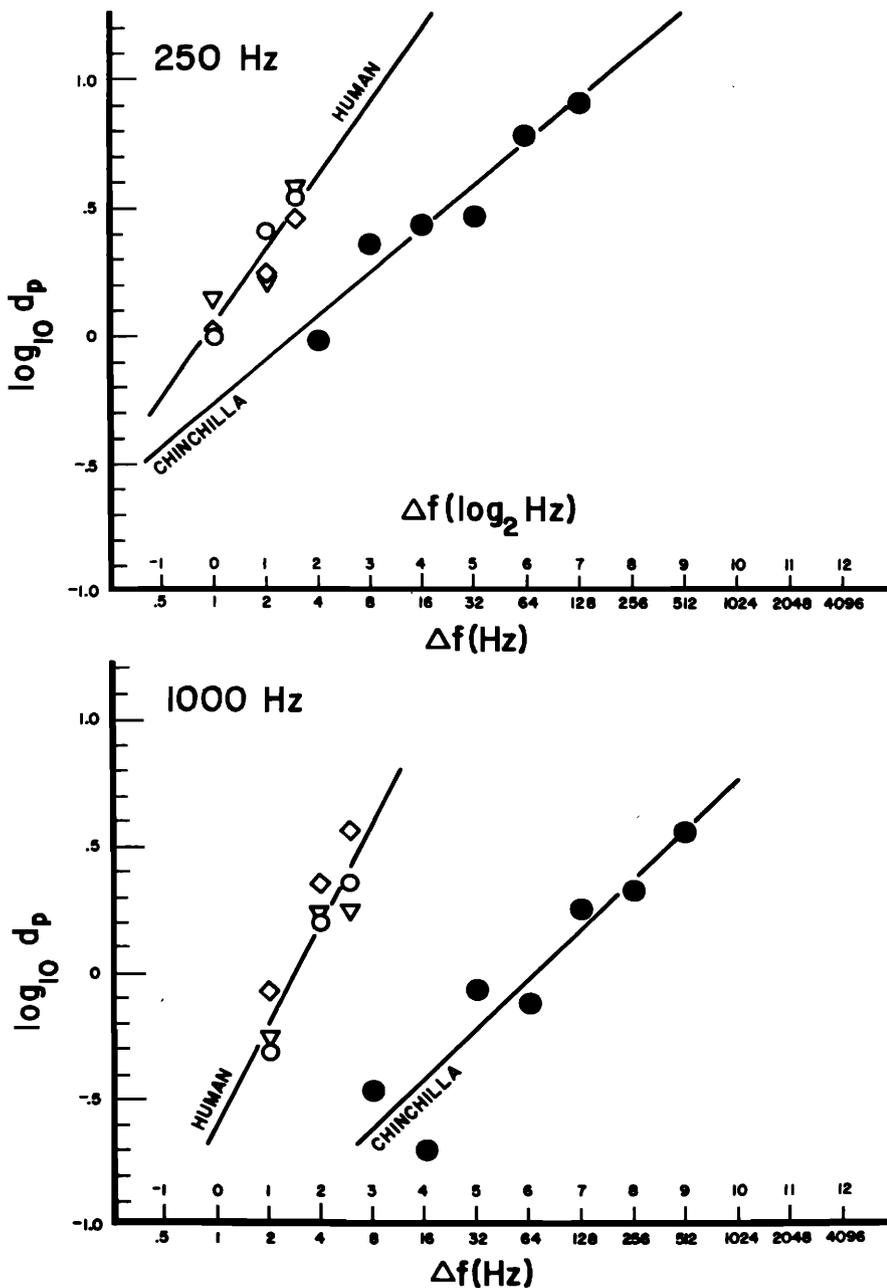


FIG. 8. Psychometric functions at 250 and 1000 Hz from chinchillas (present study) and from humans (Jesteadt and Sims, 1975). The straight lines are linear regression least squares fits to $\log_{10}d_p$ as a function of $\log_2(\Delta f)$. The abscissa includes two scales, $\log_2\Delta f$ and Δf in Hz.

