AUDITORY SENSITIVITY OF THE RINGTAIL LEMUR (LEMUR CATTA)

by

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A Thesis

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To

Jane Converse Mitchell

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Introduction

The auditory sensitivity of animals throughout the phylogenetic scale is basic knowledge in audition. A number of species within the primate order have been studied. However, the studies have been largely limited to the anthropoidea suborder. Very little information on the hearing capabilities of primates in the prosimii suborder is available.

The prosimii suborder is important because their ancestors diverged from ours 50 to 60 million years ago, long before the evolution of the New or Old World monkeys. This suborder, therefore, provides a third independent evolutionary line of primates. Due to the anatomical similarities of living lemurs to fossil remains, lemurs have been called "living fossils" (Buettner-Janusch, 1966). For this reason the lemur represents the common ancestor of all living primate species better than any monkey taxa (Jolly, 1966).

In a recent article, Masterton, Heffner and Ravizza (1969) attempted to reconstruct the evolution of human hearing. They used behavioral audiograms from a number of mammals in this reconstruction. The present study will provide lemur data pertinent to Masterton's reconstruction.

Behavioral audiograms of the lemur will add one type of quantitative information about their hearing capabilities. This quantification goes beyond naturalistic observations such as the following from a field study: "They (lemur) did not seem to hear the approach of other animals either more or less quickly than I" (Jolly, 1966). Yerkes and Yerkes (1929) gathered many observations from naturalists and hunters on chimpanzee hearing abilities and concluded that the auditory acuity was unknown. It remained for later workers to specify the auditory acuity with behavioral audiograms (Elder, 1934, 1935; Farrer and Prim, 1965).

The prosimii suborder includes animals such as the tree shrew*, lemur, loris, potto, galago and tarsier. Four studies of auditory sensitivity of prosimians are available (three became available after this study was in progress). Heffner, Ravizza and Masterton (1969a, 1969b) have reported thresholds on the tree shrew (Tupaia glis) and the bushbaby (Galago senegalensis). Heffner and Masterton (1970) have reported thresholds for the slow loris (Nycticebus coucang) and potto (Periodicticus potto). Mitchell, Gillette, Vernon and Herman (1970) have reported thresholds on the lemur (L. catta, L. macaco, L. fulvus).

Purpose of the Present Experiment

The purpose of this experiment was to obtain pure tone audiograms on an expanded sample of ringtail lemurs. The shock avoidance method used was an improvement over a previously used method. The audiograms extend from 0.1 to 40 kilohertz (kHz), with thresholds at .1, .2, .5, 1, 2, 4, 8, 15, 25, 32 and 40 kHz.

Method Considerations

The consideration of methods is a very important and essential feature of the present study. For the present, however, these may be characterized as the selection of a behavioral response, the threshold criteria and the control measurement of the sound stimulus.

Selection of Behavioral Response

Threshold determination depends on a discriminated behavioral response of some type. This highly artificial behavior involves learning and cannot be entirely separated from "natural" lemur behavior. Several general statements

^{*} The inclusion of the tree shrew in the Primate Order (and hence in the prosimii suborder) is currently under debate.

about lemur behavior can be made. The lemur, including the ringtail, does poorly on primate "intelligence tests" (Kluver, 1933; Jolly, 1964a, 1964b; Stevens, 1965). Jolly (1966) states, "It (lemur)...learns with difficulty to look into containers for food, to pull in food on strings, or even to reach with its hand into small bottles to pull out a reward." These observations have been generally supported by observations in our laboratory. For example, extensive training (2000 trials or more) were needed in an appetitive situation for these animals to learn a discriminated bar press to a tone.

In order to obtain reliable estimates of threshold the behavioral response must be controlled by the stimulus with a high degree of reliability. In the threshold testing situation one can consider two classes of behavior, the conditioned response and any behavior other than the conditioned response (see Figure 1). The conditioned response is defined operationally when a bar press registers a response on a counter. The conditioned response occurrence or nonoccurrence must be controlled by the stimulus. This is represented in Figure 1 where two behavioral classes and two stimulus conditions are shown. When the stimulus conditions control the behavioral class with a high degree of certainty the misses and false positive responses are minimized. Obtaining this control has been a persistent problem with many animal species (Culler, Finch, Girden and Brogden, 1935; Dworkin, Katzman, Hutchinson and McCabe, 1940; Fujita and Elliott, 1965). Mitchell et al. (1970) have found the ringtail no exception. As mentioned above, extensive training was needed to obtain a discriminated bar press. This discrimination tends to "break down" when threshold is approached; this results in many false positive responses.

Ideally, direct control over both the miss rate and the false positive rate will yield the best estimates of threshold. The single lever avoidance method of Clack and Herman (1963) directly controls (with shock) both misses and false positives.

	Tone On	Tone Off
Conditioned Response	Correct response	False positive
Other Behavior	Miss	True negative

Figure 1. Stimulus conditions and behavioral classes during threshold testing.

They obtained auditory thresholds on the <u>Macaca mulatta</u> which were at least as sensitive and reliable as other behavioral techniques. For these reasons, their method was chosen.

Threshold Criteria

Responding at or near threshold is a difficult task, and false positives are common. False positives (equivalent to intertrial interval responses) are usually ignored. However, if they occur frequently they tend to reduce the confidence one can have in the data. For this reason false positive responses were counted throughout all threshold determinations.

In obtaining thresholds it is desirable to present both ascending and descending series of stimuli (Seiden, 1957; Wollack, 1963). The tracking technique of Clack and Herman (1963) contains elements of both series. Tracking continued about threshold until specific criteria had been met and then a threshold was calculated. Threshold was defined as a 50% correct responses.

Control and Measurement of Sound Stimuli

Imperative in a quantitative study of auditory sensitivity is the use of calibrated and controlled sound pressure levels. As Wever (1959) and Vernon (1967) have mentioned, a number of animals have been studied qualitatively, but very few studies have yielded quantitative data. This is due primarily to the use of unspecified calibration procedures.

In calibrating pure tones both the absolute level and the variability in the sound field must be measured. The variability is the result of interactions of transmitted and reflected waves. The resulting standing wave pattern produces large differences in sound pressure at different positions in space. The standing wave pattern in this study was reduced by using sound absorbant corrugated foam rubber (3 1/2" thick) on the inside walls of the sound attenuating chamber.

However, variability at different positions was measured and reported (see Appendix 1).

The sound was measured with a B and K calibrated microphone. The microphone was attached to a simulated animal in the testing cage to approximate the pertubations that the lemurs produced during actual testing. The simulated lemur was a life-size paper mache model covered with artificial fur. The sound levels were measured at 23 positions, and the variability reported at each frequency (see Appendix I). Figure 2 illustrates the variability in the sound field with position for one frequency, 40 kHz. The variability for the behaving animal is probably less because he is sampling the sound field with both ears, hence two positions, on any given trial.

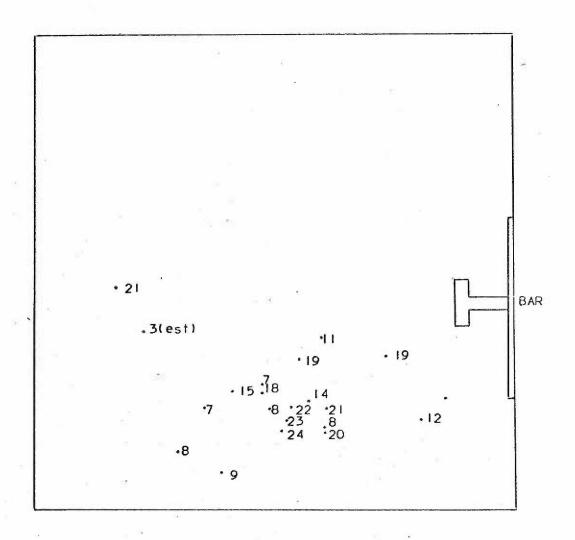
Attenuator settings (db) given in the raw data were converted to db of sound pressure relative to 1 dyne/cm² using the calibrations given in appendix 1. The mean value of the 23 positions at each frequency was used to convert from db attenuation to db re 1 dyne/cm². For example, the threshold for lemur No. 674 at 100 Hz on 2/13/70 was 11 db attenuation (see Appendix III). Seven db attenuation at 100 Hz produced -20 db re 1 dyne/cm² of sound pressure (see Appendix I). Therefore, 11db attenuation is equal to -24 db re 1 dyne/cm² and the threshold was plotted at -24 db at 100 Hz. The reference level of db re 1 dyne/cm² was chosen by convention.

Subjects

Eight ringtail lemurs, seven males and one female, served as subjects.

Consideration of their birth records, weights, breeding behavior and dentition indicated seven were adult and one was adolescent (see Table I). Lemurs No. 2023 and 2024 had been used in previous studies but all others were naive.

Figure 2. Sound field variation at 40 kHz. Top view of positions measured and db attenuation necessary to produce -20 db re 1 dyne/cm 2 of sound pressure at that point.



SPEAKER

Number	674	675	2023	2024	2311	3189	4059
Sex	male	male	male	male	male	male	female
Age (yr)	> 7	> 7	> 5	> 5	4	3	2

Table 1. Age and sex for all animals.

All lemurs were given an examination before threshold testing began.

The external auditory meatuses were free from any noticeable pathologic changes and the eardrums appeared intact and reflected light in a normal way. None of the animals could be suspected of having ototoxic drug effects.

Apparatus

A diagram of the apparatus is shown in Figure 3. The behavioral logic controlled the lights and tone, recorded responses and delivered shock according to the behavioral program. The oscillator, amplifiers, attenuators, etc. produced a pure tone stimulus with no onset transients or other noise. ** The output of the speaker was measured with a calibrated microphone (half-inch condenser) and a wave analyzer.

