# NEURAL EFFECTS OF ACOUSTIC OVERLOAD: A SINGLE UNIT ANALYSIS OF FREQUENCY-DEPENDENT DEPRESSION

by

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# INTRODUCTION

The salient features of the discharge characteristics of cochlear nerve fibers were first described by Tasaki (1954). In later studies, a number of investigators have extended Tasaki's observations and described many of the functional properties of primary cochlear nerve fibers in response to acoustic stimuli. Nevertheless, although many basic properties of cochlear nerve fibers are understood, other questions remain to be answered, because of the difficulty of studying these first-order fibers for extended periods of time. One such topic which has received little attention previously concerns the problem of acoustic overstimulation and recovery. This is an issue which has profound implications for our understanding of both normal and pathological hearing processes, yet very little is known about the behavior of single cochlear nerve fibers during exposure to intense stimulation. In the investigation to be described, the method of single unit analysis was applied to the cochlear nerve in an attempt to understand some of the mechanisms which underlie acoustic overload of the ear.

## I. Anatomy and Physiology of Peripheral Auditory System

To enable a better understanding of both the experimental rationale and the surgical and other procedures to be described in the METHODS section, it is pertinent to provide a brief review of peripheral auditory physiology.

### A. Cochlear Mechanics

The inner ear, or cochlea, is a fluid-filled bony structure that contains the specialized receptor elements of the organ of Corti and the peripheral portions of the cochlear nerve. The mechanics of the transformation of acoustic energy into neural energy which is performed by the cochlea are thought to occur in the organ of Corti, which contains the sensory hair cells, supporting cells and neural elements. The hair cells are probably the mechano-electric transducers, and are arranged in three rows of outer and one row of inner hair cells. The organ of Corti rests on the basilar membrane which appears to be one of the integral features permitting mechanical movement resulting from sound.

In normal mammalian hearing, mechanical events in the inner ear give rise to discharges in the afferent fibers of the cochlear nerve. Almost all direct knowledge of cochlear mechanics comes from the classic work of Békésy (1960). His observations of the vibratory motion of the basilar membrane in cadaver ears provided a systematic foundation for all modern acoustic theory. These observations were, however, limited to low frequency, high intensity stimuli. More recent data (collected from areas of the basilar membrane farther away from the apex, in live specimens, and using more sophisticated measurement) have corroborated Békésy's most important discovery, i.e., the fact that the basilar membrane supports a frequency-dependent travelling wave. That is to say, different acoustic frequencies will generate maximal displacement of the basilar membrane at different locations along the basilar membrane (Johnstone, Taylor, & Boyle, 1970; Rhode, 1971; Wilson & Johnstone, 1972). High frequencies are maximally effective near the base of the cochlea, and low frequencies produce their maxima closer to the apex.

## B. Cochlear Anatomy

The hair cells are specialized receptor cells that receive at their bases the peripheral ends not only of the first-order afferent fibers, but also of efferent fibers to the cochlea. The cell bodies of the afferent fibers are the spiral ganglion cells which lie in a bony core, the modiolus of the cochlea, and exhibit two processes, one extending peripherally to the organ of Corti, the other extending centrally through the internal auditory meatus to the cochlear nucleus of the medulla. Both the peripheral and central extensions are axonal in structure and are considered parts of the cochlear branch of the eighth cranial nerve. The central extensions of the spiral ganglion cells in the internal auditory meatus are covered by Schwann cells up to the point where they reach the interstitial nucleus of the cochlear nucleus and become associated with neuroglial elements.

The number of fibers in the cat's auditory nerve has been estimated at approximately 50,000 (Gacek & Rasmussen, 1961). These fibers have a unimodal distribution of diameter with almost all the fiber diameters falling between 2 and 4 μm. At the central end of the internal auditory meatus, the 600 efferent cochlear nerve fibers run in the vestibular portion of the eighth nerve (Gacek, 1969).

The description of fibers and their endings at either the peripheral end in the cochlea or at the central end in the cochlear nucleus is extremely complicated. Although all details are not completely known, extensive studies with the electron microscope during the past decade have provided some generally accepted descriptions of the intricate morphology of the synaptic connections of the cochlear nerve fibers with the hair cells.

Spoendlin (1969; 1974) has shown in the cat that whereas approximately 90% of the afferent nerve fibers originate at inner hair cells, only 10% originate at the outer hair cells. In addition, the afferent nerve fibers innervating outer hair cells connect to a large number of hair cells, each fiber supplying as many as ten cells and one hair cell being supplied by a number of fibers (Engström, Ades & Anderson, 1966); whereas those innervating inner hair cells only connect to one hair cell, each cell receiving as many as twenty fibers (Spoendlin, 1966).

### C. Neurophysiology of Cochlear Nerve Fibers

Kiang and his associates, in a series of studies dealing with discharge patterns of single units in the eighth nerve, have summarized some general electrophysiological characteristics of cochlear nerve fibers (Kiang, Watanabe, Thomas, & Clark, 1965). Such microelectrode studies have demonstrated that each nerve fiber responds to no more than a limited range of frequencies. Within that range, the particular tone frequency at which the threshold is lowest is termed the characteristic frequency (CF) of the unit. As the intensity of stimulation is raised, a broader band of frequencies is capable of exciting the fiber. The selectivity to tone frequency of single nerve fibers has often been illustrated by tuning curves which show the fiber's threshold as a function of tone frequency. The tuning curve or response area of a fiber includes all combinations of frequency and intensity of tonal stimuli for which firing rate is increased over the level of spontaneous activity (Galambos & Davis, 1943). Most fibers of the cochlear nerve have tuning curves that show a fairly sharp high frequency cut off, but respond to a wider range of low frequencies. It is assumed that the CF is the physiological correlate of the locus of innervation along the longitudinal dimension of the cochlear partition.

The tuning curve is an "iso-rate" function; i.e., stimulus frequency and intensity are varied in order to obtain a constant response rate. Another measure which provides a description of fiber response characteristics above threshold is the "iso-intensity" contour introduced by Rose and his co-workers (Hind, Anderson, Brugge, & Rose, 1967; Hind, Rose, Brugge, & Anderson, 1970; Rose, Hind, Anderson & Brugge, 1971). In this type of curve, the stimulus intensity is held constant while discharge rate is measured as a function of frequency. A set of such curves at differing intensity levels (commonly, 10 dB apart) defines the response area of the fiber.

The tonotopical organization of the fibers in the eighth nerve is such that fibers with high CF are found in the "outer layers" of the nerve bundle. Between the outer layer and the center, the CFs of the fibers decrease, so that units having the lowest CF are found in the center of the nerve bundle (Kiang et al., 1965). This pattern reflects the tonotopic organization of the cochlea itself, as fibers from the apex of the cochlea travel in the center of the nerve trunk, fibers arising from more basal regions being superimposed in successive layers (Sando, 1965).

Although there is much evidence to indicate that there is a close relationship between basilar membrane displacement and neural discharge rate, it is not known whether the critical event for impulse generation is displacement *per se* (of the basilar membrane and/or other structures), or some other function of displacement such as the velocity of displacement or the shearing forces between various structural elements. It does appear from recent observations, however, that the curves of mechanical displacement of the basilar membrane may be much closer to the neural tuning curves than had been thought (Rhode, 1971). However, there is as yet, little information relating the amplitude of membrane displacement to the corresponding rate of discharge evoked from the nerve.

## II. Literature Concerning Acoustic Overload

### A. Psychoacoustical Studies

One of the common functional characteristics of all sensory systems is a reduction in sensitivity following exposure to any stimulus of sufficient duration and intensity. The concepts of adaptation and fatigue have been used to describe the effects of various types of sensitivity-reducing stimuli upon auditory function. In the last 50 years, these phenomena have been widely studied by psychophysicists and physiologists alike, but they remain nevertheless a subject upon which considerable disagreement still exists. Although different physiological processes underlying adaptation and fatigue have often been postulated, due to imprecise definition of these terms, such hypotheses are difficult to test.

One solution to the problem of defining these terms has been to use the intensity level of the sound exposure as a way of categorizing the effect studied (Hood, 1950). Adaptation studies have been conducted using weak to moderate levels of stimulation, while on the other hand, fatigue studies have tended to be concerned with the effects of moderate to quite intense levels of stimulation (Elliot & Fraser, 1970). When the term auditory fatigue is used without explicit definition, what is usually meant is a temporary reduction in hearing sensitivity,referred to as "temporary threshold shift" (Ward, 1963).

A major finding of the study of fatigue or hearing loss resulting from exposure to sufficiently intense pure tones has been the paradoxical observation that the greatest shift in threshold occurs not at the frequency of the stimulating sound but at frequencies above it. Depending on the intensity of the acoustic overload, the major depression of hearing may be found from one-half to one octave above the stimulating frequency. This phenomenon was first demonstrated by Davis and his colleagues (1950) and has, since that time, been repeatedly confirmed and extended (Hood, 1950; Licklider, 1951; Ward, 1962, 1963; Elliott & Fraser, 1970). In particular, the depression at one-half octave above the overload frequency is so commonly found that it is often referred to as "the half-octave shift effect".

