Behavioral Measurements of Absolute and Frequency-Difference Thresholds in Guinea Pig

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Absolute and frequency-difference thresholds were determined by the conditioned-suppression technique. The results show that the average frequency range of audibility at +50 dB sound-pressure level extends from 86 Hz to 46.5 kHz, with a best frequency near 8 kHz. Individual differences in sensitivity are related to body weight and, probably, age. The average frequency-difference limen is 3.5% from 125 Hz to 42 kHz. Compared to other mammals, the auditory capacities of guinea pig are within one standard deviation of the mammalian mean on each of six dimensions: high-frequency and low-frequency cutoff, lowest intensity, best frequency, area of the audible field, and frequency discrimination.

INTRODUCTION

Although much of the knowledge concerning the anatomy and physiology of the ear is based on experimental studies of the guinea pig, little is known about the guinea pig's hearing ability as revealed by behavioral methods. In the past this lack of behavioral data has been excused through deference to a supposedly natural and pervasive recalcitrance that makes guinea pigs intractable for the usual techniques of behavioral testing.[1,2] Consequently, behavioral audiometry of guinea pigs has usually relied on techniques that are either completely unique (e.g., Ref. 2) or, at least, outside the array of techniques that are still considered acceptable by animal psychophysicists.[3-5]

In the last few years, a new technique for assessing sensory thresholds in animals has been refined.[6,7] This technique, called "conditioned suppression," has proved to be quicker, more precise, and probably more accurate than other behavioral techniques of comparable generality.[8] Since the conditioned-suppression technique has already been used to measure many different kinds of thresholds in audition (as well as in vision, olfaction, and somesthesis) and in many different kinds of animals, including some previously considered to be as intractable as guinea pigs, it seemed worthwhile to reopen the question of the hearing ability of the guinea pig.

I. METHOD

Briefly, the guinea pigs were trained to lick a spout for a water reward. After a reasonably steady lick rate was

attained, a tone was presented for 10 sec and, at its offset, a shock was delivered to the guinea pig's feet (Fig. 1). This conditioning procedure soon resulted in a cessation of licking at the onset of a tone. In test trials, this cessation, or suppression, of licking was used as evidence that a tone had been perceived.

A. Subjects

Four domestic guinea pigs (*Cavia procellus*) were used. Guinea pigs A and B were judged to be adolescents on the basis of their body weight at the beginning of the experiment, while C and D were both adults. They were maintained on a diet of rabbit pellets (Flint River Mills) supplemented with vitamins (Vitatone) and, occasionally, fruit and greens.

B. Details of Behavioral Apparatus

The animals were tested in a rectangular cage 7 in. long, 6 in. high, and 6 in. wide. The walls, ceiling, and

Fig. 1. Stimulus configuration in absolute threshold test. Duration of "safe" signal (silence) varied randomly from 15 to 600 sec.

floor of the cage were constructed of $\frac{3}{16}$-in. brass rods. A waterspout, connected by rubber tubing to a water bottle located beyond the sound field, was placed at one end of the cage. A drinkometer (Grason–Stadler, model E4690A) connected to the waterspout and floor bars recorded the number of times the animal licked the spout. The cage was placed on a wooden stand which rested on 2-in. pieces of fiberglass in a pan of pelleted cellulose. The entire testing apparatus was placed on a burlap-covered table in a sound-treated chamber (IAC, 1202A) with walls and ceiling loosely draped with burlap.

C. Details of the Stimulus-Generating Apparatus

To produce tones, sine waves from an oscillator (Hewlett-Packard, 200CD) were led first to an electronic switch (Grason–Stadler, model 829E), then to an attenuator (Hewlett–Packard, 350D) and, last, via an impedance matching transformer, to a wide-range speaker (University, model 312). The speaker was mounted on a 2-in.-thick block of fiberglass padding 30 in. from the waterspout (about 31 in. in front of the interaural line). This sound system proved to be capable of delivering undistorted tones from 54 Hz to 70 kHz at an intensity of at least 70 dB sound-pressure level (SPL). For frequency-difference thresholds, a second oscillator and attenuator were added to the sound system to produce the stimuli depicted in Fig. 2.