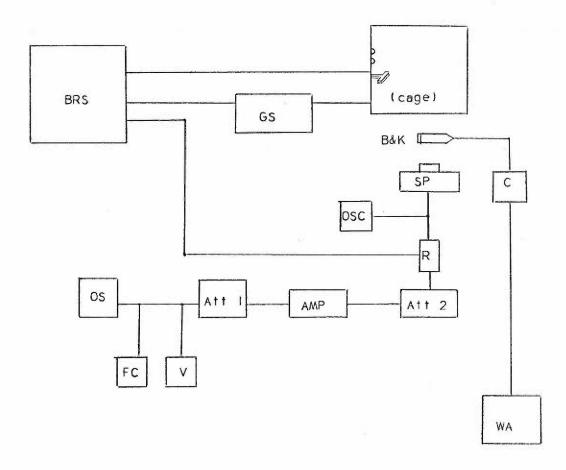
Procedure

Summary

- 1. Adaptation to the laboratory and training cage.
- 2. Escape training with tone, red light and shock. An escape response is a bar press in the presence of red light or shock.
- Avoidance training to criterion of 90% avoidance on two consecutive days (50 trials per day).

^{**} Noise could not be detected by careful listening, with a calibrated microphone and wave analyzer or on an oscilloscope.

Figure 3. Apparatus to produce, control and measure pure tone stimuli.



OS = General Radio oscillator, Type 1309A.

FC = Hewlett Packard frequency counter, 5212A.

Att I = Hewlett Packard attenuator, 3500.

V = Ballantine, electronic voltmeter, Model 300.

AMP = Dynaco Mark III amplifier.

Att 2 = Custom made attenuator, 22 db constant.

R = Raytheon raysistor, CK1123.

OSC = Tektronic oscilloscope, Type 503.

SP = Western Electric, 555W polarized speaker.

B&K = Bruel & Kjaer calibrated microphone.

C = Bruel & Kjaer cathode follower.

WA = General Radio wave analyzer, 1900-A.

BRS = BRS electronics 200 series logic.

GS = Grason-Stadler, 700 shock generator.

- 4. Introduction of two types of trials. (1) White light, Blank trial.
- (2) White light + tone, Tone trial.
- Training to 90% avoidance and less than ten per cent responses duringBlank trials.
 - 6. Conditions of elimination of the white light.
 - 7. Generalization to all frequencies.
 - 8. Threshold estimation by the tracking technique.
 - 9. Tracking until threshold estimate complete.
- Threshold estimates collected over days, until these estimated values stabilized.

Detailed Procedure

- Adaptation to the laboratory and training cage was accomplished by keeping each animal in the laboratory for several days. Adaptation to the training cage began with ten-minute periods which were gradually lengthened as urination and defecation stopped.
- 2. Escape training began with a large bar (3", T-shaped). Usually the animals investigated this bar and tended to press on it at the first encounter. Training began with ten-second tones followed by a pulsing red light and shock (each 1/2 sec.). Pulsed shock was used to facilitate avoidance (D'Amato, Keller, DiCara, 1964). The tone, with the alternating red light and shock continued until a bar press was made; this terminated all stimuli. Diagrammatically this is represented as follows:

Escape Training

Tone		
Red light		ПП
Shock		П_Г
Response	N 200	

Escape training began with a variable interval of seven to 40 sec. with an average of 30 sec. between tones (hereafter, VI 30). The method of successive approximations (shaping) was used to obtain the first few escape responses. The shock intensity was initially 0.05 millampere, below what the lemurs would visibly respond to, and was gradually raised (to .4-.8 ma). Beginning with low intensity shock was thought to prevent freezing and/or violent jumping and thus aid the acquisition of the escape response (D'Amato, Fazzaro, and Etkin, 1967). Usually escape responses were made within the first or second session (25 to 50 trials per session). After a few sessions (25 to 175 trials) a smaller bar, less likely to be accidentally pressed, was used (1 1/4", T-shaped).

3. Avoidance responses were occasionally made early in training but generally appeared after short latency escape responses had developed. A VI 30 schedule was continued until 50% avoidance was maintained for two consecutive days.

A VI 20 schedule was used until 90% avoidance was achieved on two successive days (usually 50 trials per day). If this 90% criterion was not reached in 500 trials or ten days of training the animal was not trained further. Lemurs No. 679 and No. 3183 were dropped from training because they did not reach this criterion.

4. The two types of trials to be used in final testing were introduced by aperiodic presentation of the white light. The white light was introduced in this

manner to habituate out startle and/or orienting reflexes, as the 90% avoidance criterion was approached. After the 90% avoidance criterion had been reached the white light accompanied each Tone trial as well as Blank trials.

Initially Blank trials were introduced infrequently (17 to 38% of the trials) but this appeared to confuse the animals and therefore the last two animals trained (No. 2311 and 4059, see Table 2) were introduced immediately to frequent (50%) Blank trials. The sequence of behavioral programs for each animal is shown in Table 2. The shock intensity for responses during Blank trials (false positives) was initially 0.05 ma and was gradually raised until it equalled the Tone trial shock intensity (.4-.8 ma for misses). During threshold testing the shock intensity for misses and false positives was equal.

	Programs Available						
Animal No.	VI 30 (0%)	VI 20 (0%)	VI 20 (16%)	VI II (38%)	VI 15 (50%)		
674	X	X	X	X	X		
675	X	X	X	X	X		
679	X	X					
2023	X	X	X	X	X		
2024	X	X	X	X	X		
2311	×	X			X		
3189	X	X					
4059	X	X			X		

Table 2. The sequence of programs used (X) for each lemur. (VI 20, 16% is a variable interval schedule with an average of 20 sec. between trials and 16% of the trials are Blank trials.)

5. Training on VI 15 (50%) had the goal both of 90% avoidance during
Tone trials and 10% or fewer responses during the Blank trials. This criterion
was not reached by two animals (No. 674 and No. 2024) within 2500 Tone trials,
but because their avoidance responses were over 90%, the 10% false positive

requirement was suspended. Frequency generalization and threshold estimation were begun when the above criterion had been reached or suspended.

- 6. Three animals (No's. 674, 675 and 2024) had consistently high false positives and after 4500 Tone trials the white light was eliminated during all or part of threshold testing. The Blank trials (unsignaled to the animal because the white light was eliminated) were still presented and the false positives occurring during these periods were counted exactly as in the other animals. Eliminating the white light "worked" for two of the animals (No's. 674 and 2024) as they reduced their false positive rate (58% to 42%; 45% to 21% respectively) and thresholds were obtained. Lemur No. 675, however, continued to exhibit high false positives (over 100%) and only rough estimates of threshold were obtained.
- 7. Frequency generalization was accomplished by presenting tones at successively higher and lower frequencies than the initial training tone.

 Presentation of these tones continued until 90% avoidance was seen at all frequencies. This procedure usually took three to ten sessions and about 30 Tone trials at each new frequency.
- 8. Threshold estimation was accomplished using the tracking method as follows: Each successful avoidance (hit) reduced the tone intensity by one step (5 db initially, 2 db subsequently) and an escape (now called a miss) increased the intensity by one step. The stimulus intensity was unchanged by any other response contingency.

The initial threshold estimate, at a given frequency, used 5 db steps and a modification of the above tracking procedure. During tracking, when the first miss (escape) occurred, the intensity remained unchanged for the next three Tone trials regardless of the responses that occurred. After this plateau of three presentations at the same intensity, tracking was resumed and proceeded normally. When a total of three misses out of five or fewer Tone trials were recorded at a

given intensity, the shock was suspended 5 db above that intensity. Once the shock suspension level had been set it was not free to move to a higher intensity regardless of the number of misses that occurred. The shock suspension level moved to lower intensities if three hits were recorded in five or less Tone trials or if a ratio of hits/misses equalled .6.

After this initial run, using 5 db steps, a threshold (50% hit) was calculated. Calculations were done simply by plotting the % Hit versus the db Attenuation as shown for the data point in Figure 4. The threshold in Figure 4 is estimated at 61 db Attenuation (and must be converted to db re 1 dyne/cm²). The shock suspension level for the next session would be 5 db above this point.

The next session at the same frequency used the regular tracking procedure and steps of 2 db. As above, if during a session, the equivalent of 3/5, hits to Tone trials, were recorded below the previous threshold estimate the shock suspension level was changed appropriately. Using this method the shock suspension point either remained at the level set by the previous threshold estimate or moved lower. It was not free to raise during a session. At the end of each day a threshold estimate was calculated and served for the next session at that frequency.

Reversals in the plot of % Hits versus db Attenuation were found occasionally. Examples of this are shown in Figure 5. The threshold estimates (plotted lines crossing to below the 50% hit rate) were included in the final mean threshold calculation if the reversals were 6 db or less apart. Thus, the threshold estimate in Figure 5A would not be included in the final calculation but 5B would be included.

 Threshold estimates were collected as described above. At a given frequency, tracking proceeded until the following criteria were met.

Five tone presentations were made at each of three consecutive intensities and the lowest intensity had less than a 50% hit rate.

Figure 4. Threshold estimate on a given day, called 6l db. Data from $^{\#}2023$ at 1 kHz, 12/29/69. Note: Higher attenuation is lower intensity.

