# A STUDY OF THE RELATIONSHIPS BETWEEN THE MECHANICAL RESPONSE OF THE TYMPANIC MEMBRANE AND THE ELECTROPHYSIOLOGICAL INDICATORS OF HEARING IN THE BULLFROG *(RANA CATESBEIANA)*

This report was prepared for the
National Aeronautics and Space Administration
by

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Louisiana State University Medical Center
New Orleans, Louisiana

under NASA Sustaining
Grant No. NGL-19-001-024

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## ABSTRACT

The present study was undertaken to investigate the visible mechanical response of the tympanic membrane of the bullfrog *(Rana catesbeiana)* and what relation it has to the indicators of hearing determined electrophysiologically. Seven subjects were presented with pure tones of varying frequency and intensity while the tympanic membrane was viewed under stroboscopic illumination. Thresholds of visible mechanical response were recorded for each frequency tested. Graphic data revealed a nonlinear relation between frequency and intensity with two definite areas of sensitive hearing. The areas of sensitive hearing correspond to the "best frequencies" revealed electrophysiologically. The range of frequencies eliciting mechanical response correspond to the range of frequencies eliciting electrophysiological response. The size of the membrane determines the amount of intensity necessary to elicit a visible mechanical response.

# CHAPTER I

# INTRODUCTION

## I. REVIEW OF THE LITERATURE

While the physiological investigation of the mammalian auditory system has attracted much attention [6, 10, 23, 26], that of the amphibian has not. The amphibian ear possesses all of the evolutionary rudiments of the type of auditory receptors attaining highest perfection in the mammalian cochlea [22], a perilymphatic system which develops in the amphibian for the first time in evolution [22], and the primitive parallels to the peripheral and central auditory system found in higher vertebrates [3]. McGill [16] pointed out that our present state of knowledge of hearing in amphibians is not commensurate with the importance of this class in the study of the evolution of the sense of hearing.

The auditory system of the class amphibia and, more specifically, the order anura (frogs and toads) is relatively simple anatomically. Most of the investigation has been done on the bullfrog *(Rana catesbeiana)*.

### Anatomy

Frishkopf and Goldstein [8] found that the anatomical structures of the bullfrog's peripheral auditory system consist of an external tympanic membrane, three fused middle ear bones, and an inner ear or otic capsule (Figure I).

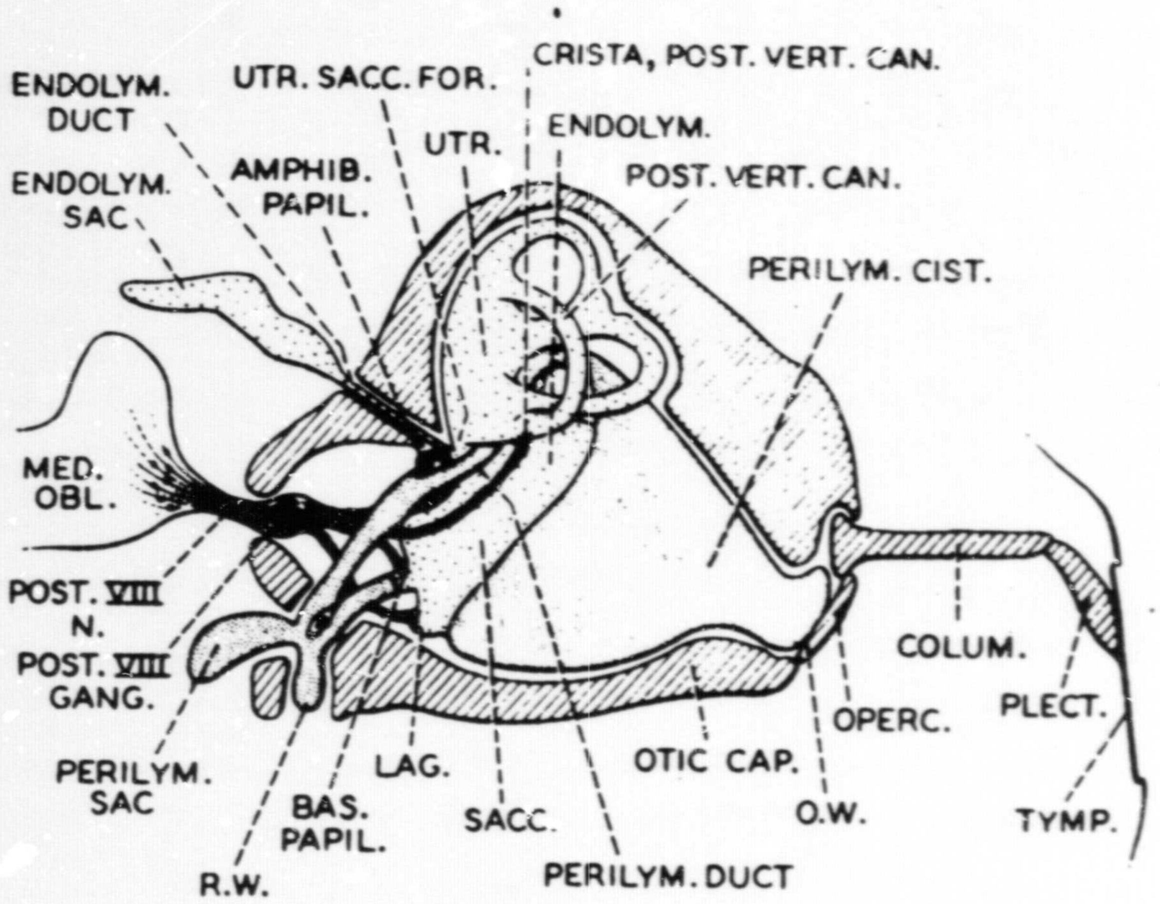

FIGURE I. Schematic Diagram of the Frog's Ear in Cross Section
(From Frishkopf and Goldstein [8])

The tympanic membrane is a circular membrane made up of a darker, more flexible, outer ring and a lighter colored, more resistent, center section located directly behind the bulging eyeball. The fused middle ear bones attach to the medial side of the center section.

The otic capsule contains eight sensory structures: three semicircular canals, the utricle, saccule, lagena, and the basilar and amphibian papillae. The two papillae appear to be auditory receptor organs because of their structure and location [11]. The basilar papilla of amphibians is probably the simplest of all vertebrate organs and is usually regarded as a homolog of the mammalian cochlea [9]. Each of the eight sensory structures in the otic capsule is innervated by a branchlet of the eighth nerve. Four of these branchlets merge to form a posterior branch, and four merge to form an anterior branch which join medially to the capsule to form the eighth nerve. Frishkopf and Goldstein [8] concluded that the ganglion on each branch contains primary cell bodies whose central processes synapse in the medulla, and whose peripheral processes terminate on hair cells of the vestibular and auditory organs.

Frishkopf and his co-workers [9] explain that sound is transmitted from the tympanic membrane by way of the fused middle ear bones--the plectrun, columella, and operculum--to the membranous oval window of the perilymphatic system. This system is a closed membranous sac that holds perilymphatic fluid and is in close proximity to the membranous endolymphatic system that contains endolymphatic fluid and houses all eight sensory organs. In the region of the papillae, perilymph and endolymph are separated only by thin contact membranes. Therefore, fluid motion in the perilymph, resulting from the motion of the tympanic membrane and middle ear bones, produces a corresponding motion in the endolymph and mechanically stimulates the tectorial membrane attached to the receptor hair cells located on the papillae.

The central connections of the auditory portion of the frog's eighth nerve have been described by Larsell [14]. He believed the majority of the fibers from the papillae terminated in the corpus posticum, corresponding to the inferior colliculus.

Strother [21] reported there is much evidence to indicate a frog does make use of sounds, especially during breeding season. Determining just how and what the frog hears, however, is not an easy task.

## Behavioral Techniques

Some researchers have used behavioral techniques, field observation, or some variation of conditioning procedures to study hearing in frogs.

Yerkes [29] was the earliest investigator to record experimental evidence of hearing in frogs. He claimed that "the sense of hearing in the frog is fairly well developed..." [29:304]. He reported that a withdrawal response by the frog could be modified by the presence of sound over a frequency range from 50 to 10,000 CPS, but his acoustic stimuli were crudely controlled.

Other investigators [4, 13] studied respiration rates of bullfrogs in response to changing auditory stimulation. Corbeille and Baldes [4] reported that tones from 128 to 8,000 CPS produced a change in the respiration rate of the frogs they tested.

Naturalistic studies [3, 5, 15] showed the instinctive response of the anuran to the mating call of its species. Capranica [3] showed that bullfrogs can distinguish between 33 species of frogs and toads and respond by calling only to other bullfrogs.

Strother's [20] attempts to condition frogs were unsuccessful. He felt that conditioning procedures, although providing much information on higher organisms, has not been fruitful on frogs. Capranica [3] revealed that naturalistic studies involving the instinctive response to the mating call can only be carried on for a very short period during their sexual peak. Thus, other indices of hearing and different ways of recording responses were investigated.

## Electrophysiological Indicators of Hearing

Other experimenters used techniques which permitted observation of unconditioned responses or measurement of the electrical response of the auditory nerve to acoustic stimulation. A much abbreviated range of frequencies was found through these techniques [21].

Earlier studies [1, 17] performed on decapitated frogs indicated either very high thresholds for the auditory fibers or no presence of auditory fibers at all. In a gross-electrode study, Adrian et al [1] supported the view that the frog is insensitive to all but loud sounds. Later studies [7, 8, 18, 20, 21] supported the idea that the auditory receptors are very sensitive in a number of species. Frishkopf and Goldstein [8] found that the thresholds of auditory fibers in the bullfrog deteriorate quickly when the blood supply fails; thus, possibly explaining the high thresholds observed in early studies on decapitated animals.

From his study of microphonic responses to pure tones, Strother [21] reports:

> The electrical responses from the auditory apparatus of vertebrate ears, though not an indicator of auditory perception per se, give an indication of peripheral auditory functioning and permit us to make certain assumptions about hearing capabilities and the nature of hearing in general. [12:160]

Strother's [21] findings suggested that the range of hearing for the bullfrog extends from a few cycles to an upper limit of 4,000 CPS. He felt this limited range was due to the "mechanical simplicity of structure inherent in its ear." [21:161]. Strother found the auditory receptors possibly sensitive to sound pressures smaller than 0.1 dyne/cm$^2$ for certain low frequencies. He also found that as one ear was being stimulated, energy was readily transmitted to the opposite ear through the Eustachian tube; and suggested a possible use of this stimulation in sound localization.