To prevent onset and offset artifacts, the electrical signal was electronically keyed with a rise and decay time of 25 msec for all frequencies except the very lowest. For frequencies less than 500 Hz, the rise and decay times were set still slower, at 50, 100, or 250 msec. The electrical signal to the speaker was continuously monitored for onset and offset transients with an oscilloscope and its frequency was monitored by an interval timer (TSI model 385R).

D. Sound-Calibration Procedure

The SPL was measured with Brüel & Kjær equipment consisting of a microphone amplifier (model 2604), a $\frac{1}{2}$- or $\frac{1}{4}$-in. condenser microphone (models 4133 and 4136), and a bandpass filter (model 1612). To verify the absence of significant overtones, an oscilloscope was connected to the recorder output of the sound-level meter.

Since initial measurements showed that the presence of the animals' heads had a negligible effect on the sound field (apparently a result of the relatively large and homogeneous sound field obtained by placing the speaker at a distance from the animal), routine measurements were taken with the animal removed from the sound field. The sound-calibrating procedure consisted of placing the microphone in the position previously occupied by the animals' heads and pointing it directly at the speaker (i.e., 0° incidence). Measurements taken on nearly every daily testing session showed that the sound field for a given frequency rarely varied by more than 1 dB.

To convert the meter readings into "free-field" SPL, free-field correction curves for 0° sound incidence were used (Brüel & Kjær manual for 4135–36 condenser microphones). No special correction was necessary for microphone 4133, as it is already calibrated for a flat free-field response. Since a free-field response does not vary significantly from the pressure response of the 4136 microphone for frequencies below 3 kHz, no corrections were necessary for low-frequency measurements with this microphone either. However, the free-field 0° incidence response curve differs significantly from the pressure response curve for frequencies above 3 kHz for the microphones. Therefore, it became necessary to show that the acoustics in the test chamber approximated a free field. The appropriate tests were made by calibrating the SPL of the audio equipment in an anechoic chamber (IAC, model 1200). For frequencies above 3 kHz the measurements taken in the anechoic chamber proved to differ by no more then 1 dB from the measurements taken in the testing chamber. Thus, there was no reason to reject the assumption that the animal testing chamber approximated a free field for frequencies above 3 kHz.

Because the animals' thresholds were below the sensitivity of the sound-level meter for most frequencies, it was necessary to measure a higher intensity and then calculate the threshold value through extrapolation. Since a change in the attenuator setting produced an equal change in the SPL of the tone throughout the dynamic range of the meter for every frequency, thresholds were calculated by linear extrapolation.

Finally, measurements of frequencies higher than 32 kHz were accomplished either by setting the bandpass filter to the 31.5 kHz band and adjusting the reading according to the theoretical attenuation of the filter, or else by setting the sound-level meter to record the linear response (20 Hz–200 kHz) and then measuring when the tone's intensity was at least 10 dB above the intensity of the background noise. Both techniques gave the same result.

Therefore, it can be concluded that the calibration of the sound system in free-field decibels SPL was probably accurate to ±1 dB.

SAFE SIGNAL   WARNING SIGNAL   SAFE SIGNAL

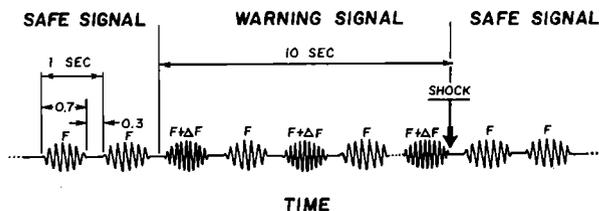FIG. 2. Stimulus configuration in frequency-difference threshold (DL) tests. During testing, ΔF was varied in increments of $(0.01)F$. Intensity of tones was fixed at 30 dB above the animal's threshold.