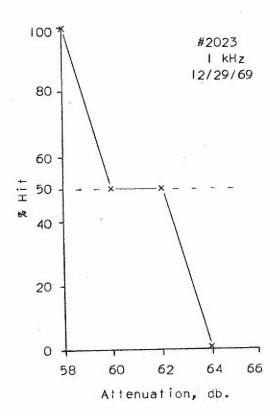
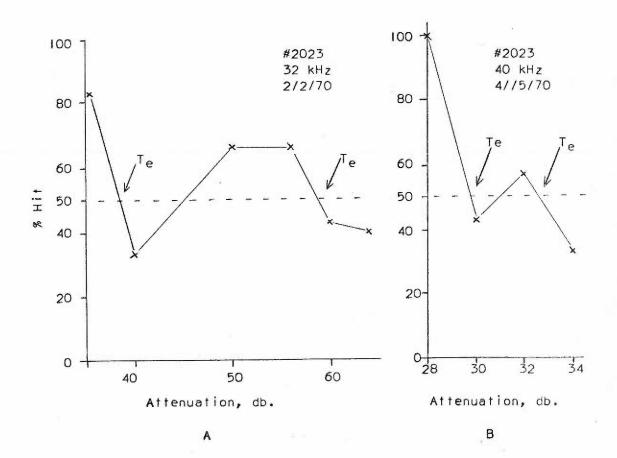


Figure 5. Reversals shown in threshold estimates. A. Threshold estimates are 39 and 59 db attenuation. These are more than 6 db apart and are therefore not included in the calculation of mean threshold. B. Threshold estimates are 30 and 32 db and are therefore included in calculating the mean.



Ten tones had been presented at any one intensity level.

When a criterion was met tracking continued until the end of the next ascending series (the next hit). This equalization of ascending and descending series avoided biasing the data in favor of either series.

10. Threshold estimates were calculated and plotted each day. When this plot of threshold estimates had three thresholds on different days within six db of the lowest threshold estimate at that frequency, the data for that frequency were considered complete. A plot of thresholds over days is shown in Figure 7.

Results

Thresholds were estimated each session by procedures 8 and 9. The data, as mentioned above, yielded a plot (e. g., Figure 6) from which a threshold estimate was calculated. The threshold estimates were plotted on a graph of intensity over days as shown in Figure 7 (Procedure 10). This plot of threshold over days allowed one to determine quickly whether the animal was shifting its threshold from day to day. As can be seen in Figure 7A, No. 4059 shifted her threshold dramatically at 15 kHz. This was common at frequencies above 8 kHz and was thought to be due to the learning of highly directional listening behavior. Figure 7B, for 2 kHz, shows very little shift in threshold estimates over days, and is characteristic for the lower frequencies.

When the threshold estimates over days had stabilized, a cut-off line was drawn 10 db above the most sensitive threshold estimate. This is shown in Figure 7 as "+10 db cut-off" line. The mean value of all threshold estimates on or below this cut-off were reported as the final threshold. After threshold stabilization

Figure 6. Plot of hits and false positives in threshold estimate. (Data from $^{\#}2023$, 2 kHz, 2/II/70).

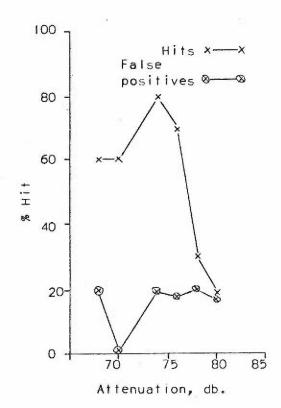
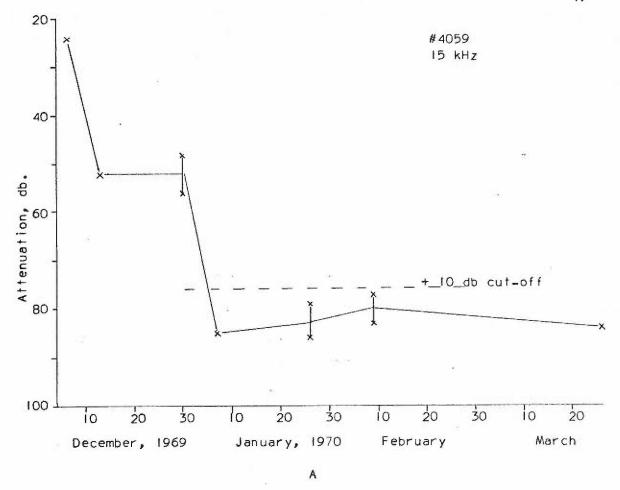
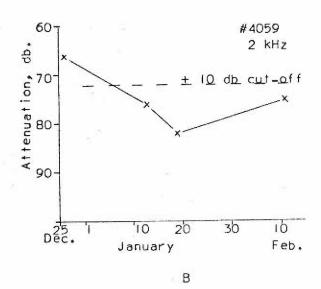


Figure 7. Threshold estimates plotted over days. This allows for detection of shifting thresholds. These data are representative for the respective frequencies.





there were very few threshold estimates above this +10 db cut-off line.*** Only for lemur No. 674 at one frequency (40 kHz) was it necessary to deviate from this procedure. Animal No. 674 at 40 kHz had continued high false positives and a large range of variability from day to day. In this case all data collected at 40 kHz were used to calculated the mean reported.

Audiograms of individual lemurs are shown in Figures 8 through 13. The mean value and ranges are shown for each animal. Figure 14 is a plot of the mean values of the individual animals (except estimated data of No. 675). A mean value of this conglomerate is shown in Figure 15 in comparing this study to the previous study as well as the lemur with other species of primate (see Figure 17).

Discussion

Lemurs: Comparison of previous and present studies

The average and range of the data from five lemurs in the present study are plotted with the average and the range from the previous study (Mitchell et al., 1970) in Figure 15. This plot suggests that the present study has yielded lower thresholds. This suggestion is supported by lemur No. 2023 which was included in both studies; the resultant audiograms for this animal from each study are shown in Figure 16.

The differences in Figure 15 were analyzed using a Mann-Whitney U test. At 100 Hz and 40 kHz the values are not significantly different (U = 15, p > .1; U = 5, p > .1, respectively). A t-test was not used because the variances were not equal. All other frequency points are different at or beyond the .04 level of significance (200 Hz and 25 kHz, .04; all others .009 or beyond). Thus it is concluded that elevated thresholds were obtained in the previous study at all

^{*** 195} threshold estimates were within the +10 db cut-off line and 18 estimates fell outside of this cut-off and were therefore not included in calculation of the mean thresholds.

Figure 8. Audiogram of lemur no. 674.

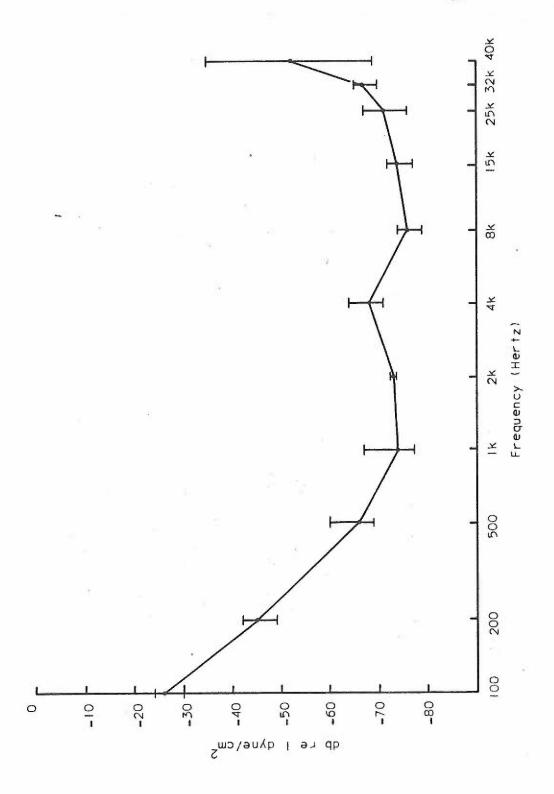


Figure 9. Estimated partial audiogram of lemur no. 675. Range values are not shown due to incomplete data (see Procedure, p. 14).

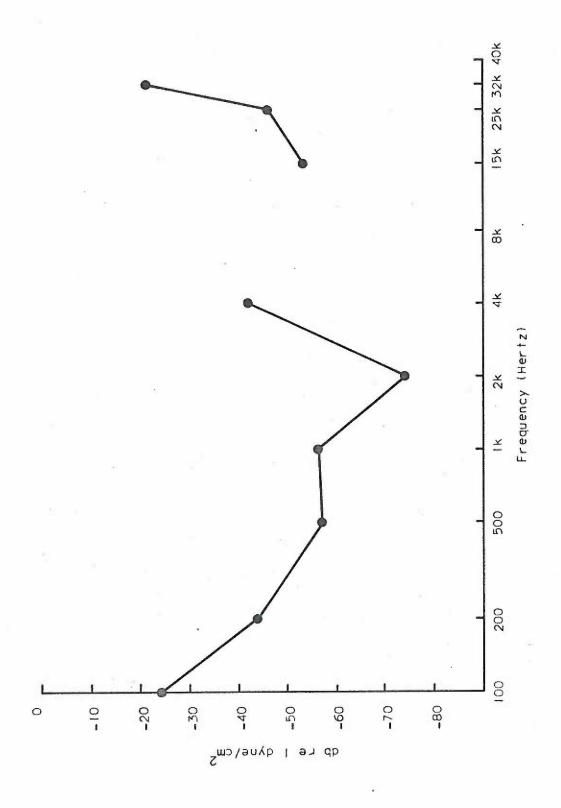


Figure 10. Audiogram of lemur no. 2023. Mean and ranges are shown.

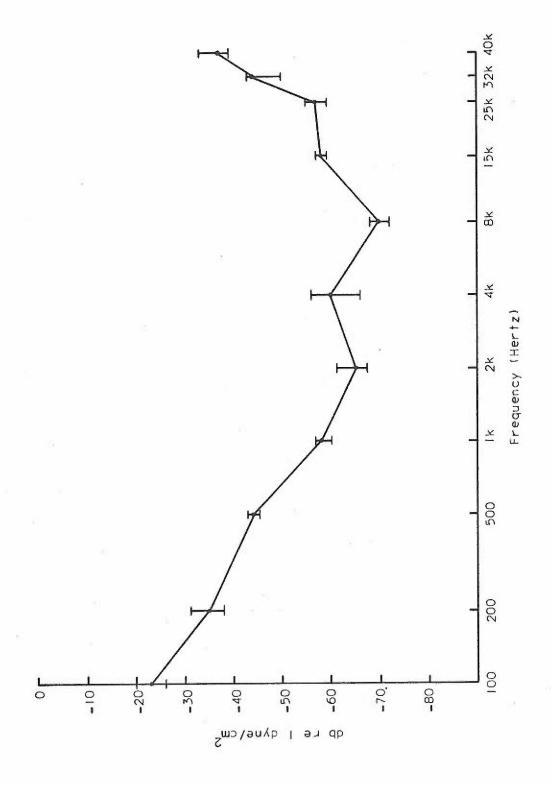


Figure II. Audiogram of lemur no. 2024. Mean and ranges are shown.