In a later study, Strother [20] used the galvanic skin response as an indicator of hearing. The frequency limits and intensity thresholds were in close agreement with his previous findings.

Some electrophysiological studies [2, 12, 25] gave no responses over 730 CPS. Axelrod [2], on the other hand, reported two types of auditory units when he recorded from single units in the eighth nerve of live *Rana pipiens*. One type responded to frequencies in the 600-700 CPS band, and the other responded to low-frequency sounds up to a certain cutoff frequency.

Frishkopf and his co-workers [7, 8] used microelectrode techniques to make detailed studies of responses to sound stimuli in the eighth nerve of bullfrogs. Thresholds were determined for tone bursts at different frequencies; and a tuning curve, or curve depicting thresholds, was made. An auditory unit can be characterized by its "best frequency", or that frequency to which it is most sensitive. Two kinds of curves tended to occur most frequently: one with its best frequency in the range of 1,000 to 1,500 CPS, and the second with its "best frequency" below 700 CPS (Figure II). The histogram in Figure III shows the number of units with best frequencies in a given interval. They were able to divide the units into two classes on the basis of best frequency and other response properties: (a) "simple units"--with best frequencies between 1,000 and 1,500 CPS, spontaneously active, and unable to be inhibited by acoustic stimuli; and (b) "complex units"--with best frequencies below 700 CPS (between 700 and 200 CPS), silent unless stimulated, easily inhibited by tones in the range of 300 to 1,000 CPS (usually 500 CPS), and also sensitive to vibration. The thresholds at best frequencies occur over a range of about 40 db. The most sensitive units of both classes have thresholds of about 25 db SPL (re 0.0002 dyne/cm$^2$). The range of frequency sensitivity lies below 3,000 CPS.

In the latter study, Frishkopf and Geisler [7] presented additional evidence to support the view that it is the basilar papilla which gives rise to simple units, and the amphibian papilla which gives rise to complex units.

Frishkopf and Goldstein [8] explain that the simple units appear to be particularly well adapted for detecting bullfrogs' croaks. Major energy peaks in the croak occur between 1,200 and 1,500 CPS; this is the frequency range which simple units respond to.

Frishkopf et al [9] go into more detail about the croak characteristics and state:

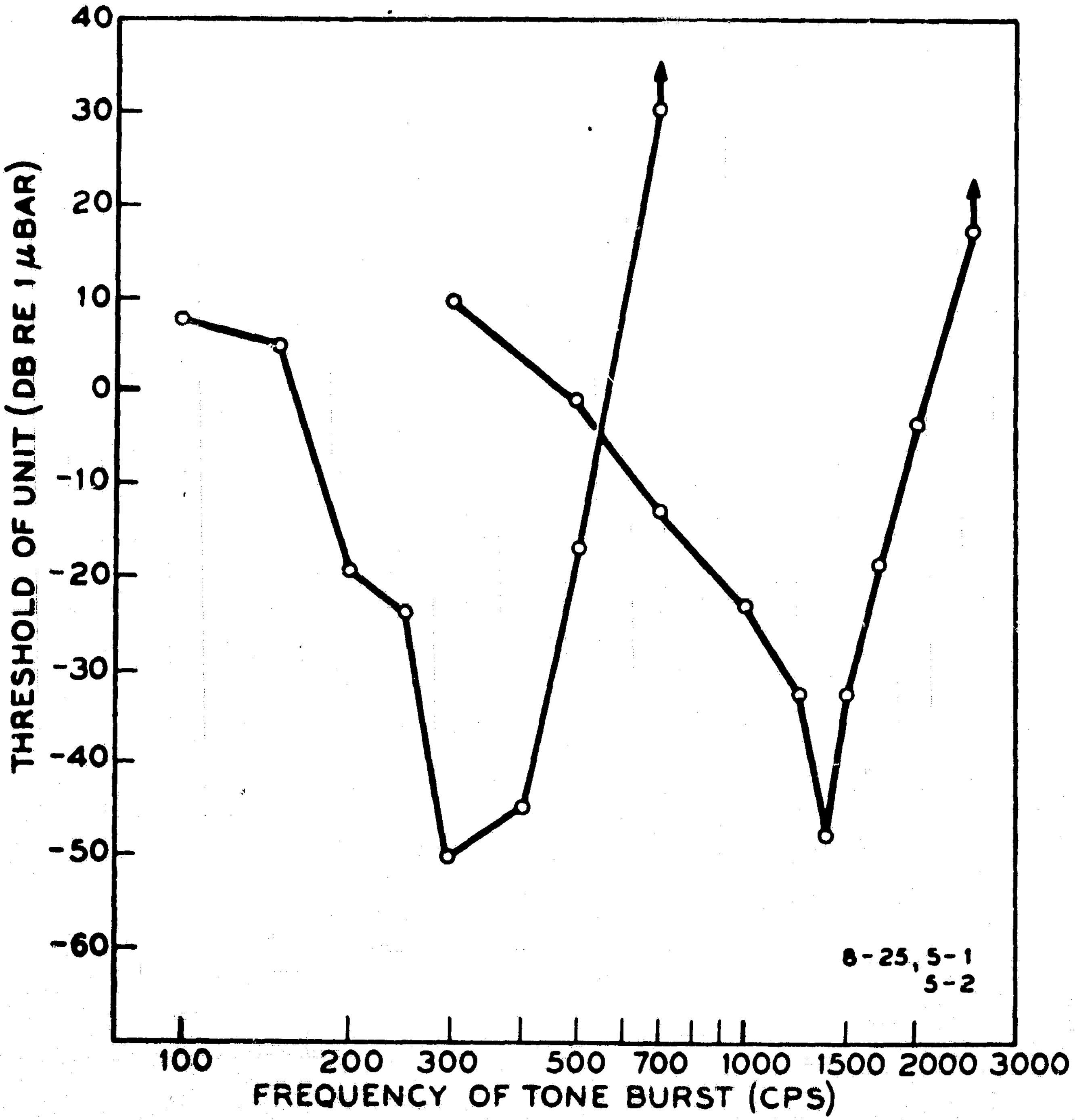

FIGURE II. Representative Tuning Curves for Simple and Complex Units (From Frishkopf and Goldstein [8])

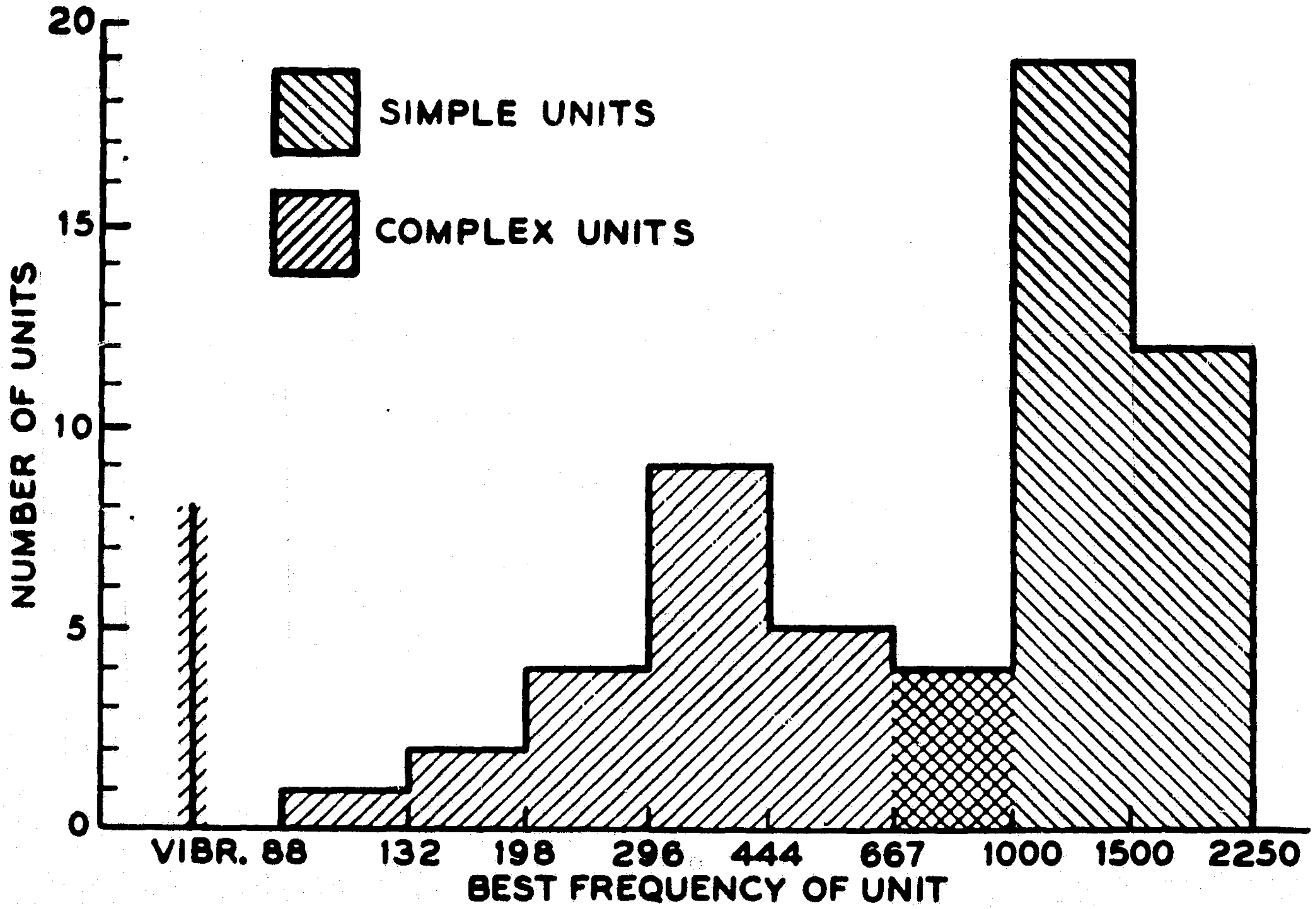

FIGURE III. Histogram of Auditory Units with Best Frequencies in the Indicated Intervals (From Frishkopf and Goldstein [8])

> Two regions consistently are found to contain considerable energy: a low-frequency region in which the spectral envelope has a relative peak, depending on the individual, between 200 and 700 Hz; and a high-frequency region--often quite broad--centered around 1400-1600 Hz. It is typical to find a dip in the spectral envelope between these two frequency regions. [9:976]

Figure IV shows peaks near 200 CPS and 1,600 CPS, and a minimum around 500 CPS. This suggests that the bullfrog hears the sound he produces [9]. Capranica [3] feels that the selective behavioral response, evoked calling, is strongly predetermined at the peripheral level of the frog's auditory nervous system and that his proposed model of evoked vocal response reflects, possibly in part, the auditory capabilities of the bullfrog.