E. Details of Procedure

1. Training

The guinea pigs were deprived of water in their home cages with the exception of small amounts they gained from an occasional fruit or green vegetable supplement. Thus, the chief source of water was the lick spout in the testing cage. Each animal was trained to lick the waterspout in order to receive small amounts of water (about 0.03 ml per reward) on a variable ratio (VR) schedule (ranging from VR 10% to VR 50%). This training provided a reasonably steady lick rate of three to six licks per second throughout the ½-h daily sessions. It was on this background of steady licking that the test trials were imposed. The steady licking also yielded a secondary benefit by maintaining the animal's head and ears in a relatively constant position with respect to the speaker.

After a steady rate of licking had been achieved at a reward schedule of 20%–30% VR, an obviously supra-threshold tone was presented for 10 sec, and at its offset, a mild shock was delivered to the feet. After a few tone–shock pairings, the animal ceased licking at the onset of a suprathreshold tone and did not begin to lick again until the tone was terminated and the shock received.

2. Threshold Testing

At each frequency octave, threshold testing was conducted in two ways: First the threshold was estimated by a modified method of limits, then a second exhaustive determination was made by the method of constant stimuli. In both methods every trial was followed by shock, whether or not the tone later proved to be subthreshold.

In the exploratory stage, the intensity of the stimulus was decreased in steps of 5 dB on each successive trial until a failure to cease licking was observed. The intensity of the stimulus was then increased until either a cessation or an obvious suppression of licking again occurred. By repeating this procedure, the threshold could be readily estimated within 5–10 dB.

In the second stage of testing (method of constant stimuli), tones with intensity levels in 5-dB increments extending from 10 dB below to 10 dB above the estimated threshold were presented in random order. After 10 presentations at each of the five preselected levels, a smooth psychophysical curve of lick suppression as a function of intensity could be plotted. The data reported are those gained from this second method only.

To ensure that the animals did not respond to possible artifacts in the sound system, sham trials were administered every session. Sham trials were identical to test trials with two exceptions: (1) the signal was attenuated to at least 50 dB below the animal's suspected threshold; and (2) the trial was not followed by an electric shock. Since the sham trial procedure never resulted in significant suppression, no further mention of this procedure need be made.

3. Frequency-Difference Limens

After the audiogram had been completed, frequency-difference limens (DLs) were determined. The animal was introduced to this new task by placing it in the test apparatus while a pulsing tone was being presented (0.7 sec on, 0.3 sec off). After the guinea pig began licking in the presence of this, now neutral, stimulus, training trials were begun. A trial consisted of 10 sec in which the tone pulses alternated between low and high frequencies (i.e., F, $F+\Delta F$, F, $F+\Delta F$, $\cdots$). At the end of the 10-sec warning signal, a shock was delivered and the pulsed tones were again of the same frequency (i.e., F, F, F, $\cdots$) (Fig. 2). After a few pairings with shock, the animal ceased licking whenever there was a large difference in the frequency of the pulsing tones and did not begin licking again until the shock was delivered and the tones had returned to the same frequency. The intensity of the tones was always 30 dB above the absolute threshold determined in the previous procedure.

In order to determine whether the animal was basing its response on artifacts such as small differences in intensity, sham trials were also given during frequency-difference testing. These sham trials were exactly like test trials except: (1) the warning period consisted of alternating pulsed tones of the same frequency, but with intensities differing by 1–6 dB; and (2) no shock was delivered.

4. Analysis of Behavioral Data

In order to use conditioned suppression to determine a sensory threshold, one must interpret a change in the rate of instrumental responding as an indication that the animal has detected the stimulus. Sidman et al.,[7] Hendricks,[6] and Kamin[9] have discussed the theoretical and practical problems involved in this method.