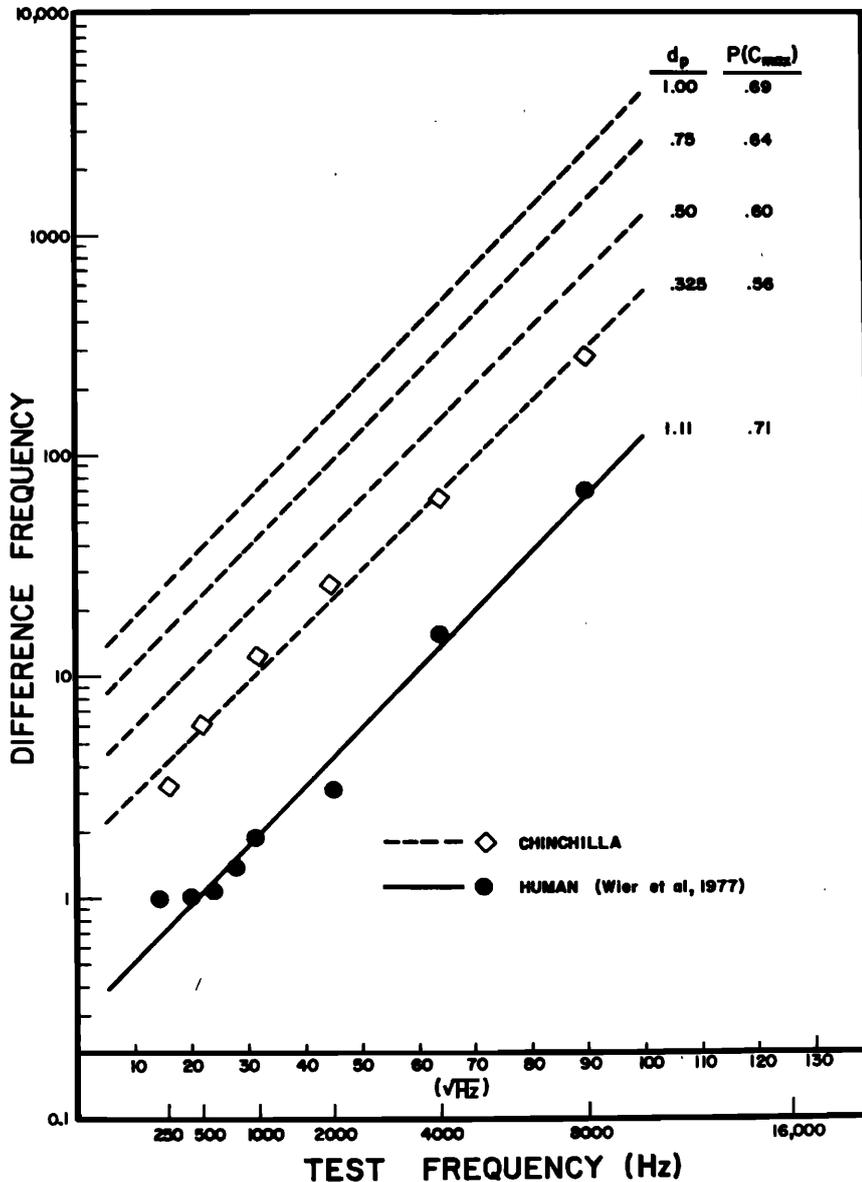


FIG. 9. Difference frequencies for equal detectability plotted against test frequency for humans (Wier, Jesteadt, and Green, 1977) and for chinchillas. The corresponding detectability indices, d_p and $P(C_{max})$, are indicated to the right of each curve. The straight lines are linear regression least squares fits to $\log_{10} \Delta f$ as a function of $f^{1/2}$.

clude from this that the human auditory system is 34 times better at detecting frequency differences between tones than the chinchilla's auditory system.

Perhaps a more reasonable comparison might be made between chinchilla and human differential frequency sensitivity at a lower point on the psychometric functions. If extrapolations are made to a $d_p = 0.325$ on the human psychometric functions in Fig. 8, i. e., at a performance index of $d_p = 0.325$, then the predicted Δf for chinchillas at $d_p = 0.325$ would be only 10 times the predicted Δf for humans. For example, at 1000 Hz the predicted Δf for chinchillas would be about 12 Hz compared with 1.2 Hz for humans.