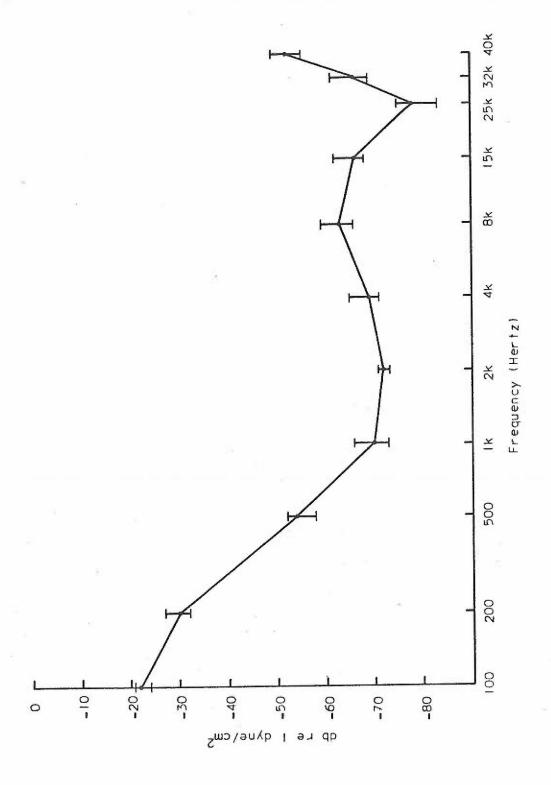


Figure 12. Audiogram of lemur no. 2311. Mean and ranges are shown.

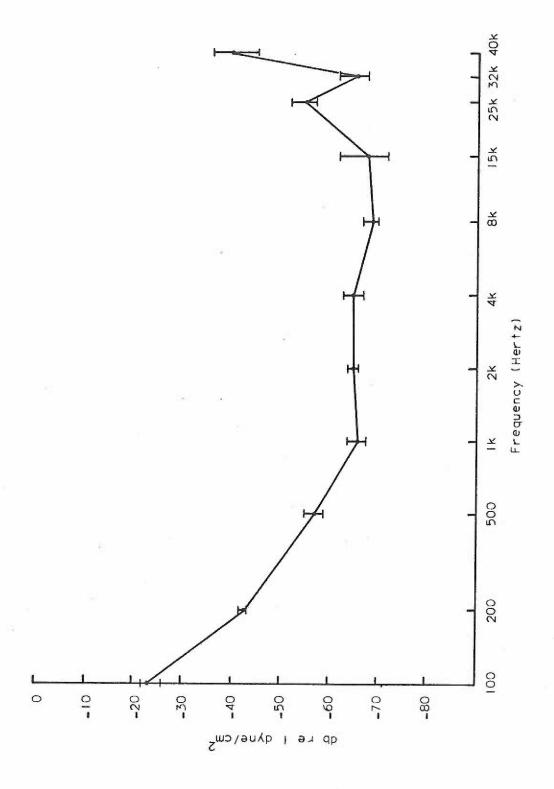


Figure 13. Audiogram of lemur no. 4059. Mean and ranges are shown.

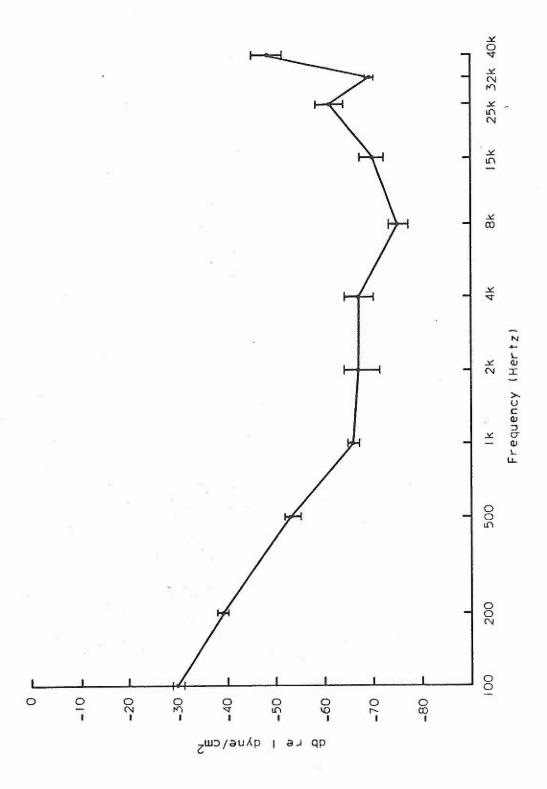


Figure 14. A plot of the mean values of all complete lemur audiograms.

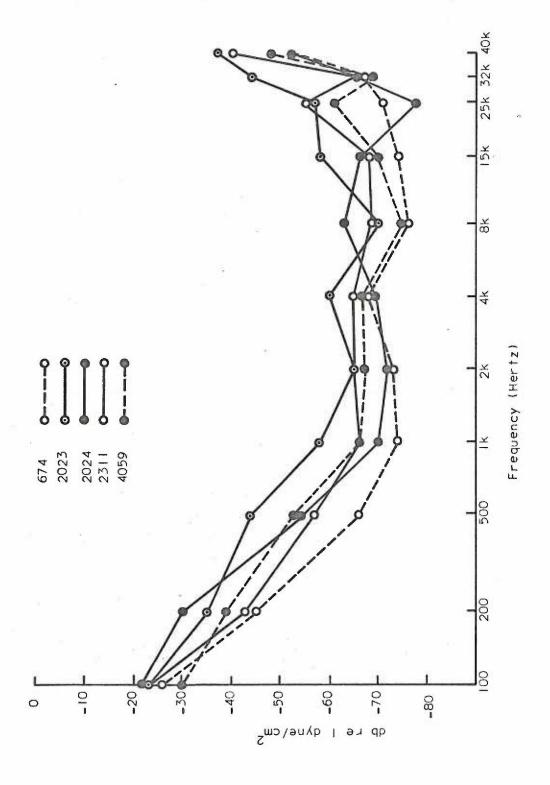


Figure 15. Combined audiograms from the present study and the previous study (Mitchell et. al., 1970). The range for some points in the present study are off-set. Lemur #2023 is included in each study.

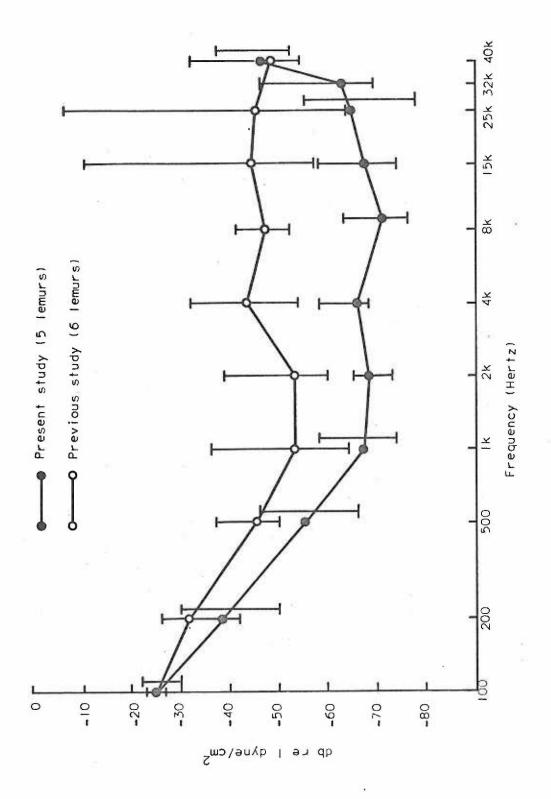
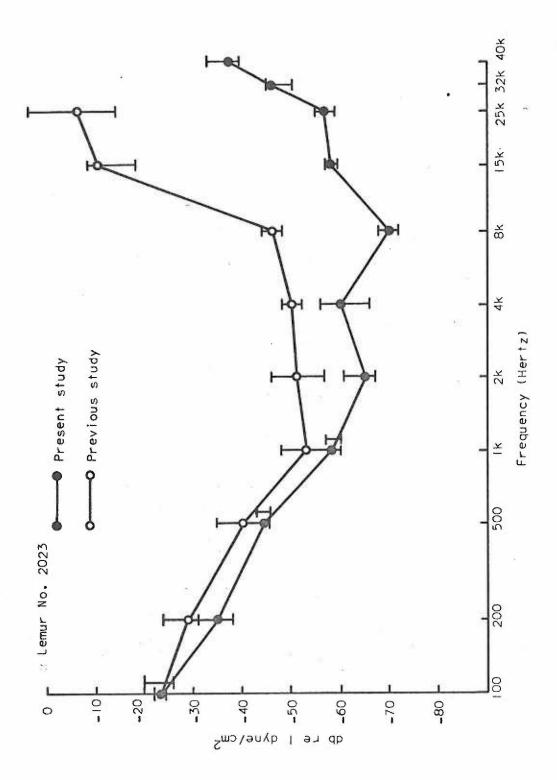


Figure 16. Lemur No. 2023 which was included in the previous as well as the present study.



frequencies except 100 Hz and 40 kHz.

In considering the differences between the previous and present study, several factors seem important: (a) speaker placement, (b) practice effects, (c) methods.