For this experiment, a unitless measure of detection was chosen which is a function of the number of licks in the 10-sec period in which the warning stimulus was present (W), and the number of licks in the 10-sec safe period (S) immediately preceding the warning period. The formula for discriminatory performance is $(S-W)/S$. Since zero values for S are eliminated by not presenting a trial when the animal is not licking, this measure varies from values near $+1$ to values near 0. A value of $+1$ means complete cessation of licking and is interpreted as indicating that the stimulus was easily detected whenever it was present. A value of 0 means that the rate of licking did not change upon presentation of the stimulus and is interpreted as indicating that the animal did not detect the signal. Intermediate values are interpreted as indicating that the subject may have detected or only occasionally de-

FIG. 3. Individual audiograms of four guinea pigs. Intensity scaled in decibels *re* 0.0002 dyn/cm². Note agreement in best frequency (8 kHz) and high-frequency cutoff. Individual differences are probably the result of age differences.
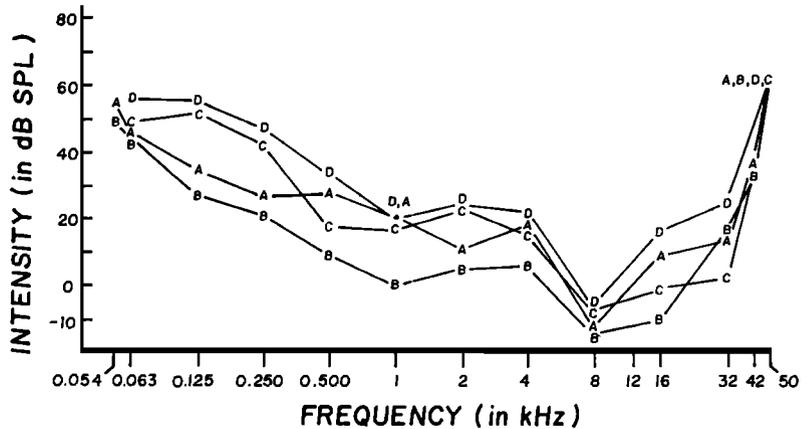
tected the signal. For the construction of standard audiograms (e.g., Fig. 3) and frequency-difference limits (Fig. 7), an average performance value of +0.50 has been arbitrarily chosen as threshold, but the result of a less conservative definition of threshold (+0.20) is shown in Fig. 5.

II. RESULTS AND DISCUSSION

The audiograms of the four guinea pigs are shown in Fig. 3. The frequency range of audibility extends more than 9.5 oct at 50 dB SPL, with an obvious best frequency near 8 kHz.

A. Individual Variation

Although the amount of variation between the four curves is not unusual for behavioral audiograms obtained with other techniques, it is large relative to the variation found in other species using the conditioned-suppression technique (cf. Refs. 10–13). In an attempt to determine whether this variance was due mostly to measurement error or, alternatively, due mostly to true individual differences among the animals, the threshold procedures were repeated on guinea pigs C and D.

Figure 4 shows two typical test–retest comparisons. The extremely close agreement between the two psycho-physical functions for each animal, together with the marked difference in thresholds between the two animals, leads to the conclusion that it is the animals themselves, and not imprecision, that is the main source of variation in the audiograms. Therefore, the question turns to the possible sources of variation among individual guinea pigs.

Routine ear examinations failed to provide evidence of injury, disease, infestation, or deformity in any of the animals. Thus, these possibilities are unlikely, although they cannot be completely ruled out. It is more likely that the differences in sensitivity are due to differences in age. Since the true ages of the guniea pigs are not known, this conclusion relies on the indirect evidence summarized in Table I. The table shows that the ordering of the four guinea pigs by body weight parallels perfectly their ordering by either low-frequency cutoff, lowest threshold, or area of the audible field. Since the probability of any one of these orderings is 1/4!, the existence of a relation between body weight and sensitivity for guinea pigs is likely.