Sachs's [18] results resembled those of Frishkopf and Goldstein [8]. He also found two types of units: (a) low-frequency units most sensitive between 150-450 CPS, and (b) high-frequency units most sensitive between 700-1,700 CPS. His work was done on green frogs.

## Mechanical Indicators of Hearing

Although several studies [19, 24, 27] have been done on human tympanic membrane movement, no research was found that investigated the mechanical response of the bullfrog's tympanic membrane to auditory stimulation. Frishkopf et al [9] tried to find some relation between the size and sex of the frog and the response characteristics of the auditory organs. No correlation was uncovered; although the tympanic membrane enlarges as the animal grows, and it is larger in the adult male than in the adult female [3, 28, 29]. The energy peaks in the bullfrog's croak match more closely the "best frequencies" of the hearing as the male

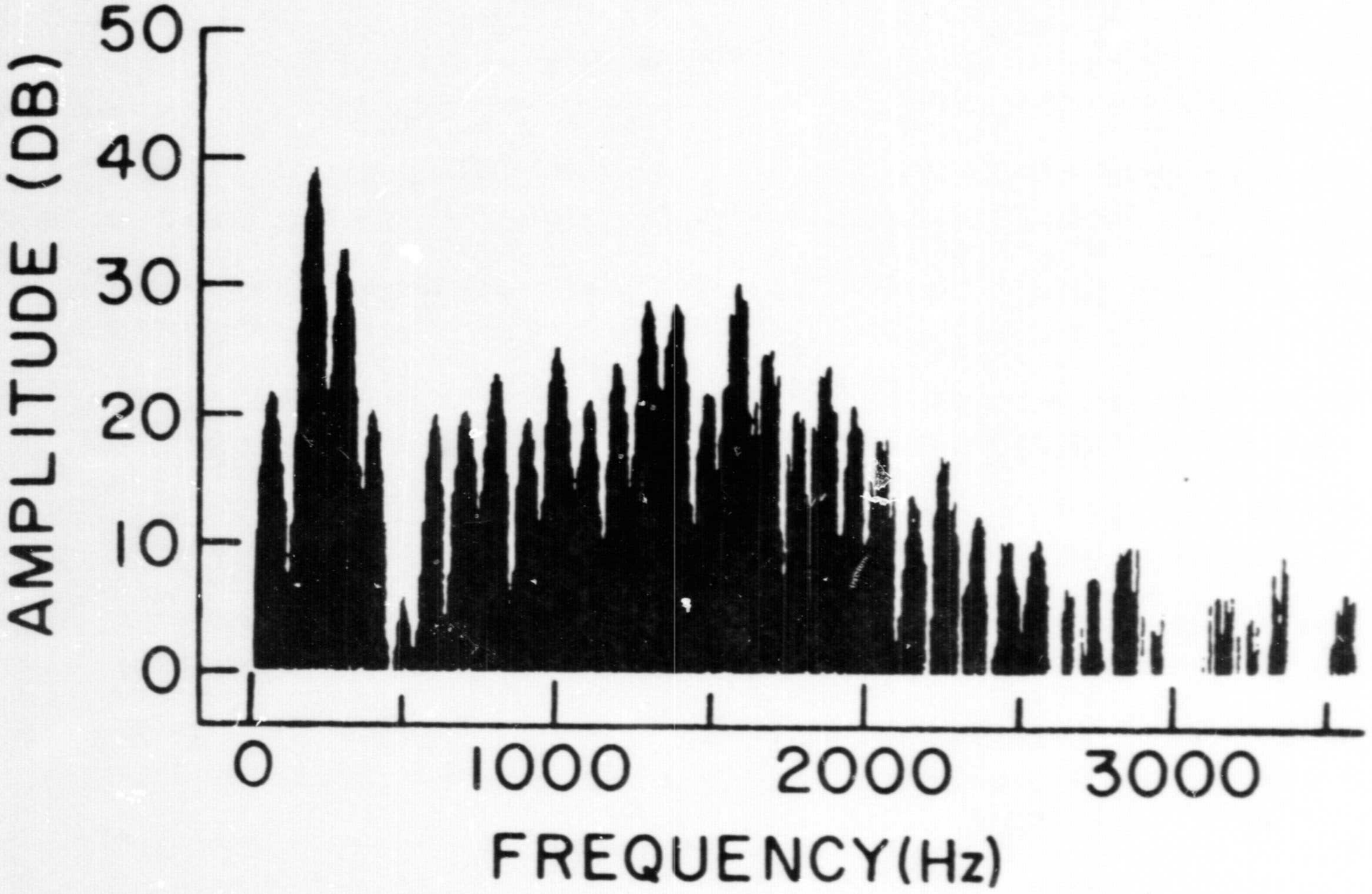

FIGURE IV. Spectrographic Section Taken Through the Middle of a Bullfrog's Croak (From Capranica [3]) bullfrog approaches adulthood [9]. It seems then, that only the mature males can act as centers for mate calling, simply as a result of growth.

## II. STATEMENT OF PURPOSE

The foregoing review of literature has indicated an increasing interest in and basic research questions that are proposed by a study of the sense of hearing in amphibians.

There are three main objectives of this study. The objectives and specific questions to be investigated follow.

### Objective I.

To describe the mechanical response of the tympanic membrane of the bullfrog *(Rana catesbeiana)* as observed from visible displacement in response to pure tone stimuli of varying intensity and frequency.

1. What intensity is required to produce a just-visible movement at each frequency tested?
2. Does this required intensity vary as a function of the stimulating frequency; that is, can sensitive frequencies or "best frequencies" be defined mechanically?
3. What range of frequencies evokes visible responses?

### Objective II.

To compare mechanical response with previous electrophysiological findings.

1. Are mechanically and electrophysiologically defined sensitive frequencies similar?
2. What is the relation of mechanical and electrophysiological responses with regard to the range of frequency sensitivity?

Objective III.

To explore the relationship between tympanic membrane size and the intensity necessary to elicit a just-visible movement.

## III. DEFINITIONS OF TERMS USED

*Mechanical response* refers to the purely physical reaction of the auditory system to an atmospheric pressure change. Such response of the tympanic membrane will be operationally defined for this study as any visible vibratory movement of the membrane accompanying an experimentally induced pressure change.

*Threshold of visible mechanical response (VMR)* refers to the highest intensity level at which no movement can be detected by the unaided eye.

*Electrophysiological indicators of hearing* refers to the unconditioned responses to acoustic stimuli as electrically recorded from the inner ear of the bullfrog.

# CHAPTER II

# PROCEDURES

## I. SUBJECTS

The subjects used in this research consisted of seven healthy bullfrogs *(Rana catesbeiana)*. This particular animal was chosen because most of the experimental data on hearing in amphibians has been concerned with this species. Bullfrogs possess large, easily viewed tympanic membranes and cooperate well during testing without being anesthetized. The objective of selecting these particular frogs was to obtain a sample of various sizes of membranes--small, medium, and large. The sizes were operationally defined as: small, those with a total surface area of from 0 to 103 $mm^2$; medium, those with a total surface area of from 104 to 207 $mm^2$; and large, those with a total surface area of from 208 $mm^2$ up. Of the animals this investigator was able to select from, one had a small tympanic membrane, four had medium-size membranes, and two had large membranes. Table I lists each frog with its corresponding membrane dimensions (length, height, and total surface area).

## II. APPARATUS

The stimulus tone was produced by a Hewlett-Packard Model 204B electronic oscillator operating into a 15-inch Altec Lansing loudspeaker attached to a resonator. Additional equipment included a McIntosh 75-watt power amplifier for increasing the intensity of the stimulus tone; a one-inch Brüel and Kjaer microphone; a Brüel and Kjaer Type 2603

## TABLE I

## TYMPANIC MEMBRANE DIMENSIONS

| FROG | LENGTH | HEIGHT | TOTAL SURFACE AREA |
|---|---|---|---|
| #1 | 20 mm | 19 mm | 298 $mm^2$ (L) |
| #2 | 17 mm | 15.5 mm | 207 $mm^2$ (M) |
| #3 | 17 mm | 17.5 mm | 234 $mm^2$ (L) |
| #4 | 10 mm | 11 mm | 86 $mm^2$ (S) |
| #5 | 15 mm | 15 mm | 177 $mm^2$ (M) |
| #6 | 15.5 mm | 15 mm | 179 $mm^2$ (M) |
| #7 | 15 mm | 15 mm | 177 $mm^2$ (M) |

(L) = Large membrane: 208 $mm^2$ and up

(M) = Medium membrane: 104-207 $mm^2$

(S) = Small membrane: 0-103 $mm^2$

microphone amplifier for measuring the intensity of the signal; and a General Radio Strobotak for stroboscopic illumination of the vibratory movement of the tympanic membrane.

## III. PROCEDURE

Each frog was labeled and his tympanic membrane measured. Two millimeter-scale measurements of the tympanic membrane were made: (1) width, from the most rostral to the most caudal point on the membrane; and (2) height, from the most dorsal to the most ventral point on the membrane. The right tympanic membrane was used in each experiment for consistency.

The investigator held the frog on a platform in front of the resonator which connected to the loudspeaker. Figure V shows the frog in a resting position (tied) with the equipment ready for testing. During testing, the tympanic membrane was positioned approximately one-fourth of an inch in front of the half-inch hole in the end of the resonator. The Strobotak was positioned and aimed to allow maximum illumination of the tympanic membrane.