(a) Speaker placement. The speaker location was changed from directly overhead (previous) to facing the animal on a horizontal plane. This might introduce differences in the sound field. Table 3 shows the previous and present sound field variations. There is only one frequency, 15 kHz, where the sound field variation could have explanatory power and this would account for only a small portion of the differences seen between the studies.

Frequency (Hertz)	Previous study (range in db of 12 positions)	Present study (range in db of 23 positions)
100	6	8
200	4	7
500	4	. 7
1 K	6	6
2 K	10	10
4 K	4	8
8 K	8	13
15 K	25 (8)	13
25 K	16	20
32 K	*	21
40 K	19	21

Table 3. Sound field variability at various positions within the testing cage. At 15 kHz one deviant point produced the 25 db range, 11 positions were within an 8 db range.

* not measured in the previous study.

Changing the speaker position would also change the direction of the "pinna shadow" for high frequency sounds and thus might bias the data. One

would expect the greatest "pinna shadow" effects at 40 kHz but this is one of the points where the audiograms are not different (see Figure 15). Thus the sound field variation and/or "pinna shadow" do not seem to be of value in explaining the differences seen between the previous and present study.

(b) Practice effects. One might suspect that inadequate frequency generalization could have produced elevated thresholds in the previous study. However, in the previous study the animals were initially trained on tones of 1 to 3 kHz with extensive training (1000 trials) from 1 to 10 kHz, and it is in this area that the elevated thresholds were obtained (see Figure 15). This would not be expected if frequency generalization were an explanation. In addition, the extreme frequencies 100 Hz or 40 kHz should logically show the largest frequency generalization effect and thus the greatest difference between studies. The fact that the audiograms agree at both 100 Hz and 40 kHz suggests that the differences are not due to inadequate frequency generalization. Thus the differences between the previous and present study do not appear to be due to inadequate frequency generalization.

Another effect of practice might be the learning of highly directional listening behavior. Directional listening behavior would be extremely important at the high frequencies. When looking at No. 2023's two audiograms in Figure 16, directional listening would seem a possibility. However, looking at the group of animals (Figure 15) this would seem less likely due to the agreement at the highest frequency, 40 kHz.

(c) Methods. Differences due to methods and response contingencies might account for some of the differences seen. One difference in the methods is the presentation of stimuli. In the previous study the tones were presented at random intensities and in the present study a tracking procedure was used. These differences in the method of stimuli presentation are not thought to have affected

the thresholds obtained (Woodworth and Schlosberg, 1954; Stebbins, 1970).

One can also consider the response contingencies. The present method could be considered an aversive method (shock avoidance) and the previous method appetitive (food reward). Two studies have produced data which bear directly on this point. Fujita and Elliott (1965) and Heffner et al. (1969a) used both appetitive and aversive methods in obtaining thresholds. Fujita and Elliott (1965) used a single lever shock avoidance and a single lever reward methods on the same individual animals (rhesus, squirrel and cynamolgus) and concluded that there were no differences in the thresholds obtained. Heffner et al. (1969a) obtained thresholds in the tree shrew testing two animals with shock avoidance (double grill box) and two others with conditioned suppression (licking for food reward). Their results likewise suggest no difference between animals attributable to the method used.

In spite of the negative findings in these published papers it is thought that the elevated thresholds in the previous study were largely a result of the method. In the previous study the method required deprived animals to press a bar when a tone was present to receive a food reward. If they pressed the bar at the wrong time they received a shock. In the present study they pressed the bar to avoid shock when they heard a tone and likewise were punished with shock if they anticipated and pressed when no tone was present.

In the previous study generally higher shock levels were used (0.5 to 1.6 ma) as compared to 0.4 to 0.8 ma used in the present study. In the previous study misses (which produce elevated thresholds) were under only indirect control and resulted in reward forfeit. In the present study misses (failure to avoid) resulted in shock. Thus the reward forfeit for misses did not allow adequate control of the miss rate, when false positives were being punished, which results in elevation of thresholds. Neither of the studies mentioned above punished

false positives with shock, and thus did not have this difficulty.

Lemurs and other primates

Masterton et al. (1969), in an original and noteworthy paper, discussed several features of mammalian hearing abilities as related to their recency of ancestry to man. Table 4 presents the thresholds for several species at low frequencies. Generally the lemur data agree with other prosimian data. The low

Investigator	Animal	Frequency (Hertz)			
		250	500	1 k	
Ravizza et al., 1969a	oppossum	> 80	72	62	
Ravizza et al., 1969b	hedgehog	69	72	62	
Heffner et al., 1969a	tree shrew	55	27	30	
Mitchell et al., 1970	lemur	39(est.)	31	21	
Present study	lemur	32 _(est.)	19	7	
Heffner et al., 1969b	bushbaby	43	25	28	
Heffner and Masterton, 1970	slow loris	35 32	30 30	23 18	
Fujita and Elliott, 1965	rhesus squirrel monkey	15 20	7 10	6	
Dalton, 1968	rhesus	_	4	12	
Behar et al., 1965	rhesus	13	8	7	
Stebbins, 1966	Macaca irus	25	17	6	
Sivian and White, 1933	Man	16	8	2	

Table 4. Absolute thresholds in db re. .0002 dyne/cm 2 for low frequency tones.

frequency sensitivity of the tree shrew, lemur, bushbaby, loris and potto appear similar, being more sensitive than primitive mammals (represented by the hedgehog and opossum) and less sensitive than other primates.

Comparing the prosimii and anthropoidea suborders at the low frequencies, 250 Hz, 500 Hz and 1 kHz, using the Mann-Whitney U on individual animals from the above studies (Table 4) shows that they are different at or beyond the .002 level of significance. These findings lend support to Masterton et al. (1969) conclusion that low frequency sensitivity is not a primitive mammalian characteristic and further that it is <u>not</u> a primitive primate characteristic.

Figure 17 shows averaged data for three species of prosimians. The lemur (present study), galago (Heffner et al., 1969b) and the tree shrew (Heffner et al., 1969a) are shown. The lemur appears to be more sensitive than other prosimians at the low frequencies (below 2 kHz) and the audiograms converge at 4k, 8k and 32 kHz.

The high frequencies need to be explored in greater detail before differences can be fully discussed. Especially important is the delivery and calibration of high frequency sound. Vernon, Dalland and Wever (1966) have an excellent discussion of the care necessary for the control of high frequency sound. Their data show variations of nearly 15 db at 25 kHz and over 20 db at 40 kHz using sophisticated techniques and near free-field conditions. Free-field conditions, such as attempted in the present study, are thought to minimize variability at the high frequencies. As a tentative conclusion the lemur does not appear to be the most sensitive of the prosimians at high frequencies. However, the broad sensitivity of the lemur from 1 k to 32 kHz appears greater than the other prosimians.

Further comparisons among the primates are shown in Figure 18. The lemur (representing the prosimian), marmoset (New World monkey), macaca (Old

Figure 17. Prosimian hearing thresholds.

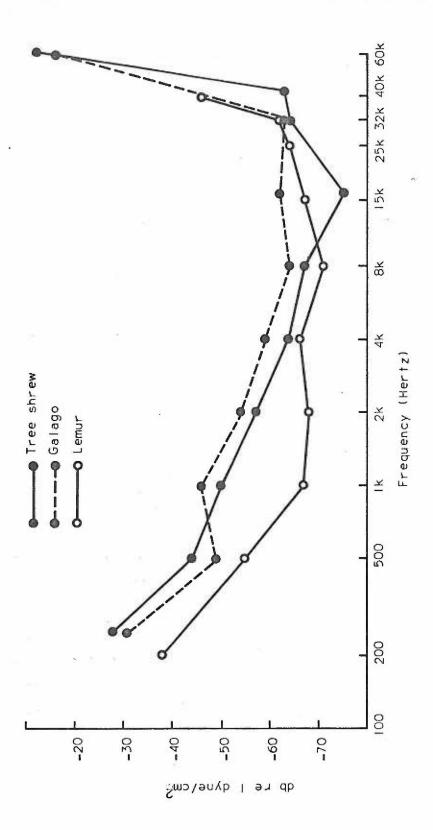
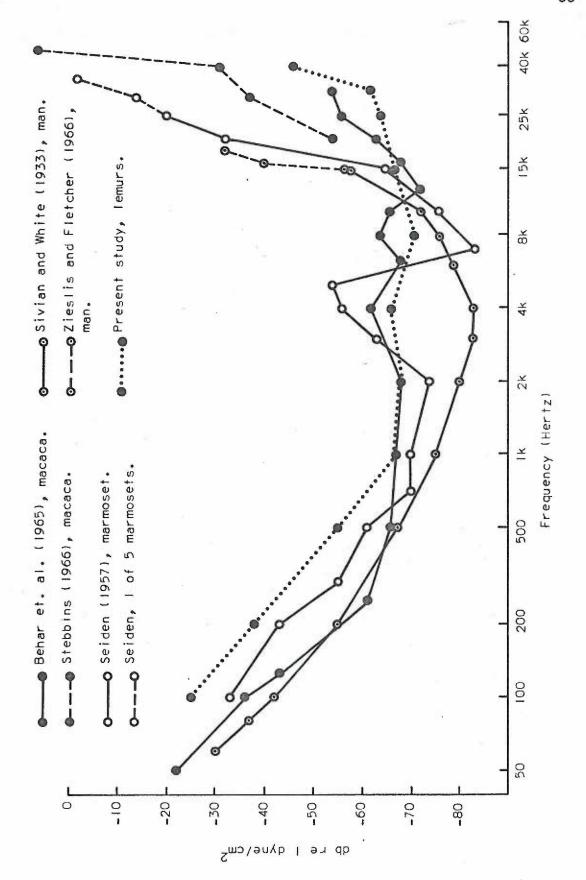


Figure 18. A comparison of prosimians, New and Old World monkeys and man.