Referring to the individual audiograms in Fig. 3, any

FIG. 4. Typical test–retest comparisons 4 months apart for subjects "C" and "D" at 4 kHz. Note close agreement between tests for each animal but marked difference between animals. Arrows indicate threshold for 0.50 performance level. 1: Test, 2: Retest.
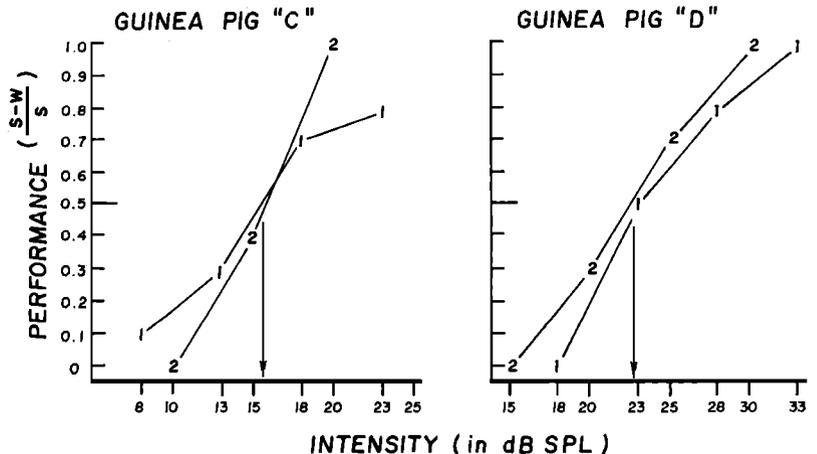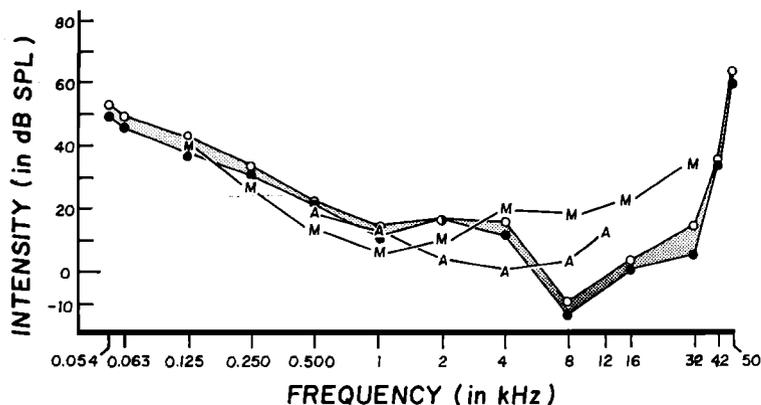
FIG. 5. Average audiogram of guinea pigs. Open circles: thresholds based on usual (0.50) performance levels; closed circles: thresholds based on less conservative (0.20) performance levels; shaded area indicates difference between audiograms based on the two criteria; A: from Anderson and Wedenberg (Ref. 2); M: from Miller and Murray (Ref. 24).

remaining doubt in the existence of this relationship is removed. The average threshold of cases A and B (the two lightest animals) is lower than the average of C and D (the two heaviest animals) at 9 of the 10 frequencies at which the four animals differ. Therefore, the body weight of the animals is a notably precise indicator of their auditory sensitivity. In seeking an explanation of this relation, the possibility that the parallel variation in weight and hearing is due to their joint dependence on age would seem too obvious to merit serious objection.

Before accepting the conclusion that the variation between individuals is due almost solely to age, it should be noted that the way in which the individual audiograms differ in guinea pigs is not typical of age effects as seen in humans (see, for example, Refs. 14 and 15). Among the four guinea pigs in these experiments, variation in sensitivity is greater at middle and low frequencies than it is at the highest frequencies. We have seen this type of variation in only two other animals— the potto[16] and the chinchilla.[17] For the chinchilla and potto, younger animals are more sensitive in the middle range of frequencies than are older animals. For the potto, we were able to rule out the possibility of neurological defects as well as otological defects as a basis for middle- and low-frequency variation. Although we cannot rule out neurological defects in the guinea pigs used here, this possibility seems unlikely in the absence of any other neurological sign. Thus, we have no further

explanation for the relation between a guinea pig's sensitivity and its body weight beyond that of growth and age, nor can we suggest a plausible reason for the similarity between potto, chinchilla, and guinea pig in the unusual way their sensitivity might be lost with aging.