B. Cochlear Mechanical Studies

One possible explanation of the origin of the half-octave shift phenomenon is that it is produced by mechanical movements of the basilar membrane. Békésy (1960) concluded from his optical observations of the patterns of motion of the cochlear partition, that with increasing intensity of sound, the peak of vibration of the basilar membrane was displaced toward the apex; i.e., in the opposite direction to that which would be predicted by the half-octave shift seen in behavioral studies. However, in the last few years, new methods have made possible more sophisticated studies of the motion of the basilar membrane.

Recently, utilizing the Mössbauer technique which permits the measurement of basilar membrane oscillations in live animals at physiological levels of sound stimulation, Rhode (1971, 1973) made an interesting observation concerning the displacement pattern of the squirrel monkey basilar membrane at high intensities of sound. He found that as the intensity of stimulation was increased, the frequency which produced the maximum displacement amplitude at a given locus became lower. This is equivalent to saying that as intensity increased, the peak of maximum membrane displacement appeared to move toward the base of the cochlea (Rhode, 1973). These findings of a basalward shift agree with the psychophysical observations that maximum changes in threshold following exposure to intense sounds occur at frequencies higher than the exposure sound.

### C. Electrophysiological Studies

#### (1) Gross Electrophysiological Studies

For a number of years there has been a great interest in the electrophysiological correlates of acoustic fatigue and/or adaptation. In general this research has involved recording of the various potentials generated within the cochlea. Most of the research has focused upon either the AC cochlear potential (often referred to as the "cochlear microphonic") or the gross evoked potential of the cochlear nerve (often referred to as "AP" or, because of its predominant negativity, "$N_1$"). In the following discussion, AP will be used to designate the gross neural response and "cochlear potential" will be used as a brief designation of the AC cochlear potential.

Many attempts have been made to correlate changes in the cochlear potential with observed hearing losses (for example: Wever, Bray & Horton, 1934; Lurie, Davis & Hawkins, 1944; Lawrence, Wolsk & Burton, 1959; Eldredge, Bilger, Davis & Covell, 1961; Beagley, 1965; Suga,Snow, Preston & Glomset, 1967). Such attempts have never revealed a close correlation between changes in the cochlear potential and hearing losses which are measured behaviorally. Although very intense sound stimulation does produce marked decrements in the cochlear potential, these losses generally extend across a broad range of frequencies even though the stimulation may have been a pure tone at only one frequency.

A number of investigators have reported decrements in the AP resulting from loud sound stimulation (for example: Derbyshire & Davis, 1935; Hawkins & Kniazuk, 1950; Rosenblith, Galambos & Hirsh, 1950; Sorenson, 1959; Moushegian, Rupert, Stillman & Weiss, 1972; Maiorello & Wilpizeski, 1972). In many cases, the changes in the AP were shown to parallel loss of threshold sensitivity in that changes in the AP were temporary and its recovery course was similar to that of hearing thresholds. However, clicks have been traditionally used as the stimulus to elicit AP in the majority of cases, and clicks are poor stimuli with which to evaluate sensitivity to different frequencies. The problem is that clicks contain a variety of frequencies (usually unspecified), and have classically been assumed to activate no more than the basal portion of the cochlea.

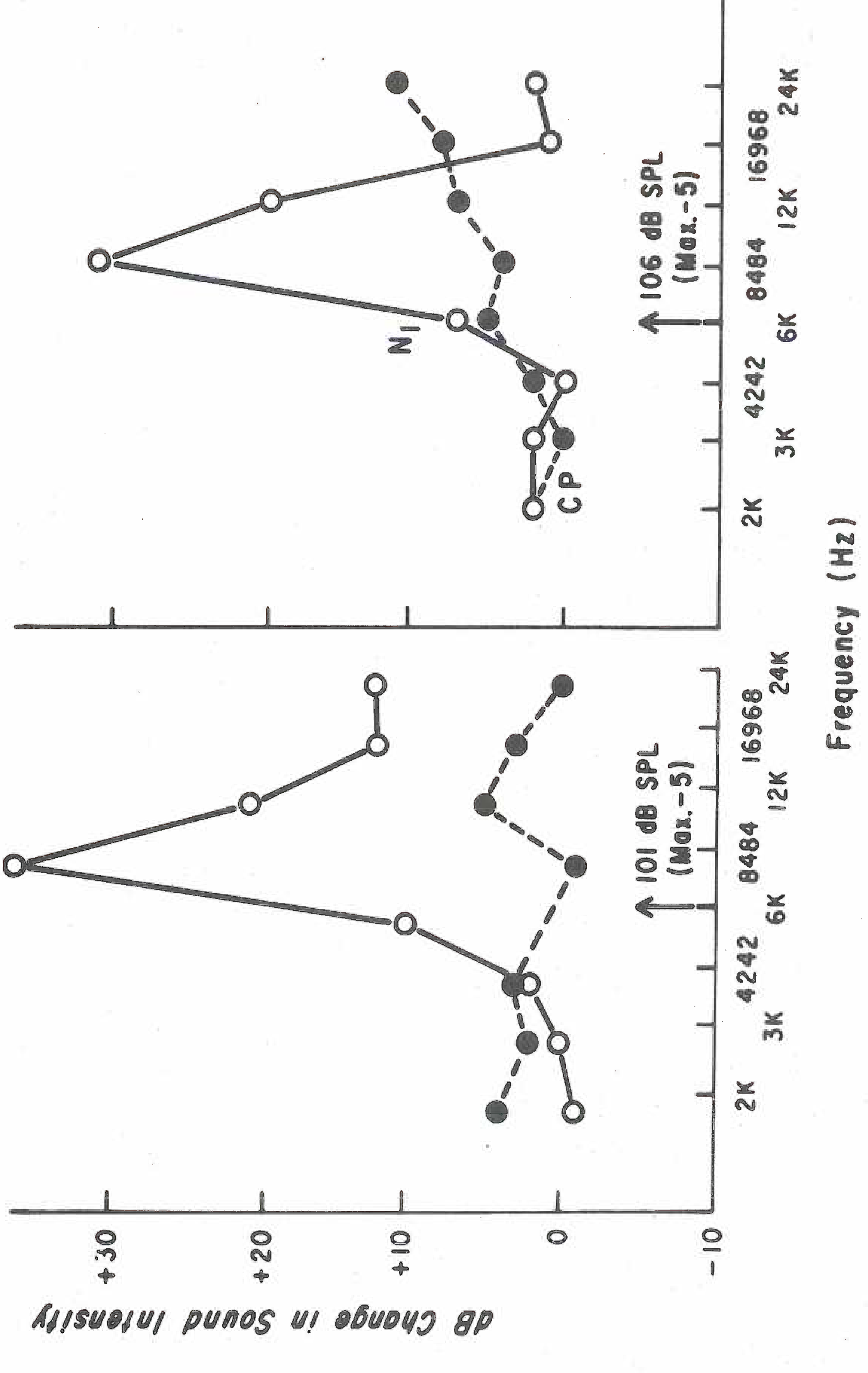
Recently, however, Mitchell (1973), using carefully-shaped tone bursts to elicit the AP, demonstrated that decrements in AP resulting from pure tone overloads (97-105 dB re 0.0002 μbar) were frequency-dependent. Specifically, he found that after exposure to an intense pure tone, the amplitude of the AP was decreased over a frequency range surrounding the exposure frequency, and showed the greatest reduction or was entirely absent at the frequency one-half octave *above* the exposure frequency. One-half octave *below* the exposure frequency, AP amplitudes were close to normal. The cochlear potential remained, by these same exposures, unaffected at all frequencies. These observations are summarized in Figure 1.

Taken together, both the AP and cochlear potential observations indicate that the measured decreases in AP were independent of such changes as receptor adaptation, alterations in stimulus energy, or mechanical injury to the organ of Corti. The decrement in AP from intense tones was shown to be temporary; i.e., recovery to pre-exposure levels had occurred when the measures were repeated 24 hours later.

It is particularly noteworthy that the reduced AP was most marked at the half octave above the stimulating frequency, thus demonstrating striking similarities to the temporary threshold shifts reported in behavioral studies. It appears then, that neural activity is a more sensitive indicator of temporary hearing depression than is the cochlear potential. There are significant limitations in the use of the AP as an indication of neural activation, however. One is that only brief stimuli are effective in eliciting the AP. A second is that interpretation of amplitude changes is difficult, for reduction of AP may result either from a reduction in the number of active neurons or from a reduction of the ability of the neurons to be fired syn-

FIGURE 1.