World monkey) and man are shown. It can be seen that the lemur shows the poorest sensitivity at frequencies below 1 kHz with increasing sensitivity in the monkeys and man.

Comparison of the high frequency points in Figure 18 are difficult. However, the lemur, shows the best sensitivity at higher frequencies. Furthermore, there appears to be a progressive loss of high frequency sensitivity in monkeys and man.

Summary and Conclusions

Audiograms were attempted on eight ringtail lemurs using the avoidance method of Clack and Herman (1963). Complete audiograms, from 100 Hz to 40 kHz, were obtained on five and a partial audiogram of a sixth lemur. The complete audiograms were combined to provide a general curve of sensitivity for the species.

The conglomerate audiogram for the species was used in several comparisons. It was compared to that obtained in another study of lemurs. Comparisons were also made between prosimians, anthropoidea and humans. The results supported the hypothesis that at low frequencies the prosimians are less sensitive than other primates.

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Appendix I

The sound levels in the following tables were measured with a one-half inch B and K calibrate microphone No. 188966. The attenuation at which the sound pressure was db re 1 dyne/cm² is recorded in the tables. The training cage was 13" X 13" X 13" and the speaker was mounted four inches outside of

Calibration of 10/31 and 11/10/69

Ceiling	2 1/4	2 1/2	2 1/4	2 1/4	2 1/2	
Wall A	3	3 1/4	2 1/4	2 1/2	2 3/4	
Wall B	7 1/2	5 1/2	8	10	7	
Frequency (Hertz)						Average
100	10	7	8	9	10	9
200	26	22	24	25	26	25
500	25	23	26	26	27	25
1k	26	25	27	29	29	27
2k	30	31	31	37	34	33
4k	38	35	36	40	35	37
8k	25	19	26	31	31	26
15k	29	32	37	36	40	35
25k	24	26	31	23	36	28
32k	15	12	25	19	26	19
40k	15	14	8	12	22	14

Wall A. Wall B was opposite the bar (see Figure 1).

A mean value of the attenuation settings was used to convert db attenuation into db re 1 dyne/cm². Note: The raw data are in db attenuation in Appendix III.

Calibration of 12/24/69

Ceiling	3	3	3 1/4	3 1/4	2 1/2	2 1/2	
Wall A	4 1/4	2 3/4	5	2 1/2	б	3 1/2	
Wall B	9 1/2	-8	10	7 1/2	2 1/4	6 1/4	
Frequency (Hertz)							Average
100	7	9	6	9	9	6	8
200	23	22	22	25	25	22	23
500	25	25	23	27	26	23	25
Ik	27	25	26	27	27	24	26
2k	31	30	31	34	34	28	31
4k	41	36	38	36	39	35	38
8k	18	27	19	30	24	23	23
15k	32	37	27	35	37	32	33
25k	25	28	25	22	30	25	26
32k	19	21	10	21	22	19	19
40k	19	21		23	21	7	18

Calibration of 1/31/70

Ceiling	3 1/4	3	3 1/2	2 1/2	2 1/4	3	
Wall A	2 1/8	1 1/4	2 1/4	5	4 1/2	4 1/4	
Wall B	8	,5	6 3/4	3	8 1/2	7	
Frequency (Hertz)							Average
100	9	9	8	est 2	5	est 4	6
200	22	25	24	19	21	21	22
500	26	26	26	20	23	23	24
Ik	26	30	28	24	25	25	26
2k	32	35	30	32	35	27	32
4k	37	40	33	40	33	34	36
8k	27	24	28	15	18	27	23
15k	39	32	37	28	33	33	34
25k	30	24	30	10	23	30	25
32k	25	16	21	5	11	21	16
40k	20	9	24	est 3	11	19	14

Calibration of 3/12/70

Ceiling	3	3	3 1/2	2 1/4	2 1/2	2 1/4	
Wall A	2 1/2	1 3/4	3 1/4	2 1/2	31/2	2 V2	
Wall B	8	3 3/4	6	6 1/2	9	4 3/4	
Frequency (Hertz)							Average
100	9	6	6	7	6	5	6
200	25	23	22	23	22	22	23
500	27	24	24	24	24	23	24
lk	27	28	26	26	26	25	26
2k	32	33	27	30	26	31	30
4k	38	39	34	40	40	40	38
8k	26	18	21	23	19	18	21
15k	36	28	33	33	29	26	31
25k	28	17	26	26	22	25	24
32k	23	10	23	16	14	17	17
40k	20	8	18	8		7	12

Appendix II

The programs available in Table 2 are shown in detail below. These programs were punched on a circular tape and could be started and stopped at any place in the program.

VI 20, 0%

VI 20, 16%

VI 11, 38%

VI 15, 50%

(T = Tone trial, B = Blank trial)

Raw Data

The data contained herein is in decibels attenuation <u>not</u> db re 1 dyne/cm², and must be converted with the aid of Appendix I as described on page 6.

Animal 674 false hit Frequency 100 Hertz pos. decibels Attenuation true RAW DATA miss neg. Date 3/30/70 Date 1/30/70. Date 2/13/70 Date 3/5/70_ Date 3/31/70 Shock .6 ma Shock .6 ma Shock .4 ma Shock .6 ma Shock .5 ma 6 8 10 8 10 10 10 12 12 16 12 14 144 16 16 18 18 20 22

Animal 674 false hit Frequency 200 Hertz pos. decibels Attenuation true DATA RAW miss neg. Date 3/27 (c) Date 3/13/70 Date 3/30/70 Date 3/5/70 Date 3/27/70 Shock .6 ma Shock .5 ma Shock .5 ma Shock .6 ma Shock .5 ma 54 36 56 36 40 38 42 40 50 44 42 46 52 46 48 48 50 50 52

Animal 674 false hit Frequency 500 Hertz pos. decibels Attenuation true RAW DATA miss neg. Date 3/21/70 Date 4/2/70 Date Date 3/5/70 · Date 3/27/70 Shock Shock .5 ma Shock .5 mg Shock .6 ma Shock .6 ma 58 62 52 60 62 64 60 😘 56 62 64 58 68 66 60 70 68 72 62 70 72 74 66 74 72 68 76 78

Animal false hit Frequency I kHz pos. decibels Attenuation true RAW DATA miss neg. Date 1/30/70 Date 4/16/70 Date 4/17/70 Date 4/20/70 Date 4/20/70 Shock .8 ma Shock .4 ma Shock .5 ma Shock .3 ma Shock .5 ma _64

Animal 674 false hit Frequency 2 kHz pos. decibels Attenuation true RAW DATA miss neg. Date 3/18/70 Date 3/21/70 Date Date 4/15/70 Date Shock .6 ma Shock Shock .6 ma Shock .5 ma Shock 70 68 70 70 72 72 74 74 76 76 78 78 76 80 80 78 82 82 84 84 2 86 84 86 86 88

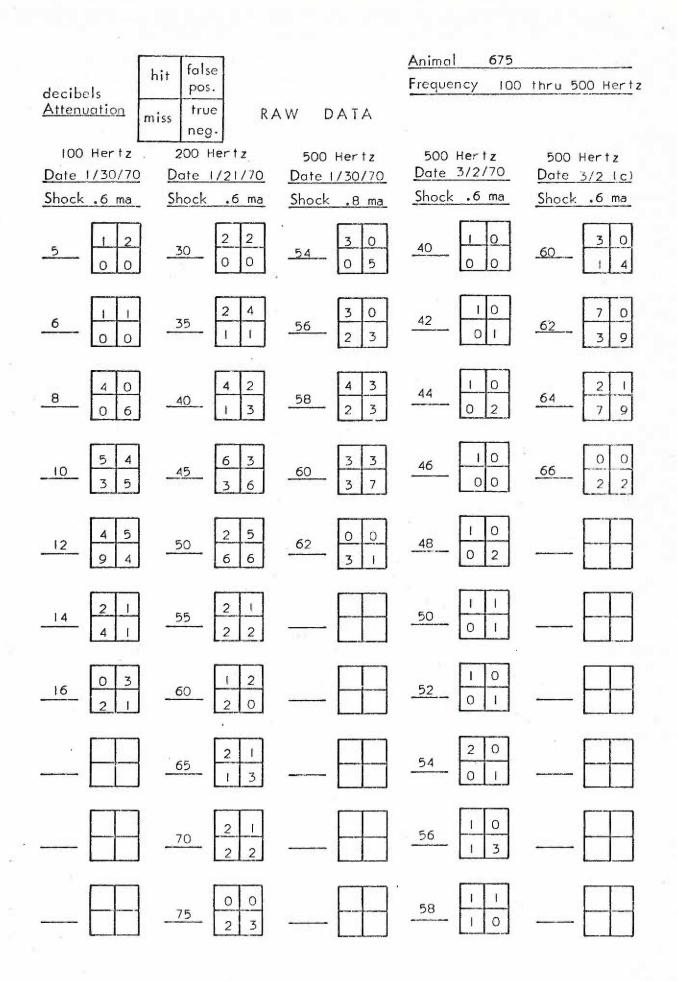
Animal false hit Frequency pos. 4 kHz decibels Attenuation true RAW DATA miss neg. Date 1/30/70 -Date 2/18/70 Date 3/11/70 Date 4/2/70 Date 2/18(c) Shock .8 ma Shock .6 ma Shock .6 ma Shock .6 ma Shock .5 ma

Animal 674 false hit Frequency 8 kHz pos. decibels Attenuation true RAW DATA miss neg. Date 1/16/70-Date 2/10/70 Date Date 3/31/70 Date Shock Shock .6 ma Shock .8 ma Shock .5 ma Shock 66 64 66 66 68 68 70 70 68 70 72 72 74 72 74 74 76 78 78 78 80 80 82 82 84