The oscillator was set at a certain frequency, and the Strobotak was set near a corresponding harmonic of the stimulus tone. Intensity of the stimulus tone was increased by a manual control on the amplifier until visible movement of the tympanic membrane was detected. If no movement was noted when the amplifier was at maximum output, the Strobotak was manipulated to determine if another setting near a harmonic of stimulus tone might produce more movement or more visible movement. When the setting on the Strobotak showing greatest visible displacement of the membrane was located, the intensity was decreased manually just

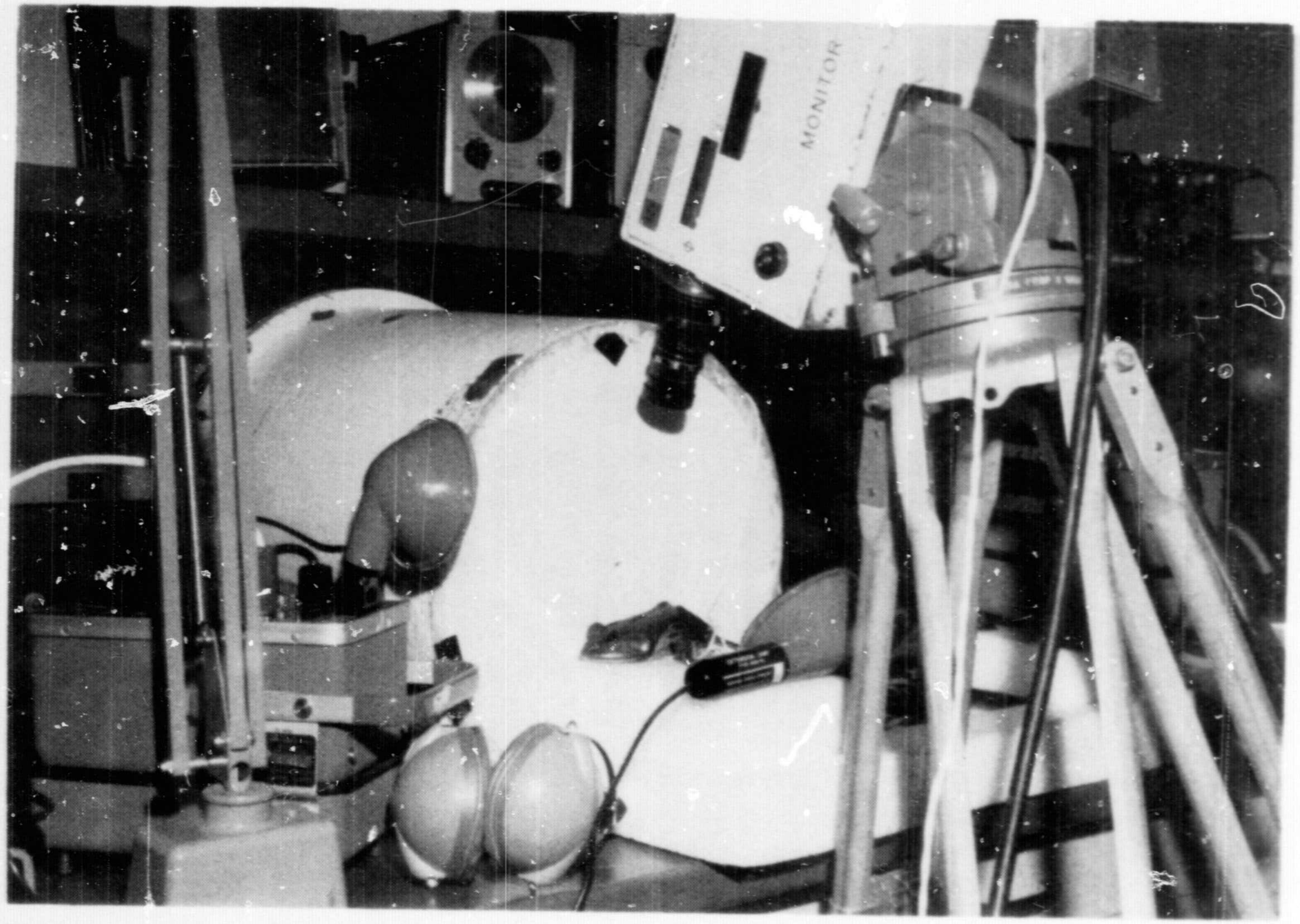

FIGURE V. Frog on Testing Stage

to the point where no movement could be visually detected. This intensity level was operationally defined as the threshold of VMR. The intensity of the stimulus tone at this point was measured by putting the Brüel and Kjaer microphone in approximately the same position as was the frog's tympanic membrane. The intensity level was read from the Brüel and Kjaer microphone amplifier and recorded as threshold.

The lowest frequency used for the stimulus tone was 40 CPS, the lowest frequency producing clear movement. Lower frequencies, down to 6 CPS, produced oscillations; but the speaker would not produce true sine waves at the low levels. Frequency was increased in steps of 20, 30, 40, and 100 CPS, depending upon the stability of the threshold curves as seen from the earliest results, until movement of the membrane was no longer visible at maximum output of the amplifier. Thresholds of visible mechanical response measured as a sound pressure level in db above 0.0002 dyne/cm$^2$ or no response (NR) were recorded for each frequency tested. The range of 670 to 4,170 rpm's on the Strobotak stroboscopically slowed the vibratory motion of the tympanic membrane so that the motion could be viewed by the unaided eye.

# CHAPTER III

# RESULTS AND DISCUSSION

## I. RESULTS

The resulting threshold of visible mechanical response for each frequency tested for each frog is given as a sound pressure level in decibels above 0.0002 dyne/cm$^2$. The table of threshold values may be found in Appendix I.

Figures VI-XII graphically represent the threshold of VMR curves for individual frogs. Specific data points are shown on each graph which plots frequency as a function of intensity. Curves within experimental error limits (± 5 db) show trends of each set of data points.

## II. DISCUSSION

Only after mathematical calculations and a preliminary pilot study did the anticipated visible displacement of the frog's tympanic membrane materialize. A frog could be tested over the desired frequencies in about two hours, resting quietly throughout the testing unless there was a sudden change in intensity and/or frequency or visual stimulation. Movement of the membrane varied from very large excursions at the lower frequencies with the membrane acting as a single unit, to a shimmering motion at the higher frequencies with a segmental vibration of the membrane.

If no mechanical tuning influenced the response of the membrane, the intensity necessary to produce threshold responses should have