Effects of acoustic overstimulation upon the $N_1$ component (the major component) of the cochlear nerve AP. The overload stimulus was a 6 kHz tone (indicated by the vertical arrow), presented for 15 minutes. The changes, compared to pre-exposure levels, in sound pressure levels required to produce 1 µV of cochlear potential (CP) or 50 µV of $N_1$ are plotted. Solid lines correspond to $N_1$ potentials, while dashed lines represent CP measurements. While there is little or no change in CP, a very pronounced depression of $N_1$ is evident at the half octave above (8,484 kHz) the overload frequency, as indicated by the fact that sound pressure levels had to be elevated by 30 dB or more in order to elicit $N_1$ at the 50 µV level. (Reproduced by permission from Mitchell, 1973).


dB Change in Sound Intensity
+30
+20
+10
0
-10
2K
3K
4242
6K
8484
12K
16968
24K
101 dB SPL
(Max.-5)
106 dB SPL
(Max.-5)
N1
CP
Frequency (Hz)

chronously. Thus, a more direct attack is to study the effects of acoustic overstimulation at the level of single cochlear nerve fibers.

(2) Single Unit Studies

In recent years there has been intense interest in the effects of acoustic stimulation at the level of single cochlear nerve fibers (Katsuki, Sumi, Uchiyama & Watanabe, 1958; Kiang, Watanabe, Thomas & Clark, 1962; Kiang et al., 1965; Rose et al., 1967; Sachs, 1969; Pfeiffer, 1970, Evans, 1972; Young & Sachs, 1973; Sachs, Young, & Lewis, 1974; Sachs & Abbas, 1974). Most of this work has been concentrated on questions related to the coding of acoustic information by the individual cochlear fibers, and has thus actively avoided fatiguing or adapting stimuli, as much as possible. However, some of these studies have provided results which also bear on the problem of overload effects. In order to describe response areas at suprathreshold levels, Rose and his coworkers have commonly used the iso-intensity function, that is, discharge rate as a function of frequency, measured at several different sound levels (Rose et al., 1967, Rose et al., 1971; Rose, 1973). Although not specifically referred to in many of their experiments, the CF (defined on the iso-intensity contour as the frequency which produced the maximum discharge rate) shifted to lower frequencies as intensity increased. An explicit description of this effect was noted by Nomoto, Suga, and Katsuki (1964) in a study investigating the relationship between discharge rate of single units and sound level at different frequencies.

More recently, Evans (1974), in a study demonstrating the effects of hypoxia, cyanide and the ototoxic drug furosemide on cat cochlear nerve fibers, demonstrated that with each of these agents, a reversible loss of 30 to 40 dB occurred but only to the low threshold, sharply tuned segments of the tuning curves. The broadly tuned, high threshold segments of the tuning curves remained, and their CFs were consistently shifted downwards in frequency. It seems quite possible that the downward shift Evans observed in CF during application of the above temporarily-damaging agents may have been produced because intense sound levels were necessary to evoke spike discharges from pathological fibers.

In a recent study designed to correlate measurements of movement of the basilar membrane in the squirrel monkey with the behavior of cochlear nerve fibers in the same species, Geisler, Rhode and Kennedy (1974) reported that for 36% of their sample of 261 nerve fibers, the apparent CF dropped slightly as the stimulus intensity increased. The fact that this effect was observed in only one third of their total fiber population was attributed by Geisler et al. to the relatively large size of the frequency steps which they used in determining their iso-intensity functions. Small shifts of CF could have occurred in the remaining fibers sampled and thus, possibly gone undetected.

One study has included specific mention of the effects of acoustic overload upon cochlear nerve fibers (Kiang, Moxon & Levine, 1970). The data were severely limited (only one fiber was described) and the overload was so intense as to produce permanent loss of hearing. Because of these restrictions, there was little information from this study which can be applied to the question of frequency dependent effects during temporarily damaging exposures.

A recent report by Young and Sachs (1973) dealt in detail with auditory adaptation at the single unit level, but that report was not concerned with the effects of different frequencies upon any one unit. Only overload stimuli equal to a given unit's CF were used. Thus this work does not provide information on the frequency shift effect.

### D. Summary and Specific Aims

From the preceding discussion it can be seen that there is experimental evidence obtained from quite different sources (cochlear mechanical data, whole-nerve AP responses, and responses of single cochlear nerve fibers) that seems to indicate that the origin of frequency shifts such as the half-octave effect seen in psychoacoustic studies is mechanical. However, since the very procedure of gaining direct access to the organ of Corti usually disrupts its normal functional state, it is possible that insight into cochlear mechanisms underlying the half-octave shift effect might better be gained indirectly, by studying the responses of cochlear nerve fibers. Since the orderly spatial arrangement of the cochlear nerve fibers permits a correlation between the electrical response characteristics of a given fiber and its place of innervation along the basilar membrane, a certain degree of prediction of cochlear mechanical data can be made from the electrophysiological findings.

It has certainly been well established from studies investigating response characteristics of single cochlear nerve fibers that acoustic signals are represented at this most peripheral stage of the auditory nervous system in such a way as to preserve much or all of the information derived from the mechanical analysis performed by the cochlea (Kiang et al., 1962; Kiang, 1965; Kiang et al., 1965; Kiang, 1968). Although gross neurophysiological data and some incidental observations of single unit responses support the notion of a basalward shift in the maximum displacement of the basilar membrane with increases in stimulus intensity, there have been no previous systematic studies at the level of single cochlear nerve fibers which might elucidate this question.

The present study was designed, therefore, to examine the possibility that the psychophysical observation of the half-octave shift has a counterpart in the cochlear nerve, and that such psychoacoustic results may be understood in terms of the input carried by the first-order auditory neurons. Toward this end, the discharge properties of cat cochlear nerve fibers following exposure to intense acoustic stimuli have been studied.

Following acoustic overstimulation, both the AP and hearing were most depressed above the exposure frequency. If the assumption is made that it is at the point of maximum displacement of the basilar membrane where fatigue or adaptation first become evident, then fibers in the nerve which would be expected to be most depressed would be those whose CFs are <u>above</u> the frequency of the exposure stimulus. From this it follows that, for any given fiber, the most depressing overload would be at a frequency <u>below</u> its CF. Depending on the intensity of stimulation, the most severely depressant overload for any given unit should be located at or near the half-octave below its CF.

Preliminary studies revealed that rather than vary the test stimulus around one particular overload frequency (as was done in the AP experiments cited earlier), corresponding effects could be observed by varying the overload frequencies and holding the test stimulus constant at the CF for any one fiber. This effect was demonstrated at the single-unit level as well as with measurements of AP. In addition, these latter measurements confirmed that the half-octave shift of AP described by Mitchell (1973) in the guinea pig also occurred in the cat.

Prior to the beginning of the current research, it was not known whether the same sound levels which might produce a half-octave shift would also permit recovery of single unit responses within reasonable lengths of time (for example, 10-20 minutes). In the early stages of the research, overload intensities ranging between 75 and 105 dB re 0.0002 μbar were evaluated in terms of their effects upon recovery time and the possibility that they might produce depression at frequencies different from the CF. It appeared from these preliminary results that stimulation levels of 85 dB and 90 dB would not only permit recovery to be observed in many instances, but also showed strong indications of severe depressant effects at the half octave below the CF. These two levels also represent a good compromise between the highest sound levels used in the experiments by Young and Sachs (1973), in which only short-lasting adaptation was observed, and the 97-105 dB levels used in the research by Mitchell (1973), in which recovery times for the whole nerve AP were on the order of several hours.

In summary, on the basis of the preliminary results just described, two parameters of the exposure stimulus were chosen to be varied systematically in the experiments to be described below. Stimulation level was either 85 dB or 90 dB; stimulation frequency was chosen relative to a given fiber's CF and was either at the half octave below the CF, at the CF, or at the half octave above it. The experiments were designed to test the following hypotheses:

(1) It was predicted that exposure frequencies one-half octave below a unit's CF, rather than above or at the CF, would most severely affect the responsiveness of a single cochlear nerve fiber. Furthermore, it was predicted that this effect would be intensity-related, in that the overload one-half octave below CF at the 90 dB level would produce the most drastic reduction in fiber response rate.

(2) It was thought that some degree of recovery of single unit responses could be measured following acoustic overloads severe enough to produce a "half-octave shift effect"; and that the recovery times would be correlated with the severity of effect of the overload. Specifically, overload at the half octave below the CF of a unit at 90 dB would be expected to produce the longest recovery times.

(3) It was anticipated that exposure frequencies one-half octave above the CF would have substantially less effect upon responsiveness of the fiber than would exposure at or below the CF.

# MATERIALS AND METHODS

The following is an outline of the experimental procedures.