Animal 674 false hit Frequency pos. 15 kHz decibels <u>Attenuation</u> true RAW DATA miss neg. Date 3/26 (c) Date 3/30/70 Date 3/26/70 Date 3/30(c) Date 4/8/70 Shock .5 ma Shock .5 ma Shock .4-.5 Shock .4-.5 Shock .6 ma 82 86 66 88 68 76 86 66 90 70 88 72 80 90 82 74 76 84 78 80 88 78 82 90 92 84

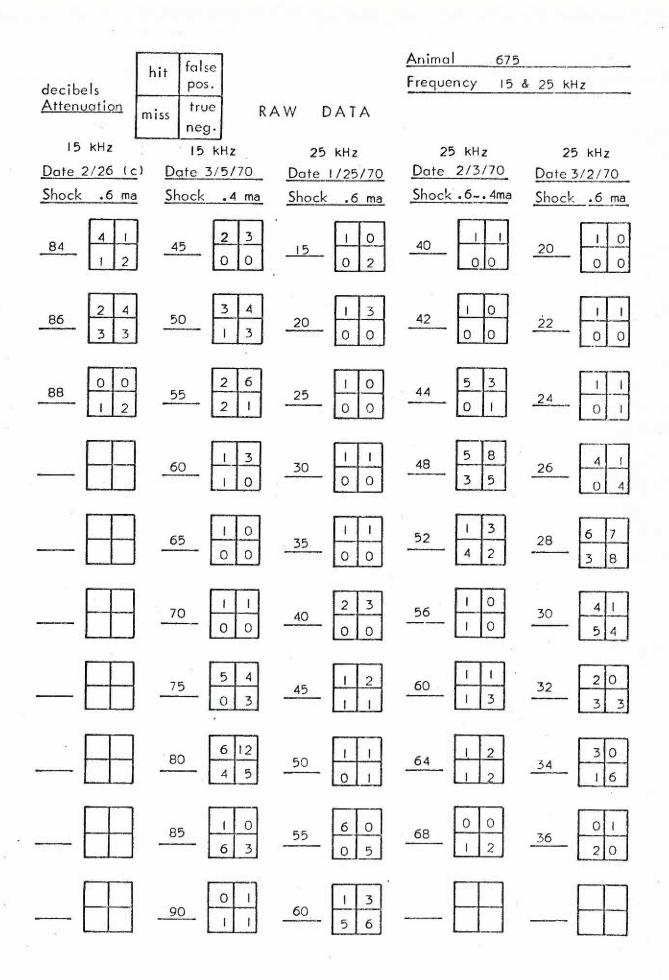
Animal 674 false hit Frequency 15 kHz pos. decibels Attenuation true RAW DATA miss neg. Date 4/10/70 Date 4/10(c) Date Date Date Shock Shock .4 ma Shock .4 ma Shock Shock 56 76 58 78 80 62 82 84 66 86 88 70 90 92

Animal 674 false hit Frequency 25 kHz pos. decibels Attenuation true RAW DATA miss neg. Date 4/8/70 Date 4/3/70 Date 4/7/70 Date 4/7/70 Date 4/8(c) Shock .6 ma Shock .5 ma Shock .6 ma Shock .5 ma Shock .5 ma 58 60 62 66 64 60 80 68 66 62 82 68 64 70 84 70 66 68 86 74 72 68 70 76 74 72 78 74 76 80 82 76



	his false		Animal 675	
decibels	pos.		Frequency	thru 8 kHz
Attenuation	miss true R.	AW DATA		
l kHz	2 kHz	4 kHz	4 kHz	8 kHz
Date 1/25/70 Shock .6 ma		Date 1/21/70	Date 1/25/70	Date 2/11/70
Shock to ma	Shock .6 ma	Shock .6 ma	Shock .6 ma	Shock .6 ma
45 0 2	45 0 0	55 0 1	50 2 0	45 2 0 3 3
50 0 0	50 12	60 0 0	55 4 2 2 4	50 0
55 0 4	55 00	65 0 0	60 4 7	55 0 1
60 2 6	60 0 1	70 0 0	65 0 0	60 0 0
65 5 2	65 00	75 2 2 0 1		65 0 1
70 0 0	70 0 0	80 4 5		70 2 0 0 1
	75 0 3	85 4 6 3 I		75 5 2
	80 5 0	90 1 3 4 0 (ceiling)		80 4 3 4 11
	85 4 I 4 8			85 3 0 3 3
	90 2 0 4 7 (Ceiling)		art-constant	90 0 0

decib		false pos.		Animal 675 Frequency 15 k	Hz
Atten	uation m	iss true RA	AW DATA		
1	5 kHz	15 kHz	15 kHz	15 kHz	15 kHz
	1/21/70	Date 1/30/70	Date 2/24/70	Date 2/24 (c) Shock .5 ma	Date 2/26/70
Snock	< .6 ma	Shock .8 ma	Shock .5 ma	310CK .3 1118	Shock .6 ma
_52	1 2	46 1 0	46 2 0	66 0 3	66 0 1
54	5 1	48 2 0	48 1 1 2	68 2 0 0 0	68 0 0
56	3 2 4 7	50 3 2 2 4	50 0 0	70 1 2	70 0 0
_58	3 1 3	52 3 0 3 5	52 1 0 0 1	72 4 0	72 1 0 0
60	2 1 3 4	54 2 1 3 3	54 0 1	74 3 1 4 3	74
62	2 3	56 2 0 2 6	56 2 0 0 4	76 2 0 3 6	76 1 0
_64	1 0	58 1 0 2 2	58 1 0	78 2 2 2 I	78 2 0 0 4
66	1 0	60 0 0	60 1 0	80 0 0	80 4 2 I 5
68	1 0		62		82 2 3 3
70	0 0		64 0 1		84 4 1



		hit false		Animal 675 Frequency 25	& 32 kHz
decil <u>Atter</u>	wation		RAW DATA	Trequency 25	G JZ KIIZ
25	kHz	25 kHz	32 kHz		
Date	3/5/70	Date 3/5 (c)	Date 3/5/70	Date	Date
Shock	k .6 ma	Shock .6 ma	Shock .64ma	Shock	Shock
20	2 I 0 0	40 0 0	8 2 1		
	4 4	42 3 0 0 2	10 3 3	<u>—</u> Ш	
_24	4 4 3 6	44 3 1 2 4	$\begin{array}{c c} & 2 & 3 \\ \hline 2 & 2 \end{array}$		
26	2 0 3 2	46 5 1 3 6	14 2 4	_ =	
_28	1 0	48 0 1 5 5			
30	1 O 0 I	_ =	18 4 4 3 5	— — —	
32	0 2		20 2 1 3 2		_ 🔲
34	0 0		22 2	🗏	
36	0 0		24 0 0		_ =
38	1 1		H		_H

Animal 2024 false hit Frequency pos. 100 Hertz decibels Attenuation true RAW DATA miss neg. Date 3/11/70 Date 2/24/70 Date Date 3/22/70 Date Shock .5 - . 6ma Shock Shock .6 ma Shock .6 ma Shock 6 10 7 12 8 10 3 11

Animal 2024 false hit Frequency 200 Hertz pos. decibels Attenuation true RAW DATA miss neg. Date 3/30/70 Date 4/13/70 Date 3/10/70 Date 3/20/70 Date 3/20 (c) Shock .5 ma Shock .5-.6 Shock .5 ma Shock ,6 ma Shock .6 ma 26 20 40 26 28 22 26 28 24 30 30 26 32 28 34 36 30 36 32 38 34 40 36 40

Animal 2024 false hit Frequency 200 Hertz pos. decibels Attenuation true DATA RAW miss neg. Date Date 4/15/70 Date Date Date Shock .5 ma Shock Shock Shock Shock 36 0

Animal 2024 false hit Frequency pos. decibels 500 Hertz Attenuation true RAW DATA miss neg. Date 2/2/70 Date 2/26/70 Date 4/1/70 Date Date Shock .8 ma Shock .4 ma Shock .5 ma Shock Shock 44 48 46 50 48 58 52 50 54 52 56 58 60 58 62 60 70 64 62 66

decibels _	hit false pos.	AW DATA	Animal 2024 Frequency 1 k	Hz
Date 1/28/70 Shock .8 ma	Date 3/24/70 Shock .6 ma	Date 4/1/70 Shock .5 ma	Date Shock	Date Shock
66 2 0 0 3	64 0 0	64 0 3		<u>— Ш</u>
68 3 2	66 0 2	66 0 0		· _
70 2 2	68 3 1	68 0 1		_
72 5 4	70 1 0 2 2	70 0 0		
74 1 1 4 6	72 0 0	72 0 1		
76 01	74 5 1 0 7	74 2 0 0 2	— III	
<u> </u>	76 5 0	76 4 0	[
	78 0 0 5 3	78 4 0 3 8	_	_
		80 2 1 3 5		🔲
		82 2 3		

Animal 2024 false hit Frequency pos. decibels 2 kHz Attenuation true RAW DATA miss neg. Date 2/26/70 Date 3/26/70 Date 3/31/70 Date Date Shock .4 ma Shock .5 ma Shock Shock Shock .5 ma 68 70 70 72 72 74 74 76 76 78 78 80 78 80 82 84 _86 86 84 86 88 88

Animal 2024 false hit Frequency pos. 4 kHz decibels Attenuation true RAW DATA miss neg. Date 3/11/70 Date 3/20/70 Date Date 4/2/70 Date Shock .6 ma Shock .6 ma Shock Shock .5 ma Shock 74 76 76 78 78 78 80 80 82 82 82 84 84 84 86 88 88 90 90 90 92

Animal 2024 false hit Frequency pos. 8 kHz decibels Attenuation true RAW DATA miss neg. Date 2/10/70 Date 4/8/70 Date 4/10/70 Date 4/9/70 Date 4/13/70 Shock .6 ma Shock .5 ma Shock .5 ma Shock .5 ma Shock .5 ma 60 62 60 62 54 62 644 64 64 66 66 64 66 68 66 68 70 _60 68 70 70 72 72 72 74 76 76 68 78