III. COMPARISON OF CHINCHILLA CR AND Δf

Fletcher (1940) presented evidence from human listeners supporting a constant relation between critical bandwidth and frequency discrimination (Δf). His measure of critical bandwidth, the ratio of signal power in

a tone at masked threshold to the noise-power/cycle in a masking noise, is now commonly referred to as the Critical Ratio (CR). Fletcher expressed the relation between CR and Δf as $CR = 10 \log K \Delta f$, with $K = 20$. Watson (1963) later determined the same relation for the cat using his own critical ratio data and frequency discrimination data from Elliott, Stein, and Harrison (1960). He demonstrated excellent agreement between critical ratios and frequency discrimination in the cat using the same constant, $K = 20$, that was used by Fletcher for man.

It was of some interest to us to determine whether the same constant relation between CR and Δf that holds for the cat and for man also holds for the chinchilla. To make that determination, critical ratios for the chinchilla were obtained from the results of Miller (1964). The average frequency-difference thresholds expressed in Hertz from Table III were used as estimates of Δf for the chinchilla. Those Δf thresholds were converted to CR equivalents using Fletcher's equation with the same

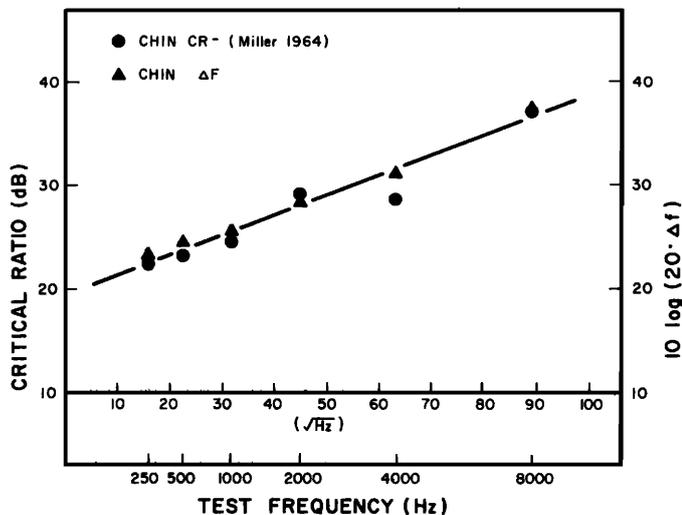


FIG. 10. Comparison of critical ratios (CR) and frequency-difference thresholds Δf in the chinchilla. Critical ratios in decibels, represented by filled circles, are plotted on the left ordinate. Frequency-difference thresholds were converted to CR equivalents with the formula $CR = 10 \log_{10} 20 \Delta f$ and are plotted along the right ordinate. Linear regression analysis on all data points, both CR and $10 \log_{10} 20 \Delta f$, yielded the solid line described by $CR = 19.57 + 0.1907f^{1/2}$. The correlation coefficient is $r = 0.97$.

constant used for man and cat, $K = 20$, and are plotted in Fig. 10 along with Miller's CR data for chinchilla. The solid line is a linear fit of the two sets of data with the formula: $CR = a + bf^{1/2}$, where the slope b is 0.1907 and the intercept a is 19.57. The goodness of fit of these data is indicated by a correlation coefficient r equal to 0.97.

It can be seen from Fig. 10, that Fletcher's formula, which describes the relation between critical ratio and frequency discrimination thresholds for man and for cat, is also a good description of the inter-relation of these variables for the chinchilla. Furthermore, the constant ($K = 20$) of proportionality that applies to data from man and from cat is also a good approximation of the constant of proportionality between CR and Δf data from the chinchilla.