I. Animal Preparation
  - (a) Preliminary Surgical Procedures (anesthetization, tracheal and venous cannulation, control of temperature, head-holder)
  - (b) Exposure of External and Middle Ear (opening of bulla, placing of round window electrode, insertion of acoustic coupler)
  - (c) Exposure of Cochlear Nerve (bone removal, sinus cauterization, cerebellar displacement)

II. Acoustic Stimulation
  - (a) Stimulus Parameters (continuous tones, tone bursts, stimulus periods)
  - (b) Stimulus Presentation Equipment (wave analyzer, control logic system, electronic switch, interval timer, attenuators, power amplifier, acoustic driver)
  - (c) Measurement of Sound (probe-tube microphone)

III. Data Recording System
  - (a) Microelectrodes (micropipets, electrolyte)
  - (b) Criteria for Identification of First-order Units
  - (c) Recording Apparatus
    - (1) Single Units (preamplifier, amplifier)
    - (2) Cochlear Potentials and Whole Nerve Potentials (amplifier, wave analyzer, signal averager)

IV. Experimental Design and Procedures
  - (a) Cochlear Potentials (1 μV frequency sensitivity function)

(b) AP (input-output functions)

(c) Single Unit Data (isolation of fibers, CF-threshold determination, experimental study)

V. Processing of Single Unit Data

(a) On-line (counter-printer system)

(b) Off-line (punch-tape system, calculator)

## I. Animal Preparation

The experimental work was conducted on young, healthy cats, free of obvious signs of respiratory impairment. The cats were approximately five to seven months old and weighed between 1.5 and 2.2 kg. Otoscopic examination of the external ear canals of all cats was used as a rough check for otitis media (indicated by excessive wax accumulation and/or a thickened tympanic membrane). Animals passing this test were anesthetized and prepared as follows.

Anesthesia was induced with an intraperitoneal injection of sodium pentobarbital (Nembutal) in a dose of 35 mg/kg of body weight. Animals were maintained at a surgical level of anesthesia with small supplemental doses given intravenously every few hours throughout the experiment. In order to combat accumulation of mucus in the trachea, a subcutaneous injection of atropine sulfate (100 μg/kg of body weight) was administered. Additional atropine was given every three to four hours. A lactated Ringer's solution was injected subcutaneously every six to eight hours to maintain proper water and electrolyte balance.

All surgical and electrophysiological recording procedures were carried out in a double-walled chamber constructed for sound isolation and electrical shielding (Industrial Acoustics Company). Operating procedures were performed at 10 to 40 X magnification using a binocular dissecting microscope (Zeiss). Throughout the experiment, respiration rate and rectal temperature were regularly monitored. The temperature was maintained at 37.5° ± 1° C by a heating pad in conjunction with a rectal thermister probe (Yellow Springs Instruments, model 46).

### A. Preliminary Surgical Procedures

The sternothyroid muscle mass overlying the trachea was sectioned and the trachea was cannulated. Although the animals were not artificially ventilated, the tracheal cannula facilitated aspiration if needed. To permit intravenous infusion of supplemental anesthetic, the femoral vein was cannulated.

To permit clear access to both the external acoustic meatus and tympanic bulla as well as to provide mechanical rigidity between the animal and the microelectrode, the subject was fitted with a specially constructed, atraumatic, rigid head-holder which was attached to the horizontal rails of a stereotaxic instrument (Kopf, model 1204). In order to fix this apparatus to the skull, the cat was temporarily held with a tooth bar and nose clamp device which positioned the animal between the rails of the rigid head-holder. A midline incision was made on the scalp and the superficial and deep temporalis muscles and connective tissue covering the cranium were reflected. Using a dental drill (Kerr, model ATM), four burr holes were drilled through the skull, one pair over the frontal cortex (0.5 cm anterior to the coronal suture and 1.0 cm lateral to the sagittal suture) and the other pair over the parietal cortex (1.0 cm posterior to the coronal suture and 1.0 cm lateral to the midline suture). These burr holes were threaded using a specially modified tap, and brass screws (2-56-1/2") were then screwed into a depth of 3.0 mm. Two brass rods (5.0 mm diameter, 11.0 cm long) were attached to the skull by cementing them with dental acrylic between the skull screws. After the dental cement had hardened, the tooth bar-nose clamp assembly was removed and the brass rods attached to the skull were clamped to the rails of the headholder.

### B. Exposure of the External and Middle Ear

The midline scalp incision was extended in a posterior direction, and the temporalis muscle of the head and the muscles of the neck were reflected downwards and away from the pinna. The pinna itself was dissected away from the cartilaginous portion of the external acoustic meatus. For most animals, it was necessary to ligate and cut the posterior auricular artery. Following isolation of the cartilaginous canal from the surrounding muscle and connective tissue, the dorsolateral portion of the bulla was exposed by sectioning the stylohyoid process and the attachment of the digastric muscle. The caudal portion of the digastric muscle overlying the bulla was reflected ventrally. At this time, the canal was cut approximately 0.5 to 1.0 cm distal to the bony ring of attachment to allow insertion of the specially constructed sound cannula. This cannula provided a rigid-walled coupler of small volume connecting the sound source to the ear.

To expose the middle ear and the cochlea, a hole was drilled in the bulla immediately posterior to the attachment of the stylohyoid. The hole was then enlarged so that the round window membrane of the cochlea could be easily visualized. A major portion of the bony septum, which partially divides the middle ear of the cat, was removed to permit careful examination of the entire middle ear in order to exclude animals with signs of otitis media.

An electrode was placed upon the round window membrane of the cochlea in order to record both cochlear potentials and APs (the whole nerve evoked potentials of the eighth nerve). For this purpose, a small guide hole, just large enough to admit the electrode, was drilled in the bulla above the larger viewing hole. The balled tip of the silver electrode wire (0.003", teflon insulated except at the tip) was led through the guide hole and fixed in position by means of a wooden peg wedged in the guide hole. This electrode-wooden peg ensemble was glued rigidly to the bulla with dental acrylic.

### C. Cochlear Nerve Exposure

The classical approach to the cochlear division of the eighth nerve through the posterior cranial fossa was used. A wide posterior craniotomy was performed over the cerebellar region. The calvarium was rongeured in an anterior direction from the lamboidal ridge to the joining of the occipital skull bone with the bony tentorium, and in a posterior direction to the edge of the atlanto-occipital membrane. To obtain hemostasis, both the inferior petrous and the lateral sinuses were carefully cauterized or when necessary, plugged with bone wax or oxygen-impregnated cellulose (Oxycel, Parke Davis). The dura was incised with the cutting edge of a surgical needle and reflected. The parafloccular lobe of the cerebellum and the brain stem on the side to be exposed were gently displaced in a medial direction by inserting very small cotton balls between the cerebellum and surrounding bone. The accumulation of these cotton balls led to the eventual exposure of the cochlear nerve as it exited from the internal acoustic meatus beneath the appendicular fossa. During this procedure, great care was necessary to avoid compression of the anterior inferior cerebellar artery, which supplies the internal auditory artery. The suctioning of cerebellar or other brain tissue was avoided, since the consequent edema changed topographical relationships between the internal auditory meatus and the intracranial portion of the eighth nerve, making successful approach with a microelectrode to the cochlear nerve extremely difficult. Following exposure of the cochlear nerve, the area around the cochlear nerve was irrigated with physiological saline at 38° C to remove any blood clots. To prevent drying, the brain and nerve were covered with warm mineral oil. With this exposure, microelectrodes could easily be inserted into the nerve under visual observation.

## II. Acoustic Stimulation: Sound System and Calibration Procedures

### A. Stimulus Parameters

Test stimuli for single-unit and AP recording consisted of tone bursts of 20 msec duration with 1.5 msec rise and fall times. Burst duration was measured from the beginning of the rising phase to the end of the falling phase. The interstimulus interval was 120 msec corresponding to a repetition rate of 8.33 per second. These stimuli were initiated by trigger pulses delivered by a digital logic system to an interval timer and electronic switch. Tone bursts could be initiated either with a random or fixed phase relation to the trigger pulse. For AP measurements, it is desirable to initiate tone bursts with a random phase relation to the trigger pulse in order to "cancel out" the cochlear potential during successive averages. Continuous pure tones were used for cochlear potential measurements and no particular phase relationships were necessary for them. Overload stimuli also consisted of sustained tones. Intensities of the test tone burst stimuli were related to threshold measurements as will be discussed in a later section. Acoustic overload tones were either 85 or 90 dB (re 0.0002 μbar). For all the above stimuli, the frequency range was 0.1 to 20.0 kHz in 100 Hz steps.

For greater efficiency in locating single units of the cochlear nerve, a "search" stimulus consisting of pulsed broadband noise (20 Hz to 50 kHz) was used. The noise bursts were generated by a random noise generator (General Radio, model 1382). The intensity of the search stimulus was chosen to be approximately 40 to 50 dB (re 0.0002 μbar).

### B. Sound Equipment and Procedures

Control of the acoustic stimuli was performed by the experimenter from outside the chamber in which the experiments were conducted. Stimuli, generated by a 1-inch condenser microphone (Brüel and Kjaer, model 4161) used as a driver, were presented to the animal using a sealed sound delivery system. By damping the condenser microphone system with nonabsorbent cotton (i.e., loosely packing the cavities with cotton), a sound system having a "flat" frequency response was produced. A rapid determination of the CF of a given fiber can only be made with a sound system that is relatively flat. The unavoidable consequence of the damping procedure was the reduction of the dynamic range of the sound system so that it was sometimes impossible to generate sound pressure levels above approximately 87 dB (re 0.0002 μbar) in some instances (i.e., depending on the calibration values obtained for a particular experiment). In general, however, the dynamic range with the 1-inch microphone extended to well above 90 dB.