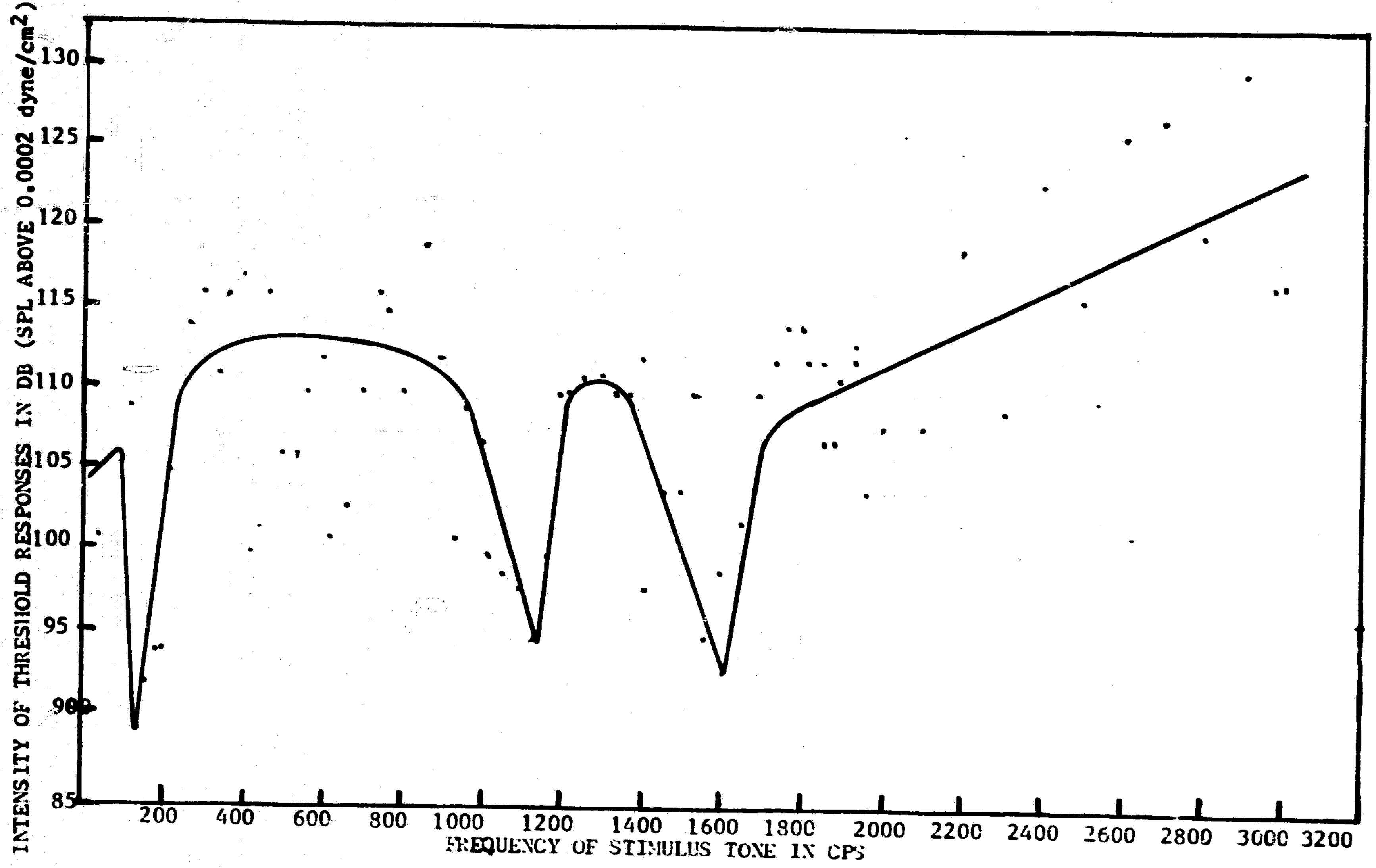

FIGURE VI. Visible Mechanical Response Curve - Frog #1

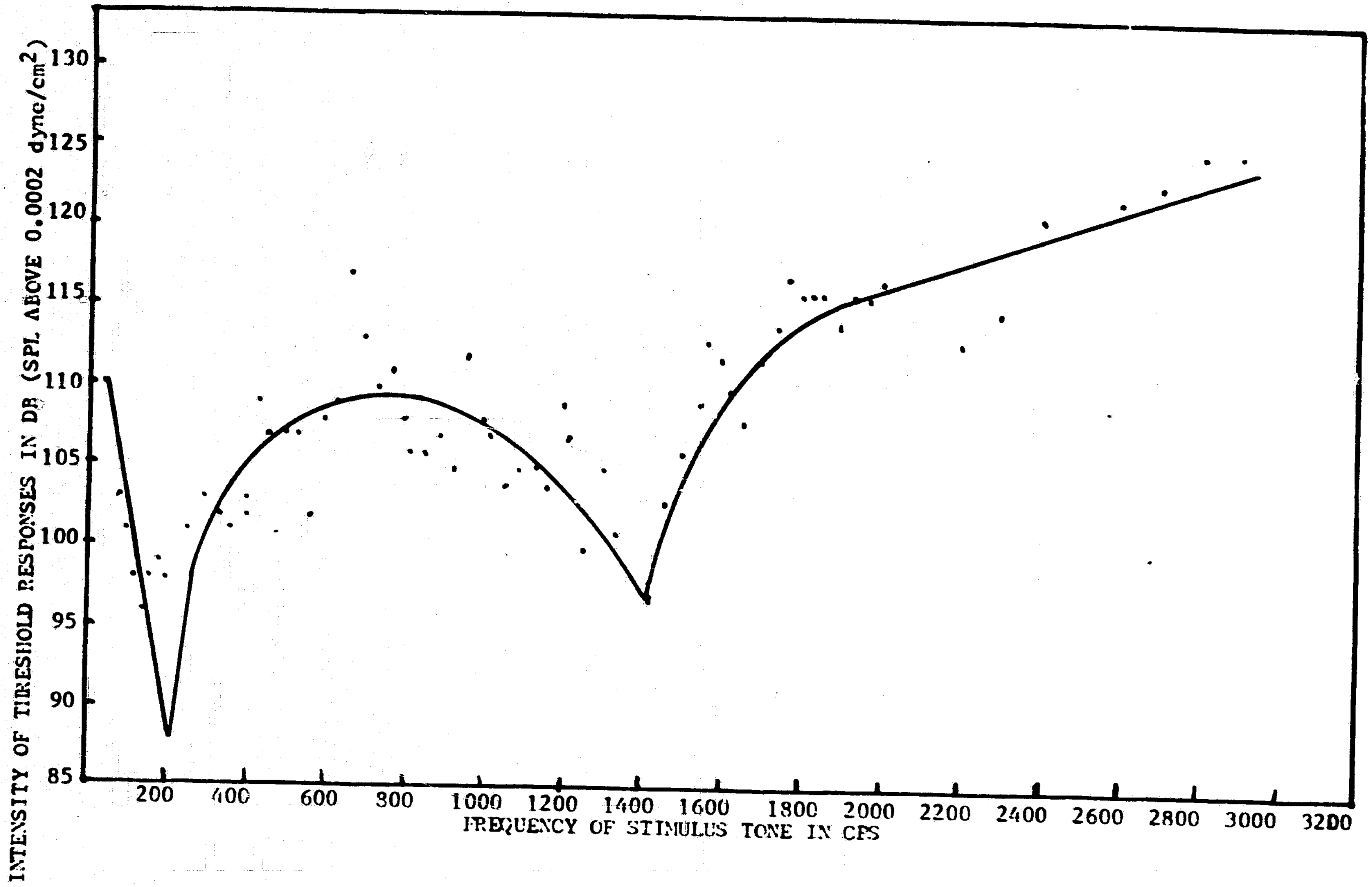

FIGURE VII. Visible Mechanical Response Curve - Frog #2

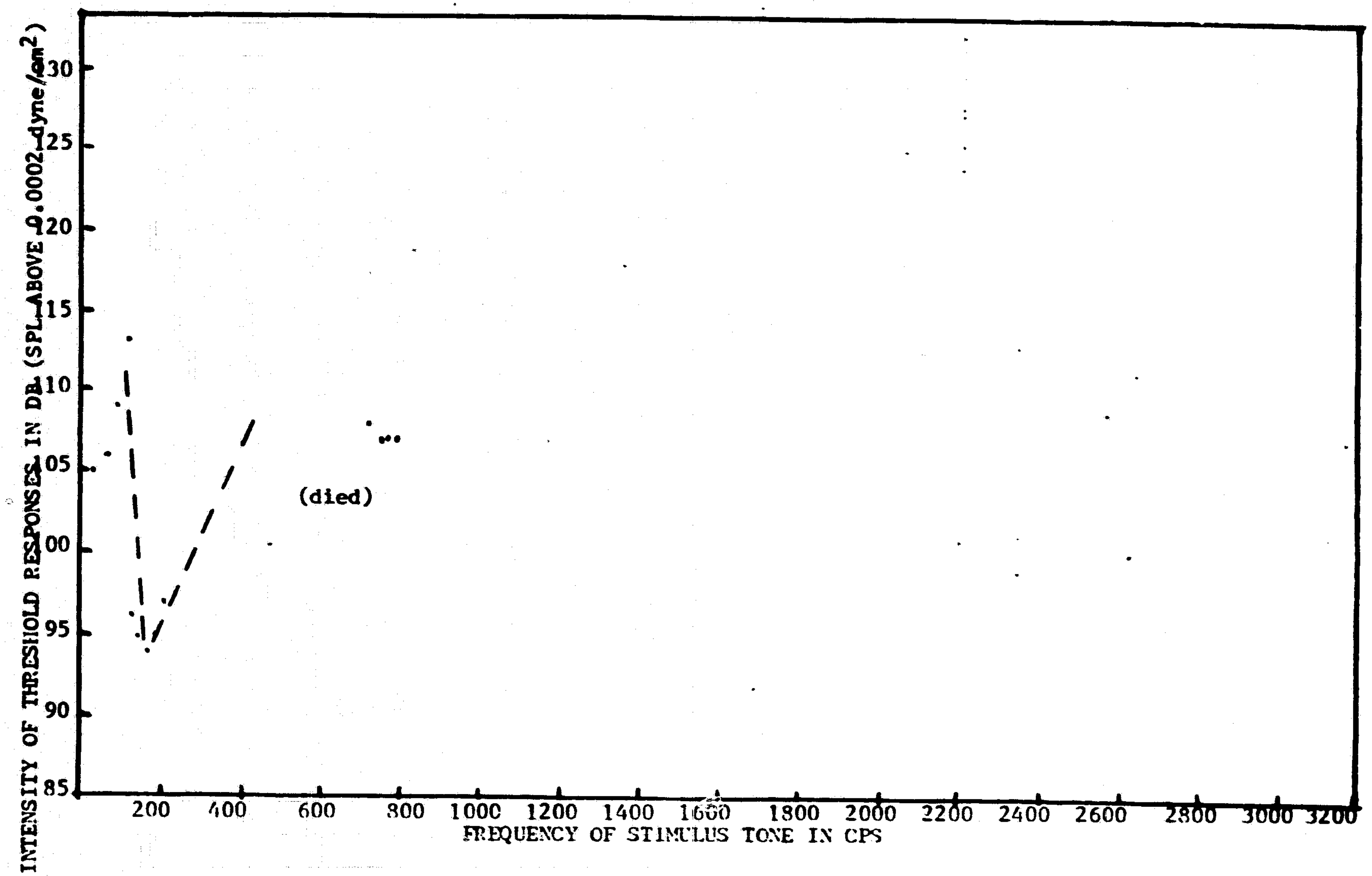

FIGURE VIII. Visible Mechanical Response Curve - Frog #3

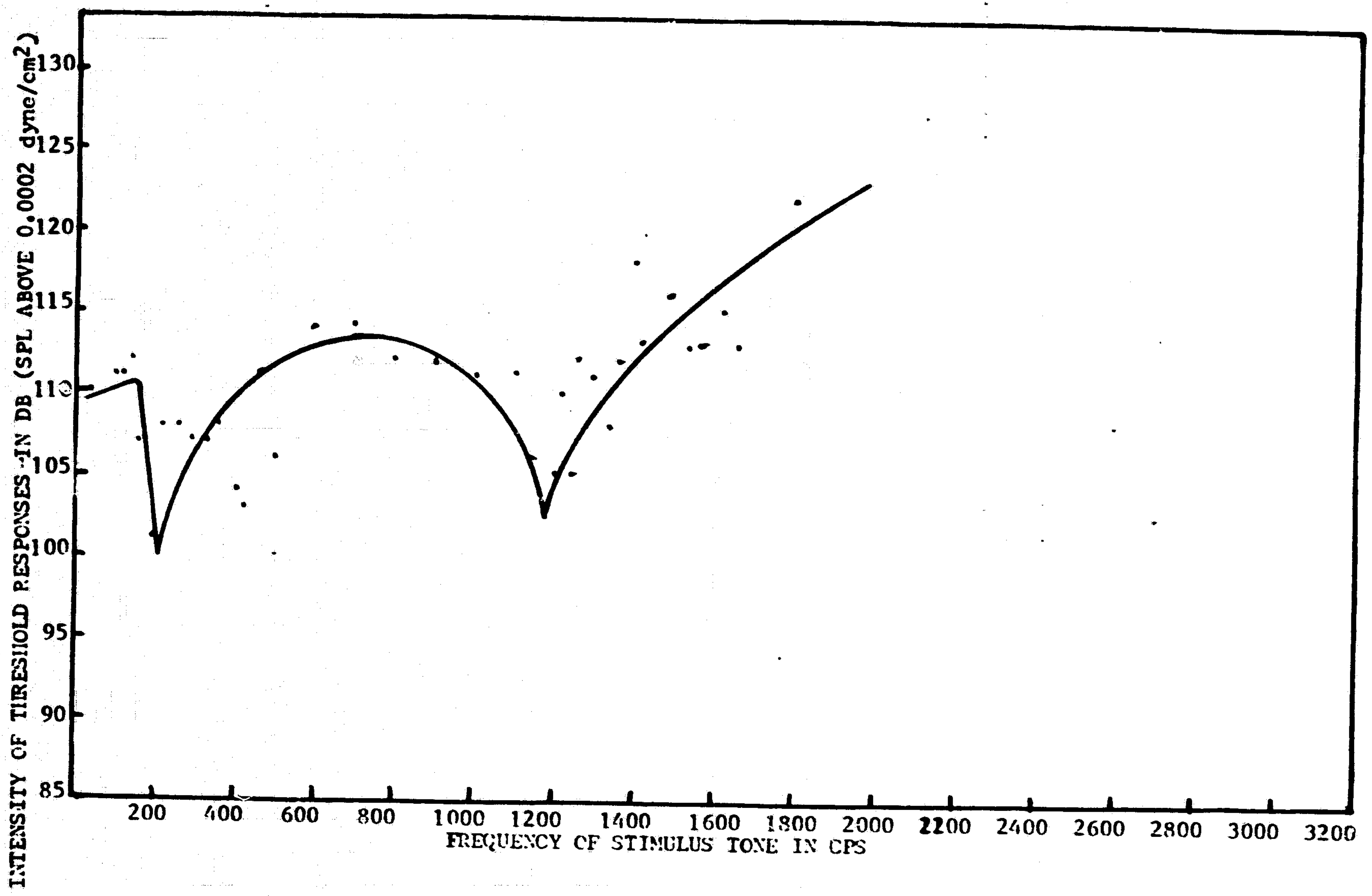

FIGURE IX. Visible Mechanical Response Curve - Frog #4

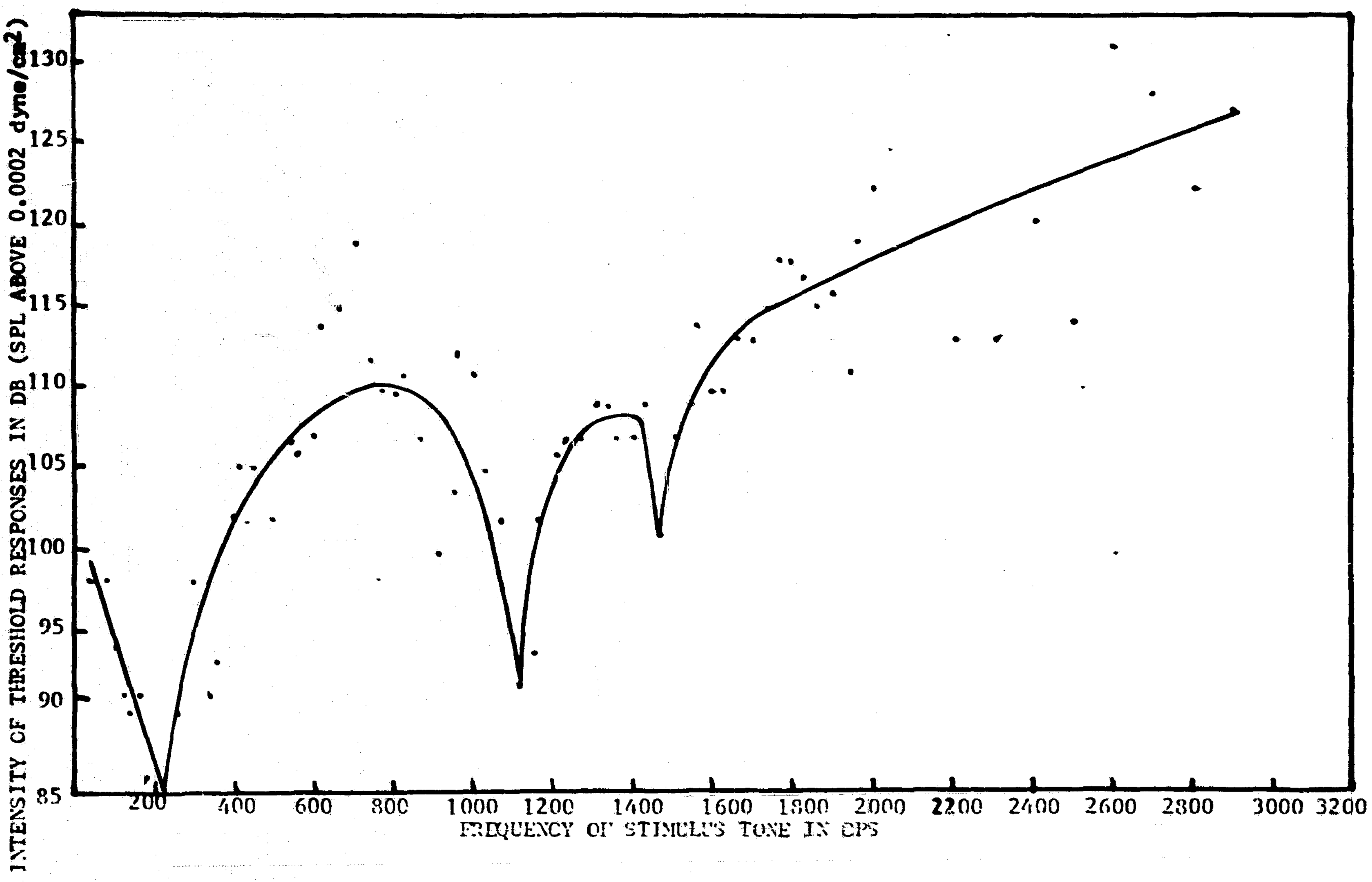

FIGURE X. Visible Mechanical Response Curve - Frog #5

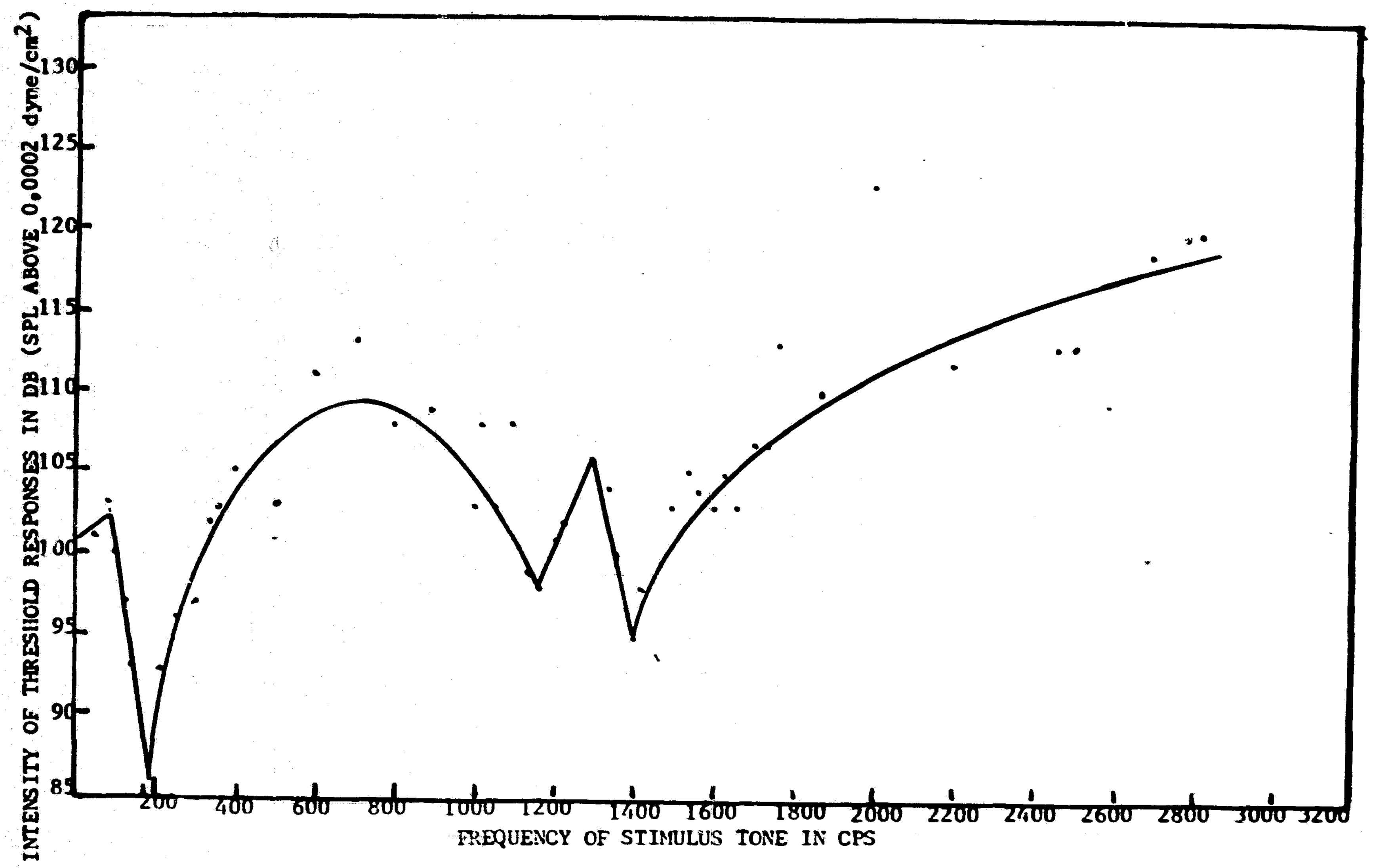

FIGURE XI. Visible Mechanical Response Curve - Frog #6

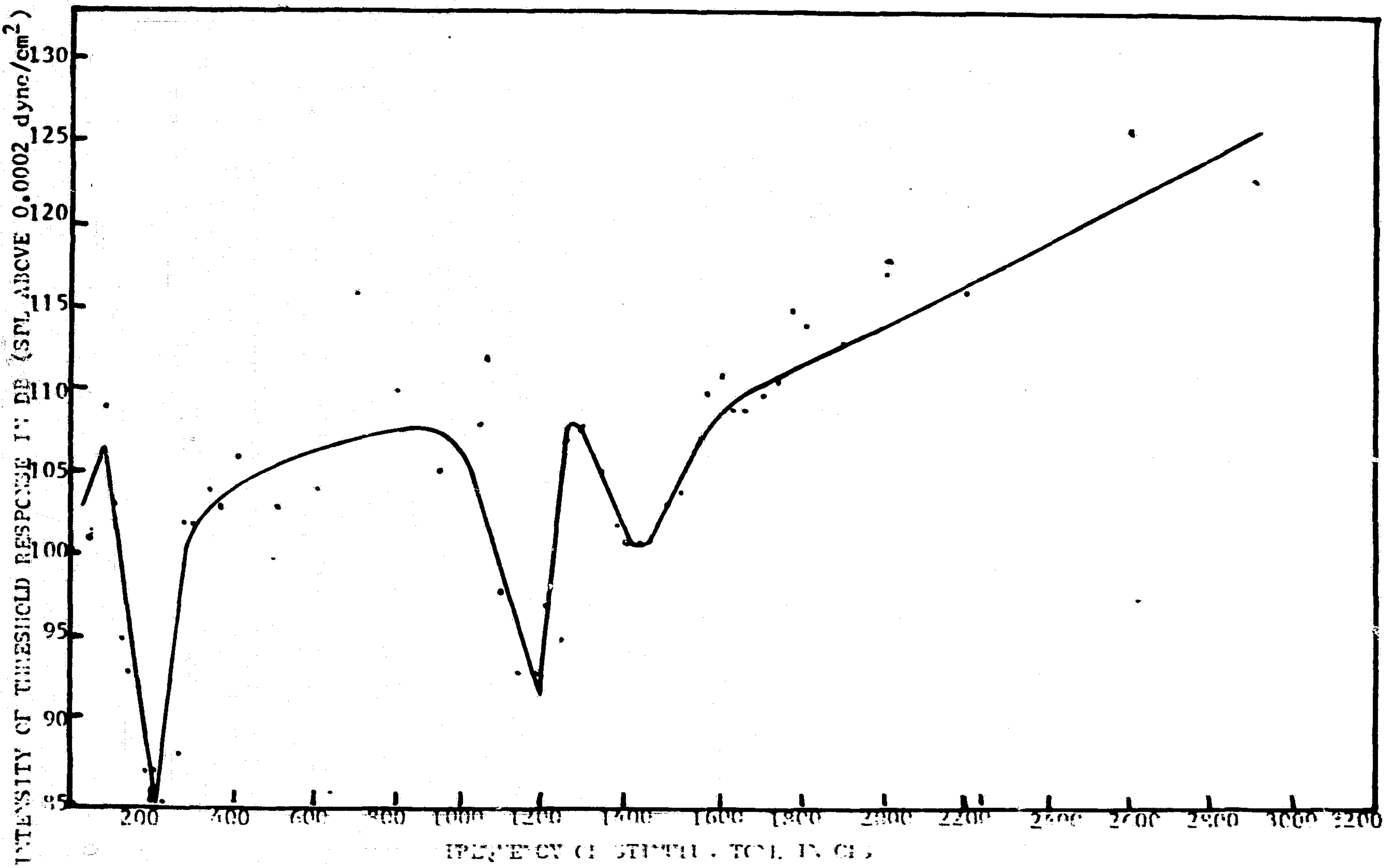

FIGURE XII. Visible Mechanical Response Curve - Frog #7 increased linearly with an increase in frequency. As Figures VI-XII show, however, this is not the case with frogs. There is not a completely linear relationship between intensity and frequency. Some type of mechanical tuning seemed to be influencing the responses of their membranes at certain frequencies. Each frog extensively tested showed two definite sensitive areas or "best frequency" areas. One sensitive area or peak normally fell below 300 CPS; usually between 150 CPS and 250 CPS. The second sensitive area or peak fell between 1,000 CPS and 1,600 CPS and often had two maxima.

It is more than coincidental that the two "best frequencies" or areas of "best frequencies" determined through the electrophysiological studies [7, 8] closely correspond with the mechanically defined sensitive frequencies found through this study. "Simple units", derived from the basilar papillae, had their best frequency between 1,000 and 1,500 CPS; while "complex units", derived from the amphibian papillae, had their best frequency below 700 CPS, usually between 700 and 200 CPS [7, 8]. With this direct relationship between the mechanical response and the electrophysiological response in the auditory system of the frog, a simple neurological system which can transmit linearly what the peripheral system receives becomes apparent for the first time in nature.