B. Previous Estimates of Guinea Pig Hearing

We are aware of 11 published reports of attempts to establish explicit behavioral audiograms for guinea pigs.[2–5,18–24] The techniques that have been used previously range from observations of the Preyer reflex (a visible flick of the pinna) to a unique technique in which the behavioral observation is an inhibition of chill-induced shivering.[2] Since the reports of Anderson and Wedenberg[2] and Miller and Murray[24] are the most recent ones that we know of and convincingly eliminate the need for considering older results, it is these reports with which comparison is required.

Figure 5 allows comparison of the average audiograms obtained in the three experiments. To begin with, it can be seen that the three sets of results are in agreement over the low-frequency range. Anderson and Wedenberg's audiogram (A, in Fig. 5) is somewhat lower than our average at 2 and 4 kHz, while Miller and Murray's audiogram (M, in Fig. 5) is lower at 0.25, 0.50, 1, and 2 kHz. These slight differences are probably accounted for by noting that the Miller and Murray audiogram is based solely on young animals and the Anderson and Wedenberg audiogram is based on only two animals, both of which may have been young. Since the audiogram of our lightest (and probably youngest) animal is lower than both of the other two audiograms (cf. B in Fig. 3), we do not attach any further significance to the small differences in the three averaged audiograms at frequencies below 4 kHz.

However, the audiograms do differ significantly at high frequencies, and these differences cannot be accounted for by the ages of the specimens. Although there is no way of knowing why Miller and Murray's subjects did not reveal their sensitivity to high-frequency tones, one obvious possibility exists. Miller and

TABLE I. Relation of body weight to sensitivity.

Animal designation	Body weight (in g)	Low-frequency cutoff at 50 dB (in Hz)	Lowest threshold (in dB SPL)	Area of audible field (in dB·oct)
B	330	54	−15	376
A	510	59	−13	308
C	710	63	− 8	284
D	850	170	− 5	231
Mean	600	86.5	−10	300

Murray used an unconditioned response (a cessation in chewing lettuce) as a behavioral indicator that their guinea pigs had detected a sound. This response is similar to the one used in the experiments reported here (a cessation in licking). The difference between the two techniques lies in the contingency we attached to the tone. In our technique, the tone is invariably followed by a shock, with the result that the subject eventually perceives the tone as a warning of impending shock. In the other technique, no shock is delivered—the animal hesitates in his feeding because of the inherent potency of unexpected sounds to elicit an alerting reaction. As noted by Miller and Murray, thresholds indicated by an unconditioned response, such as theirs, are always limited from below by the threshold as indicated by a conditioned response, such as ours. It follows that for a given animal, an audiogram generated by a procedure using conditioned responses will be no higher than one generated by a procedure using unconditioned responses. The only question is: How much lower might it be?

The answer is provided indirectly by Miller and Murray themselves. Their subjects showed a trial-by-trial increase in threshold that corresponded to the number of tones to which they were exposed. That is, the subjects were habituating their response to the tone during the course of threshold testing. Thus, after 10 presentations, the threshold seemed to be higher than after five presentations. This habituation of the response, which appears as an increase in the apparent threshold, is a direct consequence of using an unreinforced response—through repetition without reinforcement the tone loses its potency to elicit a response. Thus, the presence of habituation during testing probably explains why the Miller and Murray audiograms are higher than our youngest animal's audiogram throughout the frequency range. The further question of why the audiograms deviate more at high frequencies than they do at low frequencies is probably also accounted for by habituation. As Miller and Murray point out, among their subjects habituation seemed to proceed faster at high frequencies than at low. Although we have not studied the matter in great detail, we too have evidence suggesting the same conclusion. Therefore, the progressive deviation of the Miller and Murray audiogram from ours at higher frequencies appears to be the joint consequence of (1) a response that is continuously habituating and (2) a response that is habituating faster at higher frequencies than at lower frequencies.