At this point, it should be emphasized that when certain other classes of Δf measures are compared with CR data, the inter-relations between CR and Δf are not as clear as implied in Fig. 10. In all cases of good agreement between CR and $20\Delta f$, whether for man, cat, or chinchilla, the Δf measures used for comparison with CR measures were not obtained using psychophysical procedures that either controlled for a listener's criterion variables or eliminated a listener's criterion variables from the measure of sensory capability Δf . The Δf function for humans obtained by Wier, Jesteadt, and Green (1977) with a 2IFC procedure, and the Δf function for chinchillas based on a constant d_p index, both shown in Fig. 9, are considerably different in form than the Δf functions shown in Fig. 10. The differences largely occur for Δf 's obtained at lower test frequencies. Those Δf functions obtained with a criterion-free index of frequency discrimination tend to demonstrate lower inter-

cepts and steeper slopes. At this time, a reasonable explanation for those Δf differences, which appear to be assignable to procedural differences, has escaped us.

IV. CONCLUSIONS

The results of our work with chinchillas on a frequency-difference recognition task that involved a go-no-go response leads us to the conclusion that chinchillas do not learn this dual-response task quickly enough, nor do they learn to perform the go-no-go response task well enough for most investigators to use this recognition paradigm to measure differential sensitivity to frequency. The chinchilla can learn to discriminate large frequency differences by making an avoidance response to a large frequency difference between tone bursts, and in addition can learn to inhibit that avoidance response to no frequency difference between tone bursts. However, when the discrimination task is made more difficult by decreasing the frequency difference between tone bursts, they can no longer maintain good discrimination behavior.

Whether this failure to correctly perform frequency-difference discrimination is due to the lack of redundancy in the acoustic cues between simple pure tones differing only in frequency, or whether this failure is the result of response incompatibility between the avoidance response and the inhibition of that avoidance response, is not clear. Since the results of later experiments demonstrated differential thresholds from chinchilla that were only an order of magnitude poorer than highly trained human listeners, it is likely that response incompatibility was most responsible for the poor discrimination behavior in the go-no-go task.

When chinchillas were "asked" to detect frequency differences between alternating tone bursts in an ongoing train of tone bursts, they learned the discrimination task in less than five training sessions. With patience, they can be trained to continue that discrimination as frequency difference is reduced to the range of human differential frequency sensitivity.

When criterion-free performance indices are used to specify chinchilla differential frequency sensitivity, the chinchilla Δf function, describing differential sensitivity in terms of $\log_{10} \Delta f$ as a function of $f^{1/2}$, is parallel to the Δf function obtained from humans with comparable criterion-free performance indices. If chinchilla differential sensitivity and human differential sensitivity are compared at a performance index of $d_p = 1.0$, it appears that chinchillas require frequency differences that are about 34 times larger than required by humans. If however, a more stringent performance index of $d_p = 0.325$ is used for comparison purposes, chinchillas require frequency differences only 10 times those required by humans.

Because chinchilla psychometric functions have slopes about half the steepness of human psychometric functions, it appears that a large central variance component exists in chinchilla Δf data that does not exist in Δf data from man. Therefore, a comparison of differential sensitivity across species that is independent of perfor-

mance index cannot be made. One can only speculate that if the proper response mode was employed, a response mode more compatible with a chinchilla's normal activity than the conditioned avoidance response, differential thresholds might be realized that are even closer to those obtained from humans.

ACKNOWLEDGMENTS

This research was supported by a grant from the Deafness Research Foundation and by NIH Grant NS12125 and NS04403.