The microphone was inserted into the specially-constructed ear cannula and care was taken to seal it tightly into the external ear canal. Without a tight seal, the low frequency response of the sound system showed great variation. The microphone and sound cannula were firmly attached to the stereotaxic rail by a clamp incorporating a universal joint. A cross-section of the microphone and coupler is shown in Figure 2. The distance from the microphone diaphragm to the tympanic membrane was approximately 3.5 cm.

A block diagram of the stimulus presentation system is given in Figure 3. Stimulus initiation, period, and duration were determined by the digital control logic system (Massey Dickinson) equipped with a programmable time interval generator. Trigger pulses from the logic system were led to the interval timer (Grason Stadler, model 471-1). Sinusoidal electrical signals from the oscillator of a narrow-band wave analyzer (General Radio, model 1900) were gated with gradual (1.5 msec) rise and fall times by the electronic switch (Grason Stadler, model 829-E) triggered by the interval timer. An electronic counter (Monsanto, model 103-A) was connected to the output of the wave analyzer to monitor its exact frequency output. In addition, the output level of the wave analyzer was monitored by an external voltmeter (Simpson, model 260-5) to ensure that the output level was constant. For sustained tones used to overload the ear, a second oscillator, a digital frequency synthesizer (General Radio, model 1161-A) was used.

The "test" outputs from the electronic switch and the output from the overload oscillator were controlled by two sets of precision

FIGURE 2.

Transducer and coupler assemby for delivering and monitoring acoustic stimuli. The coupler in the upper right was used in the earlier experiments (cats 75-1 through 75-14), while that on the lower right was used for cats 75-15 through 75-17. To the left of each driver-coupler device are representative calibration curves indicating the frequency response of the different acoustic systems. All curves were obtained with the transducer/coupler assembly sealed tightly into the external auditory meatus, thus each curve incorporates variations in impedance or resonance of that particular cat's ear. The abscissa indicates the frequency range over which measurements were made. For the sake of clarity, data are plotted as a continuous line although actual measurements were made at 100 Hz intervals from 100 Hz to 20 kHz. The ordinate indicates the sound pressure level (re 0.0002 μbar) 0.5 cm from the tympanic membrane. The voltage to the attenuator was constant across frequencies for any one cat but varied slightly between cats.

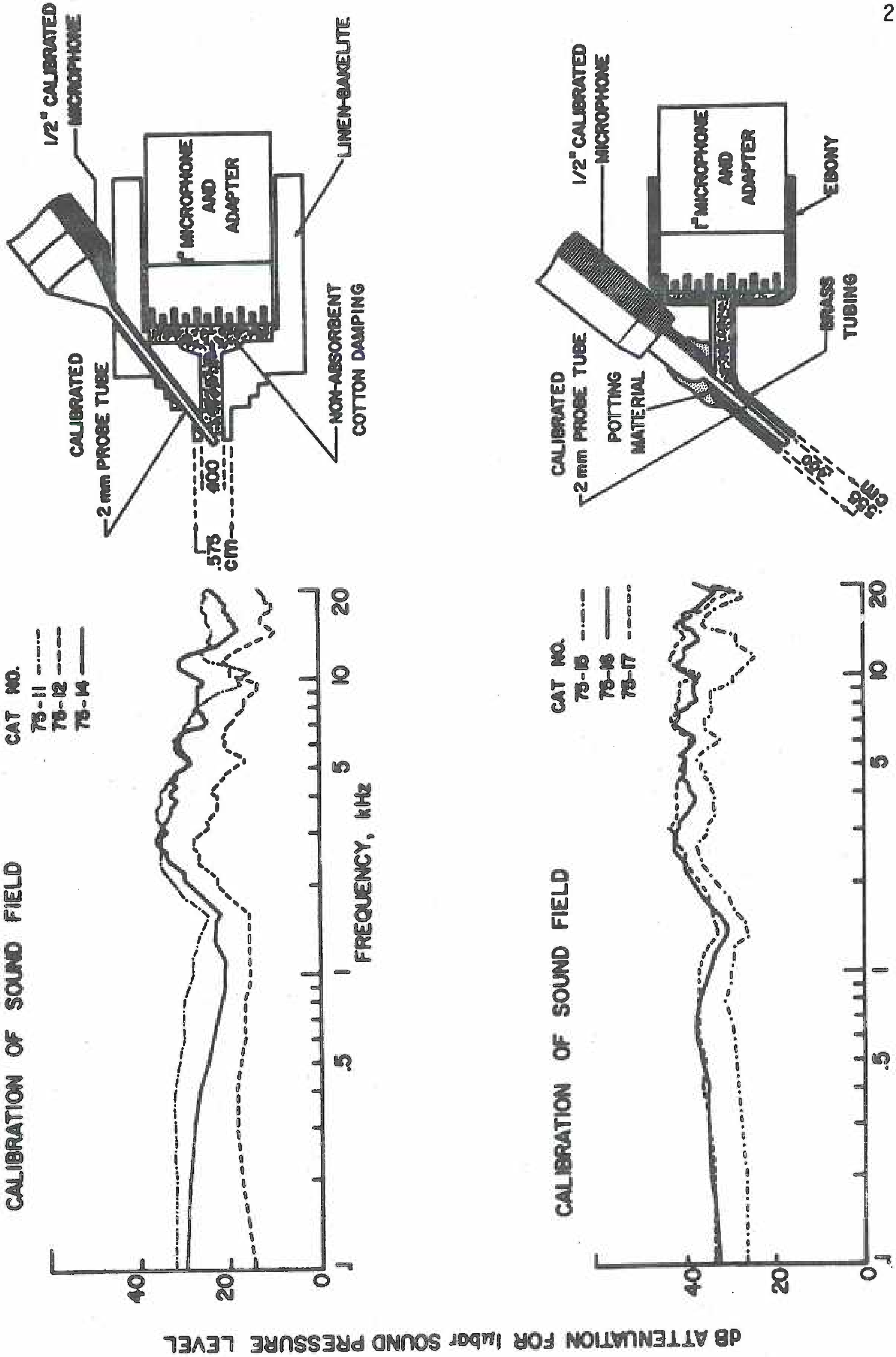
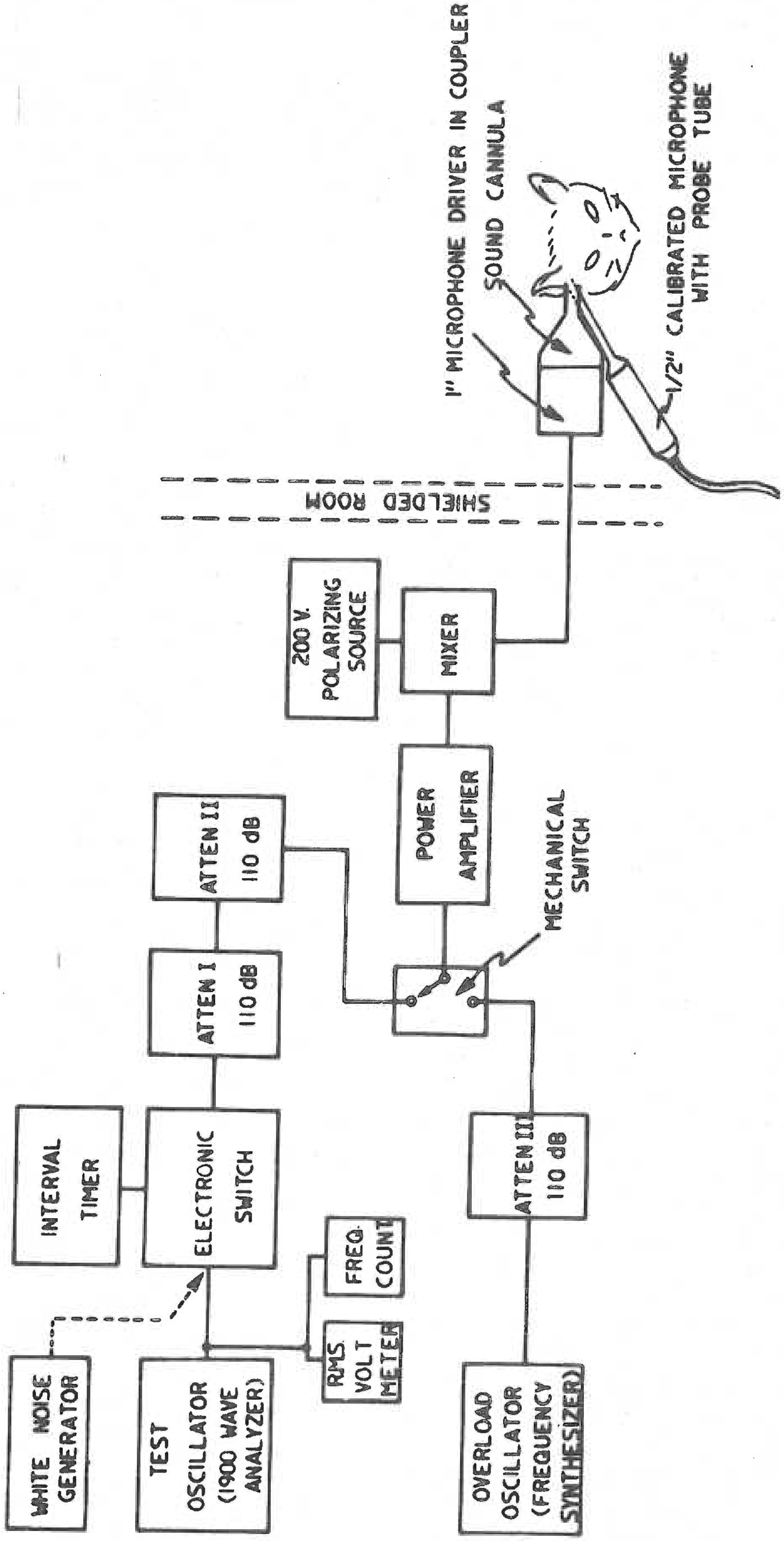