Additionally, the energy peaks in the mating croak--a low-frequency peak between 200 and 700 CPS, and a high-frequency peak centered around 1,400-1,600 CPS [9]--reveal a striking relationship between the area of greatest intensity in the mating call and the areas of greatest mechanical sensitivity of the membrane. A biological significance to the development of these sensitive areas apparently exists (Figure XIII).

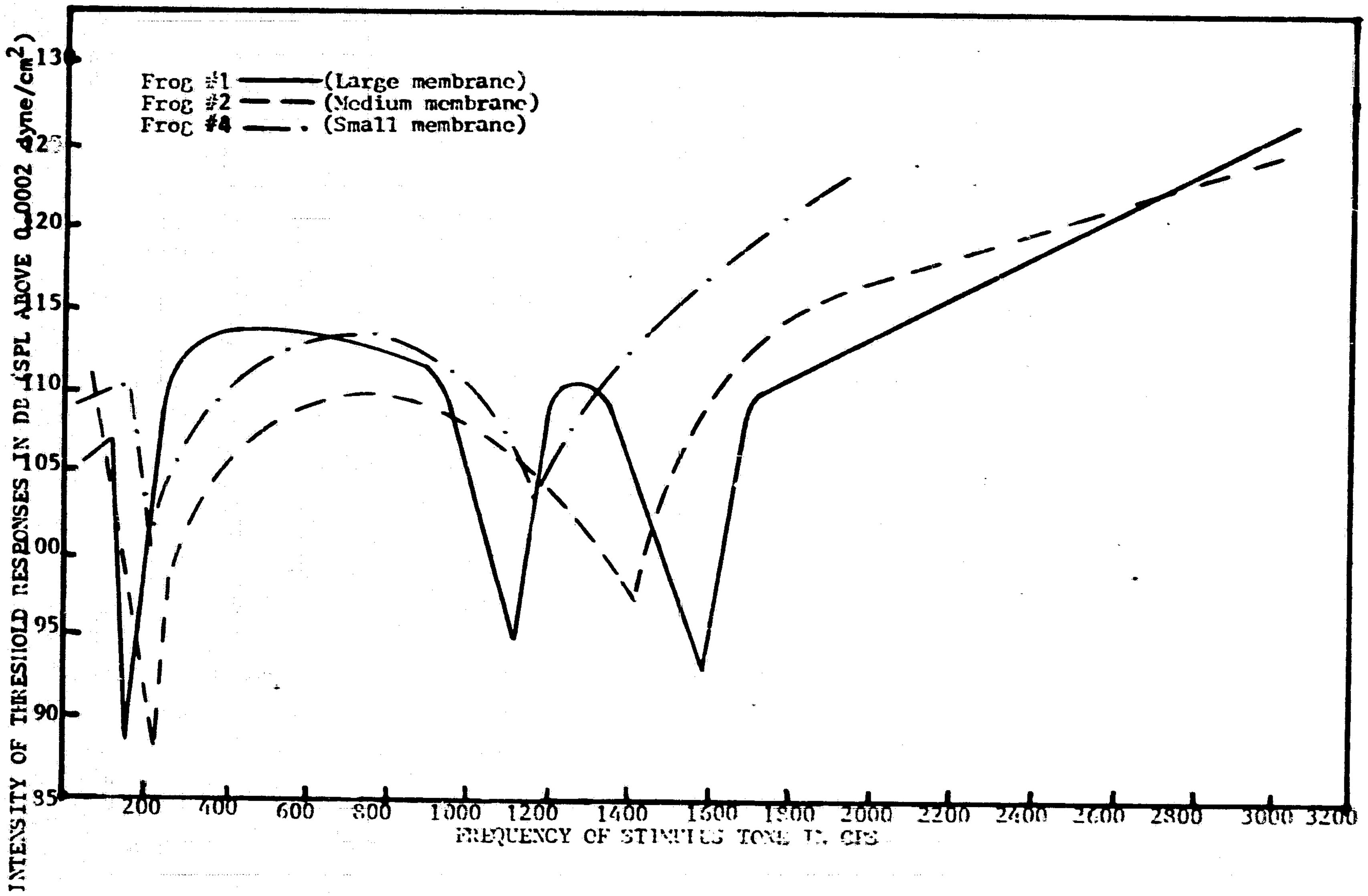

FIGURE XIII. Visible Mechanical Response Curves - Frogs #1, #2, and #4

Younger bullfrogs which possess the smaller membranes do not take part in the mating procedures; thus do not need to be sensitive to the mating call. As the frog ages, his membrane enlarges and his auditory system refines until he becomes able to hear the frequencies in the same way as an adult frog. Capranica's [3] views of the evoked calling being strongly predetermined at the peripheral level of the auditory nervous system may be true for the system as far peripherally as the tympanic membrane itself.

The curves in Figures VI-XII also show that the range of responsive frequencies varied from frog to frog. The larger the membrane, the higher the upper limit of visible response frequencies (Figure XIII). Nevertheless, no response was recorded for any frog above 3,100 CPS. The higher the stimulating frequency, the smaller the excursions of the membrane and the more difficult it became to see motion of the membrane. The unaided eye has a constant point (1' arc) beyond which any motion will be detected and below which any motion will not be detected. It is not an absolute threshold of the frog's hearing, but it can be used as an accurate repeatable measure of motion. Undoubtedly, the membrane continued to vibrate beyond what the unaided eye could detect. Yet, due to the similarity of upper limits set by both types of studies--mechanical and electrophysiological--it suggests that the actual upper limit of mechanical response is near the limit of VMR. The upper frequency limit as determined by the electrophysiological studies was not above 3,000-4,000 CPS [7, 8, 21].