- Burdick, C. K., and Miller, J. D. (1975). "Speech perception by the chinchilla: discrimination of sustained /a/ and /i/," *J. Acoust. Soc. Am.* **58**, 415-427.
- Butler, R. A., Diamond, I. T., and Neff, W. D. (1957). "Role of auditory cortex in discrimination of changes in frequency," *J. Neurophysiol.* **20**, 108-120.
- Cornsweet, T. N. (1962). "The staircase method in psychophysics," *Am. J. Psychol.* **75**, 485-491.
- Cornwell, P. (1967). "Loss of auditory pattern discrimination following insular-temporal lesions in cats," *J. Comp. Physiol. Psychol.* **63**, 165-168.
- Egan, J. P., Greenberg, G. Z., and Schulman, A. I. (1961). "Operating characteristics, signal detectability, and the method of free response," *J. Acoust. Soc. Am.* **33**, 993-1007.
- Elliott, D. N., Stein, L., and Harrison, M. J. (1969). "Determination of absolute-intensity and frequency-difference thresholds in cats," *J. Acoust. Soc. Am.* **32**, 380-384.
- Evans, E. F. (1972). "The frequency response and other properties of single fibers in the guinea-pig cochlear nerve," *J. Physiol.* **226**, 263-287.
- Fletcher, H. (1940). "Auditory patterns," *Rev. Mod. Phys.* **12**, 47-65.
- Goldberg, J. M., and Neff, W. D. (1961). "Frequency discrimination after ablation of cortical auditory areas," *J. Neurophysiol.* **24**, 119-128.
- Henderson, D. (1969). "Temporal summation of acoustic signals by the chinchilla," *J. Acoust. Soc. Am.* **46**, 474-475.
- Henning, G. B. (1966). "Frequency discrimination of random-amplitude tones," *J. Acoust. Soc. Am.* **39**, 336-339.
- Jesteadt, W. and Sims, S. L. (1975). "Decision processes in frequency discrimination," *J. Acoust. Soc. Am.* **57**, 1161-1168.
- Kuhl, P. K. (1976). "Speech perception by the chinchilla: Categorical perception of synthetic alveolar plosive consonants," *J. Acoust. Soc. Am.* **60**, S81(A).
- Luz, G. A. (1969). "Conditioning of the chinchilla to make avoidance responses to novel sounds," *J. Comp. Physiol. Psych.* **68**, 348-354.
- Luz, G. A., and Burdick, C. K. (1972). "Auditory discrimination in the chinchilla: II. Detectability of the deletion of a tone from a tonal pattern," U.S. Army Res. Lab. Rep. No. 977 (Ft. Knox, KY).
- Luz, G. A., and Nugen, R. D. (1972). "Auditory discrimination in the chinchilla: I. Reaction time," U. S. Army Res. Lab. Rep. No. 976 (Ft. Knox, KY).
- McGee, T., Ryan, A., and Dallos, P. (1976). "Psychophysical tuning curves of chinchillas," *J. Acoust. Soc. Am.* **60**, 1146-1150.
- Miller, J. D. (1964). "Auditory sensitivity of the chinchilla in quiet and in noise," *J. Acoust. Soc. Am.* **35**, S2010(A).
- Miller, J. D. (1970). "Audibility curve of the chinchilla," *J. Acoust. Soc. Am.* **48**, 513-523.
- Miller, J. D., and Luz, G. A. (1970). "A 'learning set' procedure for sound quality discriminations by chinchillas," *J. Aud. Res.* **10**, 136-146.
- Nelson, D. A., Kiester, T. E., Turner, C. W., and Ward, W. D. (1976). "Automated conditioned-avoidance audiometry in the chinchilla," *J. Aud. Res.* **16** (Suppl. 6), 209-237.
- Seaton, W. H., and Trahiotis, C. (1975). "Comparison of critical ratios and critical bands in the monaural chinchilla," *J. Acoust. Soc. Am.* **57**, 193-199.
- Swets, J. A. (1964). *Signal Detection and Recognition by Human Observers* (Wiley, New York).
- Thompson, R. F. (1960). "Function of auditory cortex of cat in frequency discrimination," *J. Neurophysiol.* **23**, 321-334.
- Trahiotis, C., and Elliott, D. N. (1970). "Extension of the Neff neural model to situations demanding discrimination among complex stimuli," *J. Acoust. Soc. Am.* **47**, 1116-1127.
- Watson, C. S. (1963). "Masking of tones by noise for the cat," *J. Acoust. Soc. Am.* **35**, 167-172.
- Watson, C. S., and Nichols, T. L. (1976). "Detectability of auditory signals presented without defined observation intervals," *J. Acoust. Soc. Am.* **59**, 655-668.
- Wier, C. C., Jesteadt, W., and Green, D. M. (1977). "Frequency discrimination as a function of frequency and sensation level," *J. Acoust. Soc. Am.* **61**, 178-184.