CALIBRATION OF SOUND FIELD
CAT NO.
75-11
75-12
75-14
40
20
0
.1
.5
1
5
10
20
FREQUENCY, kHz
1/2" CALIBRATED MICROPHONE
1" MICROPHONE AND ADAPTER
LINEN-BAKELITE
CALIBRATED 2 mm PROBE TUBE
NON-ABSORBENT COTTON DAMPING
.575 cm
.400
CALIBRATION OF SOUND FIELD
CAT NO.
75-15
75-16
75-17
40
20
0
.1
.5
1
5
10
20
FREQUENCY, kHz
1/2" CALIBRATED MICROPHONE
1" MICROPHONE AND ADAPTER
EBONY
CALIBRATED 2 mm PROBE TUBE
POTTING MATERIAL
BRASS TUBING
.350
.355 cm
dB ATTENUATION FOR 1μbar SOUND PRESSURE LEVEL

FIGURE 3.

Block diagram of stimulus presentation system. The mechanical switch was in the "up" position for generation of tone bursts for evoking AP and single unit activity as well as continuous tones for measurements of the cochlear potential. The switch was "down" for generation of acoustic overload stimuli. No external voltage or frequency monitors were required for the overload oscillator as these features were self-contained in the frequency synthesizer.


1" MICROPHONE DRIVER IN COUPLER
SOUND CANNULA
1/2" CALIBRATED MICROPHONE WITH PROBE TUBE
SHIELDED ROOM
200 V. POLARIZING SOURCE
MIXER
POWER AMPLIFIER
MECHANICAL SWITCH
ATTEN II 110 dB
ATTEN I 110 dB
INTERVAL TIMER
ELECTRONIC SWITCH
ATTEN III 110 dB
FREQ. COUNT
RMS VOLT METER
WHITE NOISE GENERATOR
TEST OSCILLATOR (1900 WAVE ANALYZER)
OVERLOAD OSCILLATOR (FREQUENCY SYNTHESIZER)

attenuators (General Radio, model 1450-TA), providing a range of attenuation of 220 dB in either 1 dB or 10 dB steps. A two-position mechanical switch was used to select either the test stimuli or the overload stimulus to be led to the power amplifier (Marantz, model 16). The amplifier signal was then led through a mixer circuit to the 1-inch microphone-driver, which was biased with 200 V from its power supply (Brüel and Kjaer, model 2801).

For recording of the cochlear potential from the round window, continuous pure tones were generated by the wave analyzer. For these measurements, the output signal of the wave analyzer was attenuated and amplified as described above with the mechanical switching device in the test position.

### C. Measurement of Sound Pressure Levels

Sound pressure levels were determined as follows. A calibrated probe tube and microphone (Brüel and Kjaer 1/2-inch condenser microphone fitted with a probe tube of 2 mm diameter and 30 mm length) were incorporated in the specially-constructed sound cannula. In early experiments (cats 75-1 to 75-14) the sound cannula used was slightly different in size than the one utilized in later experiments (cats 75-15 to 75-17). As Figure 2 showed, the tip of the probe tube was located flush with the bottom of the sound cannula, so that the distance from probe tube to eardrum was minimal (approximately 0.5 cm). Prior to each experiment, the attenuator settings in decibels required to obtain 0.1 μbar sound pressure at the tip of the probe tube were identified for every frequency to be used in that experiment. The frequencies used ranged from 100 Hz-20 kHz in 100 Hz steps. Thus, individual measurements were made at each of 200 different frequencies. Sample calibration curves are shown in Figure 2.

All sound pressure levels reported in this paper are given in dB relative to a reference pressure level (0 dB) of 0.0002 μbar (0.0002 dynes/$cm^2$). A sound pressure of 1 μbar corresponds to a level 74 dB above the 0.0002 μbar reference pressure.

## III. Data Recording System

### A. Microelectrodes

The activity of single units in the cochlear nerve was recorded using hyperfine glass micropipets (tip diameters of less than 1.0 μ), filled with 3 M KCl. Impedances of these electrodes were in the range of approximately 15-50 megohms, when measured at 1.0 kHz using an impedance bridge (Transidyne General, model 1275). These micropipets were produced by drawing 0.65-0.8 mm (O.D.) capillary tubing (Corning Glass Works, type M-247) with a vertical pipet puller (Kopf, model 700-C).

The filling of the micropipet with electrolyte was done using the method of Tasaki, Tsukahara, Ito, Wayner, and Yu (1968). In this method, fine fiberglass strands (approximately 14 μ in diameter) were introduced into the pipets prior to pulling. At the time of the experiment, the micropipets were filled using a syringe fitted with a 3-inch, 30 gauge hypodermic needle (Hamilton, type N-730). The fiberglass strands, which were drawn into extremely fine strands during the pulling of the pipet, facilitated the flow of electrolyte solution into the tip by capillary action. After filling, the micropipet was placed under a light microscope (600 X) for visual inspection of the tip region.

To permit gross placement of electrodes, an electrode carrier (Kopf, model 1260) was mounted on the stereotaxic rail contralateral to the exposed nerve. Before lowering the microelectrode to the surface of the nerve, cerebrospinal fluid covering the nerve was taken up with fine absorbent wicks. Under microscopic observation, the micropipet was advanced until contact was made with the nerve at approximate angles of 32° and 20° to the horizontal and sagittal planes respectively. By approaching the nerve at the proper angle, the micropipet could travel deep into the internal acoustic meatus. During penetration of the nerve, compression or tearing of the small vessels located on the surface of the nerve was carefully avoided.

In order to contact and hold single nerve fibers, fine microelectrode advancement in the nerve bundle was accomplished with a remotely-operated, hydraulically-coupled microdrive system (Trent Wells) attached to the electrode carrier. This apparatus consisted of a cylinder and piston advance connected by a plastic tube filled with a viscous fluid to a calibrated drive system located outside the recording chamber. The microdrive system advanced the microelectrode in increments of approximately 1 $\mu$. After satisfactory introduction of the micropipet, it was sometimes necessary to inject 2% clear agar in physiological saline at 38° C into the space above the nerve in order to stabilize the recording site by minimizing pulsations of the brain.

### B. Identification of Units as First-Order Nerve Fibers

The major difficulty in recording from primary cochlear nerve fibers is a consequence of the cat's anatomy in that the length of nerve that is completely free of cell bodies belonging to the interstitial nucleus of the second-order cochlear nucleus complex is extremely short (Kiang et al., 1965). By approaching the nerve intracranially through the posterior fossa at the proper angle so that the micropipet is located in that part of the nerve that was inside the internal acoustic meatus (i.e., peripheral to the glial septum), the cell bodies and dendritic endings of the interstitial nucleus, the vestibular branch of the eighth nerve, and the efferent bundle to the cochlea can be avoided (Kiang et al., 1965).

The major problem is that the glial cell-Schwann cell boundary cannot be discerned without histological verification. Certain criteria for maximizing the probability of recording first-order units were therefore adopted. First-order nerve fibers display predominantly positive spikes with irregular time patterns of both spontaneous and driven discharge (Kiang et al., 1962; 1965). In addition to the standard physiological criterion of spike polarity (Frank, 1959), several additional physiological criteria were utilized. When micropipets were thrust into the nerve at an angle that carried them into the internal acoustic meatus, units were encountered in close succession; when contact with one unit was lost, a slight advance of the micropipet established contact with another unit. In other words, the microelectrode appeared to be penetrating a region densely packed with small units that probably were cochlear nerve fibers.