In general, therefore, a comparison of the three sets of results suggests that there is a high degree of agreement at frequencies up to 4 kHz, and disagreement at higher frequencies. We think that the disagreement at high frequencies stems from the high rate of habituation that is a consequence of using unreinforced responses to estimate thresholds. However, we do not think that the disagreement at high frequencies should detract from the remarkable agreement at low frequencies.
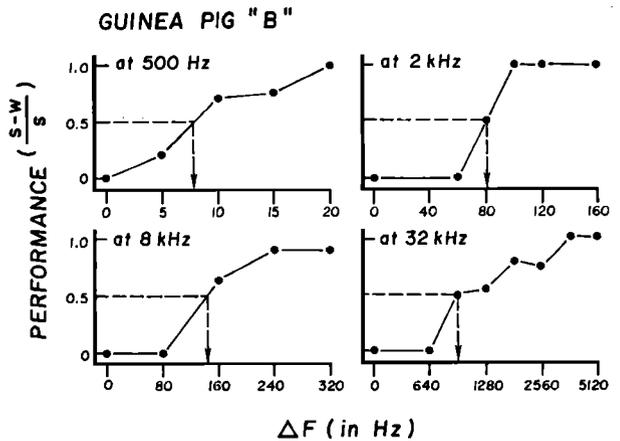
GUINEA PIG "B"

FIG. 6. Typical psychophysical functions obtained in frequency DL tests. Arrows indicate thresholds for 0.50 performance level.

Accepting the age–sensitivity relationship described above, the agreement among the three audiograms at low frequencies is sufficiently close that it may reflect the achievement of a new stage of precision in the history of animal psychophysics.[25]

Beyond the extra measure of confidence that is evoked by independent verification, the close agreement in the results at low frequencies also suggests that there is little reason to choose one technique over either of the others for a quick behavioral assessment of the kind that might be required for physiological or pharmacological research. We are *not* convinced that our technique is faster or easier than the others. The main advantages of the technique used here seem to be (1) it is not restricted to lower frequencies, (2) it minimizes intensity variations due to differing locations of the animal within the sound field, and (3) it allows a large number of trials to be presented without fear of complications arising owing to behavioral habituation or extinction.

C. Guinea Pig Hearing Compared to Hearing in Other Mammals

Table II allows comparison of guinea pigs with other mammals on five parameters of hearing. The table shows that the guinea pig is within one standard devia-

TABLE II. Auditory characteristics of guinea pigs compared with mammalia.

Taxon	High-frequency cutoff (in kHz)	Low-frequency cutoff (in kHz)	Lowest threshold (in dB)	Best frequency (in kHz)	Area of audible field (in dB·oct)
Guinea pig	46.5	0.086	−10	8	300
Mammalia[a] average	57.62	0.409	−2	10.1	250
(±SD)	(0.806 oct)	(2.76 oct)	(10)	(1.15 oct)	(85)

[a] The mammalian averages and standard deviations are based on samples that are within 5% of the true distribution of mammalian genera per order except for primates (overweighted with eight genera instead of one) and rodentia (underweighted with three genera instead of seven).

TABLE III. Frequency difference thresholds ($\Delta F/F$; $\bar{X}=24.4$, $S=16.7$).