Animal 2024 false hit Frequency pos. 15 kHz decibels Attenuation true RAW DATA miss neg. Date 4/13/70 Date 4/14/70 Date Date 4/15/70 Date Shock .5 ma Shock .5 ma Shock .5 ma Shock Shock 68 70 76 72 78 74 80 76 82 78 84 80 86 82 88 84 90 86 (celling)

Animal 2024 false hit Frequency 25 kHz pos. decibels Attenuation true RAW DATA miss neg. Date 3/13/70 Date 3/28/70 Date 4/8/70 Date 4/2/70 Date 4/9/70 Shock .6 ma Shock .5 ma Shock .5 ma Shock .5 ma Shock .5 ma 76 74 76 78 76 78 70 78 80 80 72 82 80 82 84 82 84 76 86 78 88 80 88 84 90 82 90 92

2024 Animal false hit Frequency 25 kHz pos. decibels Attenuation true RAW DATA miss neg. Date Date 4/14/70 Date 4/10/70 Date Date Shock Shock .5 ma Shock Shock Shock .5 ma 68 72 76 78 80 84 86 82 84 _88_ 90

Animal 2024 false hit Frequency pos. 32 kHz decibels Attenuation true RAW DATA miss neg. Date 4/1/70 Date 4/3/70 Date 4/7/70 Date 4/6/70 Date 4/8/70 Shock .5 ma 54 58 56 58 56 58 60 60 58 60 62 60 62 64 64 62 64 66 66 64 68 66 68 70 68 70 74 72 76

Animal 2024 false hit Frequency pos. 40 kHz decibels Attenuation true RAW DATA miss neg. Date 3/28/70 Date 3/31/70 Date Date 4/6/70 Date Shock .5 ma Shock .5 ma Shock Shock .5 ma Shock 38 40 42 42 44 44 46 46 48 50 50 52 52 54 56

Animal 4059 false hit Frequency pos. 100 Hertz decibels Attenuation true DATA RAW miss neg. Date 2/20/70 Date 2/3/70 Date 12/13 Date 1/3/70 Date 1/16/70 Shock 0.5ma Shock none Shock 0.8ma Shock 0.6 ma Shock 0.6 ma 6 15 8 6 10 8 8 25 12 10 10 12 12 16 10 14 16 12 13

	h: false		Animal 4059	
decibels Attenuation	pos.	W DATA	Frequency 100 H	ler t z
Zivenodi In	niss neg.	AW DATA	23	
Date 2/20(c)	Date 2/23/70	<u>Date 2/23(c)</u>	Date 2/26/70	Date 2/26(c)
Shock 0.5ma.	Shock O.5ma.	Shock O.5ma.	Shock O.4ma	Shock 0.4ma
15 2 0	6 0 0	16 2 0 6 9	7 0 0	
	7 0 0	17 3 0 2 0	8 00	18 4 2 3 7
17 4 0 4 6	8 2 1	18 0 0 3 5	9 00	19 12
18 5 0 3 8	9 2 1	 	10 0 1	20 0 0
	10 1 2	[11 0 0 3	
20 2 7	11 0 0 0		12 0 0	
21 0 0	12 0 0 1		13 0 1	[]
_ =	13 0 1		14 3 0 0 3	
			15 2 1	
	15 6 3 5 12		16 5 0 1 7	

Animal 4059 false hit Frequency pos. 200 Hertz decibels Attenuation true RAW DATA miss neg. Date 12/11/70 Date 12/16/69 Date 1/6 (c) Date 1/6/70 Date 1/19/70 Shock Shock .8 ma Shock .8 ma .8 ma Shock .8 ma Shock .6 ma 52 36 32 38 54 56 36 58 __38 44 40 46 50 44 46 48 50

Animal 4059 false hit Frequency 500 Hertz pos. decibels Attenuation true RAW DATA miss neg. Date 2/11/70 Date 12/17/69 Date 1/8/70 Date 2/3/70 Date Shock .4 ma Shock .6 ma Shock .6 ma Shock Shock .6 ma 48 48 50 50 50 52 52 54 56 56 56 58 60 58 60 60 62

Animal. 4059 false hit Frequency pos. 1 kHz decibels Attenuation true RAW DATA miss neg. Date 12/16/69 Date 1/5/70 Date 3/27/70 Date 2/20/70 Date Shock .8 ma Shock .6 ma Shock .6 ma Shock Shock .5 ma 60 40 64 62 62 64 66 64 50 68 66 66 68 70 68 60 72 70 70 72 72 76 76 78

Animal 4059 false hit Frequency 2 k Hz pos. decibels Attenuation true RAW DATA miss neg. Date 12/26/69 Date 1/12/70 Date 1/12(c) Date 1/21/70 Date 1/21(c) Shock .4 ma Shock .6 ma Shock .6 ma Shock .6 ma Shock .6 ma _56 40 62 76 82 64 45 58 78 66 60 86 62 68 60 64 70 66 72 70 68 74 70 76 72 78 80

Animal 4059 false hit Frequency pos. 2 kHz decibels Attenuation true RAW DATA miss neg. Date 2/11/70 Date Date Date Date Shock .6 ma Shock Shock Shock Shock 72 _76 78 _80

Animal 4059 false hit Frequency pos. 4 k Hz decibels Attenuation true RAW DATA miss neg. Date 11/24/69 Date 11/26/69 Date 11/26(c) Date 1/26/70 Date 2/23/70 Shock .6 ma 74 84 76 64 40 _45 66 78 76 . 86 88 80 68 78 90 82 70 80 72 84 82 74 86 76 75 _80

Animal 4059 false hit Frequency pos. 8 kHz decibels Attenuation true RAW DATA miss neg. Date 12/5/69 Date 1/6/70 Date:1/30/70 Date 1/16/70 Date Shock .6 ma Shock .8 ma Shock .6-.8ma Shock Shock .6 ma 66 62 64 2 68 40 64 66 70 66 68 72 68 50 70 70 55 . 72 74 72 74 60 76 65 76 78 78 76 80 75 78 80 82 80 82 84

Animal 4059 false hit Frequency pos. 15 kHz decibels Attenuation true RAW DATA miss neg. Date 12/4/69 Date 12/13/69 Date 12/13 (c) Date 12/13 (c) Date 12/16/69 Shock ? Shock .8 ma Shock .8 ma Shock .8 ma Shock .8 ma 54 20 16 36 _56_ 46 25 18 58 _38_ 48 20 __60_ 40 50 22 62 26 66 28 68 48 __30 50 60 32

Animal 4059 false hit Frequency pos. 15 kHz decibels Attenuation true RAW DATA miss neg. Date 12/29/69 Date 1/8/70 Date 1/8 (c) Date 1/8 (c) Date 1/25/70 Shock Shock Shock .6 ma .6 ma ,6 ma Shock .6 ma Shock .6 ma 62 82 70 46 44 64 84 48 86 46 66 48 88 68 76 0 70 50 78 52 72 80 54 82 74 76 84 0 58 60 78 86 62 80 88

Animal 4059 false hit Frequency pos. 15 KHZ decibels Attenuation true RAW DATA miss neg. Date 1/25 (c) Date 2/9/70 Date Date 3/26/70 Date Shock .6 ma Shock Shock .4 ma Shock .5 ma Shock 72 76 74 78 76 78 80 82 86 84 86

Animal 4059 false hit Frequency pos. 25 kHz decibels Attenuation true RAW DATA miss neg. Date 12/9/70 Date 12/26/69 Date 1/16/70 Date 1/25/70 Date 1/25 (c) Shock .6 ma Shock Shock Shock .6 ma . 4 ma Shock .6 ma 32 30 28 62 35 34 64 36 46 36 66 38 48 40 40 50 44 _70 52 42 48 60 54 46 56 56 76 48 58 70 60 78 60 64 80

4059 Animal false hit Frequency 25 kHz pos. decibels <u>Attenuation</u> true DATA RAW miss neg. Date 1/30/70 Date 2/9/70 Date Date Date Shock .6 ma Shock .5 ma Shock Shock Shock 50 54 54 58 58 66 70

Animal 4059 false hit Frequency pos. decibels 32 kHz Attenuation true RAW DATA miss neg. Date 12/26/69 Date 1/19/70 Date 2/3/70 Date 1/21/70 Date 1/19 (c) Shock .5 ma Shock .6 ma Shock .6 ma Shock .6 ma Shock .6 ma _28 20 16 56 20 36 60 40 50 28 32 48 52 36 56 58 60 60 48 64

Animal 4059 false hit Frequency pos. 32 kHz decibels Attenuation true RAW DATA miss neg. Date 2/3 (c) Date 2/11/70 Date 2/26 (c) Date 2/26/70 Date 3/25/70 Shock .6 ma Shock .6 ma Shock .4 ma Shock .4 ma Shock .6 ma 64 44 44 52 66 46 66 46 48 68 68 48 56 50 70 50 52 60 54 54 56 56 64 58 66 58 60 60 68 62

	hit false		Animal 4059	
decibels Attenuation	pos.	AW DATA	Frequency 32	kHz
<u>Date 3/26/70</u>	Date	Date	<u>Date</u>	Date
Shock .5 ma		Shock	Shock	Shock
54 1 0				
56 0 1				
58 0 1				
60 0 2				
62 0 0				
64 0 5				
66 3 5			<u>—</u> Ш	
68 6 0 3 9			_ =	
70 0 0				
_ []	[

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Animal 4059 false hit Frequency 40 kHz pos. decibels Attenuation true DATA RAW miss neg. Date 1/12 (c) Date 1/19/70 Date 12/26/69 Date 12/29/69 Date 1/12/70 Shock .6 ma Shock .6 ma Shock .5 ma Shock .6 ma Shock .6 ma 42 18 46 22 10 50 30 10 14 15 .18 34 22 38 42 26 30 46 30 50 35 34 38