Intensity necessary to produce threshold responses also varied between frogs (Figure XIII). As one would expect, the smaller the membrane the more intensity it required to drive it to a visible displacement. Figure XIII shows that with an increase in size, the intensity necessary to elicit a response is decreased. The necessary intensity to produce threshold responses ranged from 85 db to 142 db.

The largest and smallest membranes differed in total surface area by 212 $mm^2$. Table II shows the percentage of frequencies tested which differed in threshold values by ± 0 through ± 12 db. Only 69 percent of the frequencies tested were within experimental error limits. The small membrane showed sensitive areas just as the large membrane did within the electrophysiologically defined "best frequencies", but the areas were not as pronounced and sensitive as those of the large membrane. Table III shows the percentage of frequencies in each frequency range group indicated which were similar (within a ± 5 db limit) or not similar. Ranges with the highest percentages of non-similar frequencies are those which encompass peak areas and the high frequencies in which the small membrane stopped responding.

Frogs number 5 and 7 possessed identical membrane dimensions. Table IV denotes the percentage of frequencies tested which differed in threshold values by ± 0 through ± 6 db. Ninety-three percent of the frequencies tested were within experimental error limits.

The frog is a much neglected, although excellent, subject for basic auditory research. He possesses a simple neurological system which lends itself to the evolutionary study of a highly complicated vertebrate system. Through study of the amphibians' hearing, we may be able to advance our state of knowledge to become commensurate with its importance in the study of the evolution of the sense of hearing.