	0.125	0.25	0.5	1	2	4	8	16	32	42	Average
					kHz of standard						
Man[a]			0.007	0.004	0.002	0.003	0.004				0.004
M. Mulatta[b]			0.008	0.009	0.006	0.009	0.008	0.009			0.008
Seal[c]			0.014	0.012	0.015	0.014	0.018		0.010	0.010	0.012
Cotton rat[d]					0.015	0.020			0.019	0.010[j]	0.016
Bush baby[e]	0.040		0.014		0.012	0.012	0.006		0.022		0.018
Cat[f]	0.055	0.032	0.017	0.008	0.007	0.010	0.012	0.015	0.017		0.019
Hedgehog[g]										0.024	0.024
Treeshrew[e]			0.036	0.025	0.021	0.031	0.045			0.030	0.031
Guinea pig	*0.030*	*0.050*	*0.016*	*0.040*	*0.040*	*0.040*	*0.017*	*0.055*	*0.040*	*0.040*	*0.035*
Opossum[g]										0.036	0.036
Wild mouse[h]						0.056		0.031		0.023[j]	0.037
White rat[i]				0.060		0.070				0.060	0.063

[a] Ref. 27. [c] Ref. 29. [e] Refs. 12 and 13. [g] Refs. 10 and 11. [i] Ref. 33.
[b] Ref. 28. [d] Ref. 30. [f] Ref. 31. [h] Ref. 32. [j] These values are for 64 kHz.

tion of the mammalian mean for each parameter. Since the mammalian means and standard deviations are based on reasonably representative samples, it can be concluded that the guinea pig is an unexceptional mammal.[26,16]

We have shown elsewhere that the high-frequency cutoff in mammals is highly correlated with the functional distance between the two ears.[26] Using the regression equation derived from other mammals and an interaural distance of 55 mm, the expected high-frequency cutoff in guinea pigs is 51.4 kHz. Table II shows that the cutoff is, in fact, 46.5 kHz—only 1/7 oct below the expected value. Thus, even in this very indirect relationship the guinea pig is a good approximation to a "typical" mammal.

D. Frequency Discrimination

Two guinea pigs (A and B) were tested for frequency DLs after their audiograms were complete. Representative psychophysical functions are shown in Fig. 6. It can be seen that the curves are quite steep, but steeper at middle frequencies than at either extreme. Although the psychological and physiological significance of this detail is debatable, for present purposes, it means that
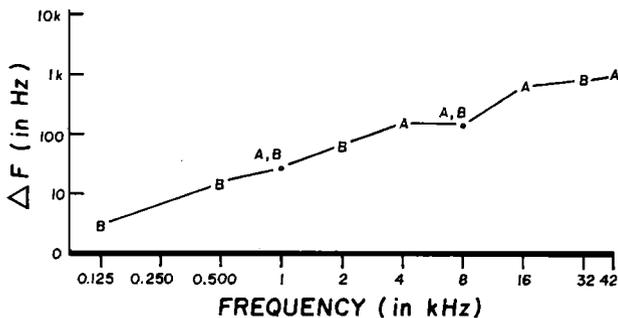
the frequency DLs at extreme frequencies are less precise than at middle frequencies. Nevertheless, the relation of ΔF to F is nearly linear, and there is close agreement at the two frequencies at which both guinea pigs were tested (Fig. 7).

The value of the Weber fraction ($\Delta F/F$) averages 3.5% over the frequency range from 125 Hz to 42 kHz. This value is higher than the value for cats, monkeys, bush babies, wild rats, seals, and humans; but lower than the value for white rats and, apparently, wild mice, (as shown in Table III[10–13,27–33]). Nevertheless, $\Delta F/F$ for guinea pig is within one standard deviation of the mammalian mean. Since the measurement error is reasonably small for all of the animals (in monkey and man it is very small), the difference in average frequency DL among the mammals listed in Table III probably is not a matter of chance. However, in contrast to behavioral absolute-threshold procedures, behavioral frequency-DL procedures do not evoke a high degree of confidence. For animals, frequency discrimination is always more difficult to learn and to retain, apparently requiring a much higher level of vigilance for stable performance. For these reasons, we would hesitate to cite this or any other set of behavioral frequency DLs as crucial evidence either for or against a particular theory of frequency discrimination.

FIG. 7. Frequency DL (ΔF) as a function of frequency. $\Delta F/F$ is 3.5%.

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