Additional support for this conclusion was obtained by the fact that only very small micropipets were able to record potentials. It may well be that the extracellular electric fields of cochlear nerve fibers are too weak and too localized to be satisfactorily recorded by larger microelectrodes (Tasaki, 1952a; Kiang, 1965; Kiang et al., 1965).

By the above criteria, however, vestibular nerve fibers were not excluded. Since the vestibular division of the eighth nerve travels with the cochlear nerve in the ventroanterior portion of the eighth nerve at the level of the internal acoustic meatus, it was necessary to distinguish between action potentials from vestibular first-order afferent fibers and those from cochlear nerve fibers. However, when the microelectrode was inserted into what appeared to be the vestibular branch of the eighth nerve, units were encountered that showed large regular spike discharges in the absence of sound. These units did not respond to sound even at high stimulus levels.

Efferent fibers of the eighth nerve were excluded from the present study on the basis of a latency criterion. A number of investigators have shown that such fibers respond to acoustic stimuli with long latencies of 20 to 50 msec (Fex, 1962; Pfalz, 1969; Wiederhold, 1970). Furthermore, the efferent fibers have a resting activity of 1 to 10 spikes per second with a regular firing rate in response to sound stimulation (Fex, 1962), while the afferent fibers often show discharge rates up to several hundred spikes per second with irregular bursts. In addition, at the level of the eighth nerve, not only is the number of efferent fibers exceedingly small, 600 efferent fibers versus 50,000 afferent fibers (Gacek, 1960, Rasmussen, 1960), but also, it is likely that activity in these fibers is drastically reduced by anesthesia (Fex, 1962; Kiang et al., 1965).

One last assurance that the electrode probably was not in an area containing cell bodies was lack of evidence of the presence of injury discharges as a result of micropipet insertion. Injury discharge behavior is characterized by very high initial spike rates, which drop to zero over a period of less than a minute, during which time the fiber is not responsive to sound. It was assumed that injury discharges were probably recorded near second-order dendrites or cell bodies since when a micropipet is near a dendritic-soma region, it can affect the cell's "spike generator" (Kiang et al., 1965). In these cases, the microelectrode was advanced further into the internal acoustic meatus until injury discharge behavior was no longer apparent.

### C. Recording Apparatus

Cochlear potential and neural AP responses were recorded differentially between the silver ball active electrode placed on the round window membrane of the cochlea and an indifferent stainless steel needle in the muscle near the bulla. Individual action potentials from the eighth nerve were also recorded differentially between the micropipet electrode in the cochlear nerve and the same indifferent neck electrode. The grounding connection, a stainless steel needle electrode, was placed in the ipsilateral hind foot. Figure 4 illustrates the recording system for cochlear potentials, APs, and single units.

#### (1) Single Units

Because of the high impedances of the micropipet electrodes, the first stage of amplification for single unit activity was provided by a unity-gain preamplifier (Picometric, model 181) which possessed extremely high input impedance and negative capacitance feedback. This preamplifier, located close to the animal, was connected to the micropipet with a stainless steel wire which was inserted into the electrolyte and pushed as close as possible to the tip of the pipet.

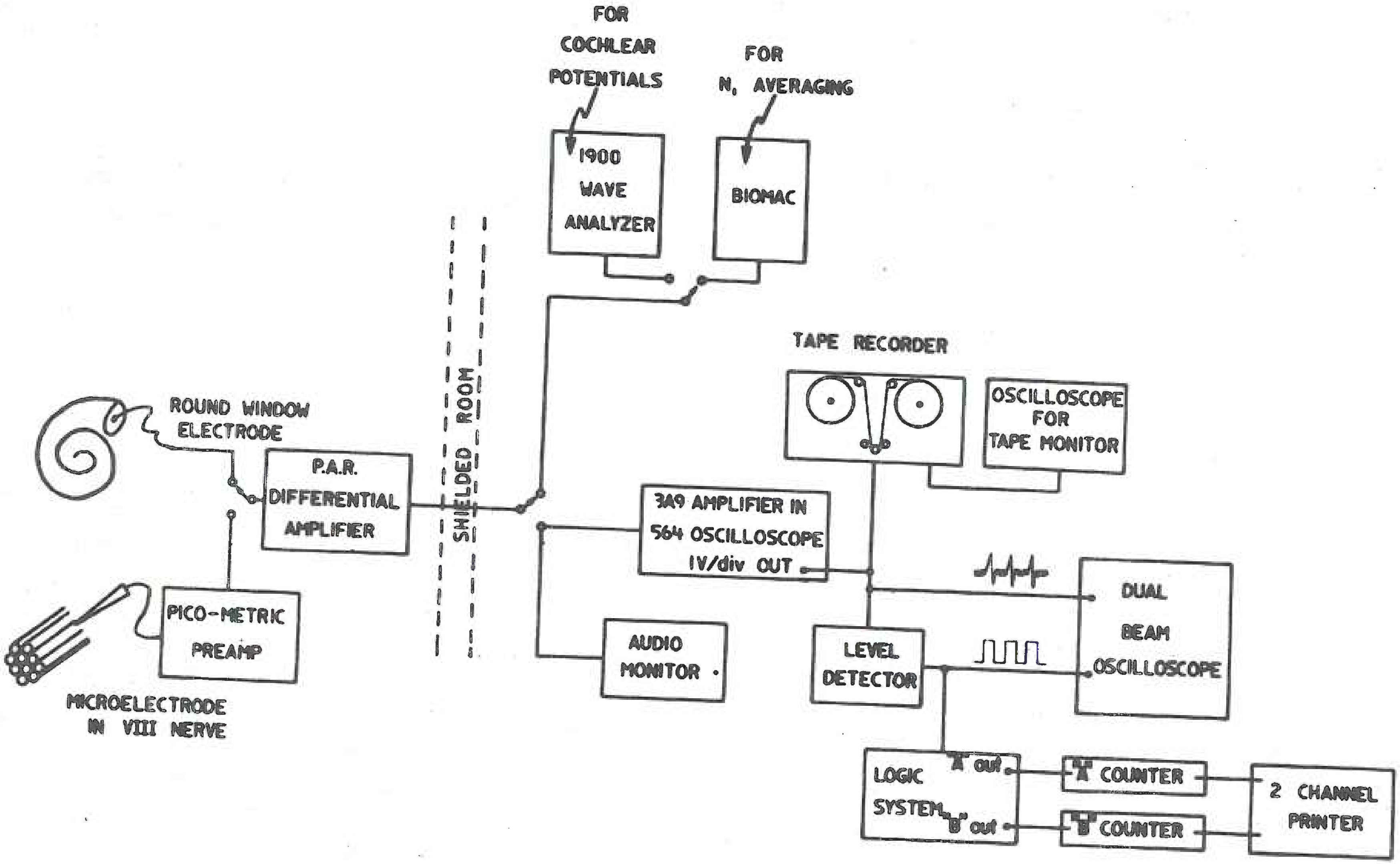
The output of the preamplifier stage was connected via a short length of shielded low-noise cable (Microdot, type 260-3816) to a capacitively-coupled differential amplifier (Princeton Applied Research, model 113) which provided 5,000 X amplification. The amplifier filters were set to pass the band 300 Hz to 3.0 kHz. The amplified output was led to an oscilloscope (Tektronix, model 654-B) containing a low-level amplifier (Tektronix, model 3A9) used single-ended. The vertical signal output (1 volt/division) of the oscilloscope was fed in parallel to the digital logic system for on-line counting of spike discharge rate and to an audiomonitor. The amplified neural data were also recorded on magnetic tape using an FM channel of an instrumentation recorder (Hewlett-Packard, model 3690).

(2) Cochlear Potentials and Whole Nerve Potentials (AP)

Due to lower impedance of the electrode used to record round window potentials (cochlear potentials and AP responses), amplifier requirements were less stringent than for the microelectrode amplifier. A second low-noise differential amplifier (Princeton, model 113), with a gain of 1,000 X and filters set at 30 Hz to 100 kHz, was used for this purpose. For cochlear potential measurements, the output of the biological amplifier was fed directly to the wave analyzer. For measurement of AP, the amplifier output was led to a small, special-purpose computer (Data Laboratories, model Biomac 1000). To obtain precise measurements of latency, amplitude and duration, the averaged AP responses were either displayed on an oscilloscope and photographed or plotted by an X-Y recorder (Electro Instruments, model 320).

FIGURE 4.

Block diagram of recording system used to record cochlear potential, AP, and single unit activity. Equipment used for on-line data analysis is also included in the lower right-hand portion of the figure.