TABLE II

THRESHOLD DIFFERENCES BETWEEN LARGE AND SMALL MEMBRANES

| DIFFERENCE OF | % OF FREQUENCIES | CUMULATIVE % |
|---|---|---|
| ± 0 db | 15% | 15% |
| ± 1 db | 13% | 28% |
| ± 2 db | 23% | 51% |
| ± 3 db | 5% | 56% |
| ± 4 db | 13% | 69% |
| ± 5 db | 0% | 69% |
| ± 6 db | 15% | 84% |
| ± 7 db | 0% | 84% |
| ± 8 db | 5% | 89% |
| ± 9 db | 5% | 94% |
| ± 10 db | 0% | 94% |
| ± 11 db | 3% | 97% |
| ± 12 db | 3% | 100% |

## TABLE III

## SIMILAR AND NON-SIMILAR FREQUENCY RANGES IN LARGE AND SMALL MEMBRANES

| FREQUENCY RANGE | % SIMILAR | % NON-SIMILAR |
|---|---|---|
| 40-100 CPS | 100% | 0% |
| 100-300 CPS | 62% | 38% |
| 300-1000 CPS | 91% | 9% |
| 1000-1600 CPS | 60% | 40% |
| 1600 CPS and up | 5% | 95% |

## TABLE IV

## THRESHOLD DIFFERENCES BETWEEN IDENTICAL MEMBRANES

| DIFFERENCE OF | % OF FREQUENCIES | CUMULATIVE % |
|---|---|---|
| ± 0 db | 20% | 20% |
| ± 1 db | 15% | 35% |
| ± 2 db | 40% | 75% |
| ± 3 db | 4% | 79% |
| ± 4 db | 8% | 87% |
| ± 5 db | 6% | 93% |
| ± 6 db | 8% | 101%* |

*error by rounding

# CHAPTER IV

# SUMMARY AND CONCLUSIONS

## I. SUMMARY

The purpose of this study was to investigate the mechanical response of the tympanic membrane of the bullfrog *(Rana catesbeiana)* and its relationship to the hearing curves found previously by electrophysiological techniques. Seven subjects were employed in this study. Each bullfrog was subjected to pure tones ranging from 40 CPS to 3,100 CPS at intensities ranging from 85 db to 142 db SPL. The tympanic membrane was viewed under stroboscopic illumination, and thresholds of visible mechanical response were recorded.

## II. CONCLUSIONS

1. The intensity necessary to produce a just-visible movement of the bullfrog's tympanic membrane varies as a function of the stimulating frequency, and sensitive frequencies or "best frequencies" can be defined mechanically.
2. Two sensitive areas are defined mechanically. One area falls below 300 CPS, usually between 150 and 250 CPS. The second area falls between 1,000 and 1,600 CPS.
3. These sensitive areas fall within the "best frequency" limits as defined electrophysiologically.
4. Less intensity is necessary to elicit a just-visible response.

5. A range of frequencies from 40 CPS to 3,100 CPS produced visible mechanical responses.
6. With a direct relationship between mechanical response and electrophysiological response in the auditory system of the frog, a simple neurological system transmitting linearly what the peripheral system receives is apparent for the first time in nature.

## III. IMPLICATIONS FOR FURTHER STUDY

1. A study of the mechanical response of the tympanic membrane after disarticulating the ossicular chain.
2. A study of the mechanical response of the ear not being directly stimulated. Observations during testing revealed a mechanical response 180 degrees out of phase with the ear being stimulated directly.
3. A study of the mechanical response of the tympanic membrane of the green frog.
4. A histological study of the relationship between basilar papillae development and tympanic membrane growth.

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# APPENDIX

## TABLE V

## THRESHOLDS OF VISIBLE MECHANICAL RESPONSE
SPL IN DB ABOVE 0.0002 dyne/cm$^2$

| CPS | FROG 1 | FROG 2 | FROG 3 | FROG 4 | FROG 5 | FROG 6 | FROG 7 |
|---|---|---|---|---|---|---|---|
| 40 | 101 | 110 | 105 | 110 | 98 | 101 | 101 |
| 50 | 103 | 114 | 107 | --- | 93 | 101 | 103 |
| 60 | 106 | 102 | 106 | --- | 98 | 98 | 107 |
| 70 | 110 | 103 | 107 | --- | 95 | 104 | 105 |
| 80 | 110 | 103 | 106 | --- | 98 | 103 | 109 |
| 90 | 111 | 106 | 107 | --- | 92 | 100 | 105 |
| 100 | 111 | 101 | 109 | 111 | 94 | 100 | 103 |
| 120 | 109 | 98 | 113 | 111 | 91 | 97 | 95 |
| 140 | 89 | 96 | 96 | 112 | 90 | 93 | 93 |
| 160 | 92 | 98 | 95 | 107 | 91 | 85 | 92 |
| 180 | 94 | 99 | 94 | 107 | 86 | 85 | 87 |
| 200 | 94 | 98 | 95 | 101 | 85 | 85 | 87 |
| 230 | 105 | 88 | 97 | 108 | 85 | 93 | 85 |
| 260 | 114 | 101 | --- | 108 | 90 | 96 | 88 |
| 300 | 116 | 103 | --- | 107 | 98 | 97 | 102 |
| 330 | 111 | 102 | --- | 107 | 91 | 102 | 104 |
| 360 | 116 | 101 | --- | 108 | 93 | 103 | 103 |
| 400 | 117 | 103 | --- | 104 | 102 | 105 | 106 |
| 430 | 100 | 109 | --- | 103 | 105 | --- | --- |
| 460 | 116 | 107 | --- | 111 | 105 | --- | --- |
| 500 | 106 | 107 | --- | 106 | 102 | 103 | 103 |
| 530 | 106 | 107 | --- | --- | 107 | --- | --- |
| 560 | 110 | 102 | --- | --- | 106 | --- | --- |
| 600 | 112 | 108 | --- | 114 | 107 | 111 | 104 |
| 630 | 101 | 109 | --- | --- | 114 | --- | --- |
| 660 | 103 | 117 | --- | --- | 115 | --- | --- |
| 700 | 110 | 113 | --- | 114 | 119 | 113 | 116 |
| 730 | 116 | 110 | 108 | --- | 112 | --- | --- |
| 760 | 115 | 111 | 107 | --- | 110 | --- | --- |
| 800 | 110 | 108 | 107 | 112 | 110 | 108 | 110 |
| 830 | NR 117 | 106 | --- | --- | 111 | --- | --- |
| 860 | 118 | 106 | --- | --- | 107 | --- | --- |
| 900 | 112 | 107 | --- | 112 | 100 | 109 | 105 |
| 930 | 101 | 105 | --- | --- | 104 | --- | --- |
| 960 | 109 | 112 | --- | --- | 112 | --- | --- |
| 1000 | 107 | 108 | --- | 111 | 111 | 103 | 108 |
| 1030 | 100 | 107 | --- | --- | 105 | 108 | 112 |
| 1060 | 99 | 104 | --- | --- | 102 | 103 | 98 |
| 1100 | 98 | 105 | --- | 111 | 92 | 108 | 93 |
| 1130 | 95 | 105 | --- | 106 | 94 | 99 | 93 |
| 1160 | 100 | 104 | --- | 103 | 102 | 98 | 97 |

## TABLE V (CONTINUED)

### THRESHOLDS OF VISIBLE MECHANICAL RESPONSE
### SPL IN DB ABOVE 0.0002 dyne/cm$^2$

| CPS | FROG 1 | FROG 2 | FROG 3 | FROG 4 | FROG 5 | FROG 6 | FROG 7 |
|---|---|---|---|---|---|---|---|
| 1200 | 110 | 109 | --- | 105 | 106 | 101 | 95 |
| 1230 | 110 | 107 | --- | 110 | 107 | 102 | 107 |
| 1260 | 111 | 100 | --- | 112 | 107 | 101 | 108 |
| 1300 | 111 | 105 | --- | 111 | 109 | 106 | 105 |
| 1330 | 110 | 101 | --- | 108 | 109 | 104 | 103 |
| 1360 | 110 | NR 115 | --- | 112 | 107 | 100 | 102 |
| 1400 | 112 | 104 | --- | 118 | 107 | 95 | 102 |
| 1430 | 98 | 97 | --- | 113 | 109 | 98 | 102 |
| 1460 | 104 | 103 | --- | NR 117 | 101 | 94 | 104 |
| 1500 | 104 | 106 | --- | 116 | 107 | 103 | 105 |
| 1530 | 110 | 109 | --- | 113 | 109 | 105 | 108 |
| 1560 | 95 | 113 | --- | 113 | 114 | 104 | 111 |
| 1600 | 99 | 112 | --- | 117 | 110 | 103 | 112 |
| 1630 | 93 | 110 | --- | 115 | 110 | 105 | 110 |
| 1660 | 102 | 108 | --- | 113 | 113 | 103 | 110 |
| 1700 | 110 | 112 | --- | NR 120 | 113 | 107 | 111 |
| 1730 | 112 | 114 | --- | --- | 115 | 107 | 112 |
| 1760 | 114 | 117 | --- | --- | 118 | 113 | 116 |
| 1800 | 114 | 116 | --- | 122 | 118 | 116 | 115 |
| 1830 | 112 | 116 | --- | --- | 117 | --- | --- |
| 1860 | 107 | 116 | --- | --- | 115 | --- | --- |
| 1900 | 111 | 114 | --- | NR 123 | 116 | 110 | 114 |
| 1930 | 113 | 116 | --- | --- | 111 | --- | --- |
| 1960 | 104 | 116 | --- | --- | 119 | --- | --- |
| 2000 | 108 | 117 | --- | NR 126 | 122 | 123 | 118 |
| 2100 | 108 | NR 116 | --- | --- | NR 116 | --- | NR 120 |
| 2200 | 119 | 113 | --- | --- | 113 | 112 | 116 |
| 2300 | 109 | 115 | --- | --- | 113 | --- | --- |
| 2400 | 123 | 121 | --- | --- | 120 | --- | --- |
| 2500 | 116 | NR 116 | --- | --- | 114 | 113 | --- |
| 2600 | 126 | 122 | --- | --- | 131 | --- | --- |
| 2700 | 127 | 123 | --- | --- | 128 | 119 | 126 |
| 2800 | 120 | 125 | --- | --- | 122 | --- | --- |
| 2900 | 130 | 125 | --- | --- | 127 | 120 | 123 |
| 3000 | 117 | --- | --- | --- | NR 122 | NR 123 | NR 123 |
| 3100 | 142 | NR 125 | --- | --- | --- | --- | --- |
| 3200 | NR 145 | --- | --- | --- | --- | --- | --- |
| 3600 | NR 130 | NR 110 | --- | --- | NR 112 | NR 113 | NR 112 |
| 4000 | NR 110 | NR 103 | --- | --- | NR 107 | NR 103 | NR 105 |
| 5000 | NR 125 | NR 112 | --- | --- | NR 115 | NR 113 | NR 113 |
| 6000 | NR 126 | NR 80 | --- | --- | NR 97 | NR 98 | NR 97 |

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