FOR
COCHLEAR
POTENTIALS
FOR
N, AVERAGING
1900
WAVE
ANALYZER
BIOMAC
TAPE RECORDER
OSCILLOSCOPE
FOR
TAPE MONITOR
ROUND WINDOW
ELECTRODE
P.A.R.
DIFFERENTIAL
AMPLIFIER
SHIELDED ROOM
3A9 AMPLIFIER IN
564 OSCILLOSCOPE
1V/div OUT
DUAL
BEAM
OSCILLOSCOPE
PICO-METRIC
PREAMP
AUDIO
MONITOR
LEVEL
DETECTOR
MICROELECTRODE
IN VIII NERVE
LOGIC
SYSTEM
"A" out
"B" out
"A" COUNTER
"B" COUNTER
2 CHANNEL
PRINTER

## IV. Experimental Design and Procedures

### A. Cochlear Potentials

The main purpose of cochlear potential measurements was to check the sensitivity of the peripheral auditory system. Continuous pure tones at eight frequencies (0.2, 0.5, 1.0, 3.0, 5.0, 10.0, 15.0, and 20.0 kHz) were presented. The sound pressure levels needed to produce a 1 μvolt output of the cochlear potential as measured on a wave analyzer were recorded.

### B. Whole Nerve Potentials (AP)

Measurements of AP were used to monitor possible changes in the nerve's normal response as well as to monitor the physiological condition of the preparation. Tone bursts (with random starting phases) at five frequencies (3.0, 5.0, 10.0, 15.0, and 20.0 kHz) were used to obtain AP measurements. Brief input-output functions (i.e., three intensity levels at each frequency) were obtained. All AP data were measured by averaging the evoked gross responses to 32 successive tone bursts. Latency and peak-to-peak (p-p) amplitude were recorded for each frequency and intensity.

### C. Action Potentials of Single Units

Immediately after a fiber was isolated, its characteristic frequency (CF) to tone burst stimuli was identified using audiovisual response criteria (Kiang et al., 1965); i.e., searching for that frequency at which an alteration in spontaneous activity was just noticeable. This was achieved by keeping the intensity of the acoustic stimuli constant while the frequency of the tone burst was varied through the complete frequency range (0.1-20.0 kHz) until the CF was determined. The threshold at the CF was then measured.

At this point, the fiber under observation was assigned on a random basis to one of three possible acoustic overload frequency conditions: (1) at the CF; (2) at the frequency one-half octave above the CF; or (3) at the frequency one-half octave below the CF. In addition, the fiber was randomly assigned to an overload intensity level of either 85 or 90 dB. Thus, there were in all, six overload conditions. For brevity in further discussions these groups will be referred to as:

| | |
|---|---|
| (1) $CF_{85}$ | (4) $-1/2\ OCT_{90}$ |
| (2) $CF_{90}$ | (5) $+1/2\ OCT_{85}$ |
| (3) $-1/2\ OCT_{85}$ | (6) $+1/2\ OCT_{90}$ |

Following these determinations, the experimental protocol (see Figure 5) consisted of four major steps: (1) the fiber was exposed to a TEST CF condition; (2) a sample of SPONTANEOUS activity was obtained; (3) acoustic overload or LOAD at one of three frequencies and two intensities was presented; and (4) a RECOVERY TEST CF condition was alternated with a RECOVERY SPONTANEOUS condition until either the nerve fiber recovered from the effects of the LOAD stimulus or contact with the fiber was lost.

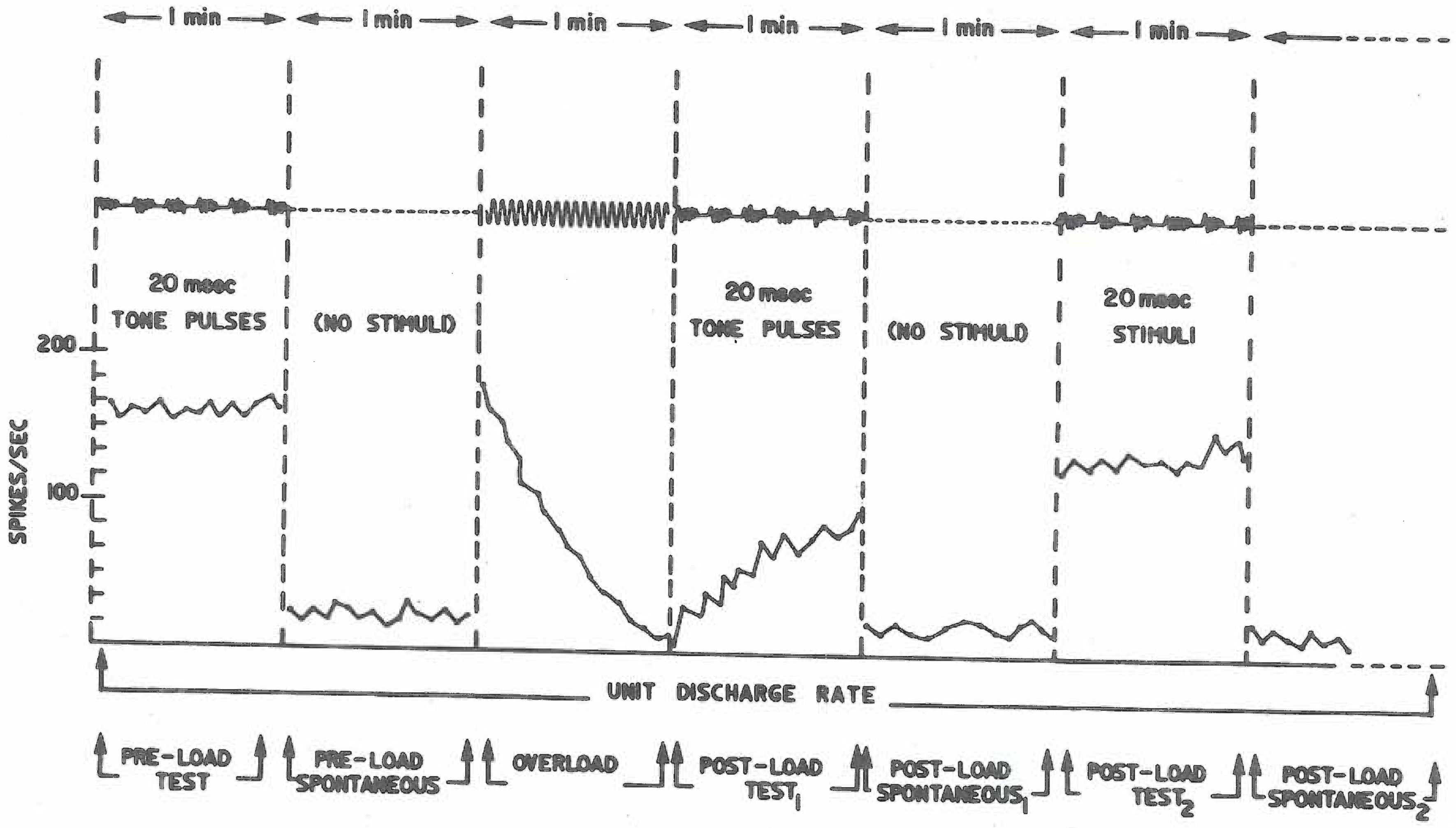
The details of the experimental procedures were as follows:

(1) TEST CF condition: The discharge rate of a nerve fiber in response to one minute of tone bursts at its CF was recorded. The stimulus level was 10-15 dB above the threshold of the fiber [a stimulus level relatively free from adaptation (Young & Sachs, 1973)].

(2) SPONTANEOUS condition: The test stimulus was turned off and

FIGURE 5.

Experimental protocol. The duration (1 minute) of each experimental condition is shown at the top of the figure and the stimulus is represented below. Pre- and post-overload tests consisted of a series of 20 msec tone bursts at the fiber's CF. Tone bursts were separated by 100 msec, giving a repetition rate of 8.3/second. The overload stimulus was a sustained pure tone either at the fiber's CF or at the half-octave above or below CF. A quiet period of 60 seconds intervened between the pre-overload test and the overload period and alternated with post-overload test periods during recovery. A typical discharge function for a cochlear nerve fiber during the various parts of the experimental protocol is indicated in each section, corresponding to the "spikes/second" rulings on the ordinate.



EXACT NUMBER OF POST-PERIODS DEPENDENT
ON RECOVERY OF UNIT DISCHARGE RATE

a one minute sample of spontaneous discharge rate of the fiber was obtained.

(3) LOAD condition: Following the SPONTANEOUS period, the fiber was subjected to an acoustic overload for one minute. The frequency and intensity of the continuous overload stimulus were chosen as described above.

(4) RECOVERY condition: Immediately upon termination of the LOAD period, test stimuli were reinstated as in (1) above for a one minute RECOVERY TEST CF period. Such test periods alternated with one minute RECOVERY SPONTANEOUS periods until either the fiber activity recovered to its pre-LOAD level or as long as contact with the fiber was maintained.

The overload levels were chosen so as to permit recovery within short periods of time. The LOAD and RECOVERY conditions were then presented anew, at a different frequency, for the same fiber, and this procedure was repeated as long as the fiber could be held. When contact with the fiber was lost, a new fiber was isolated and the entire experimental protocol (steps one through four) reinitiated.

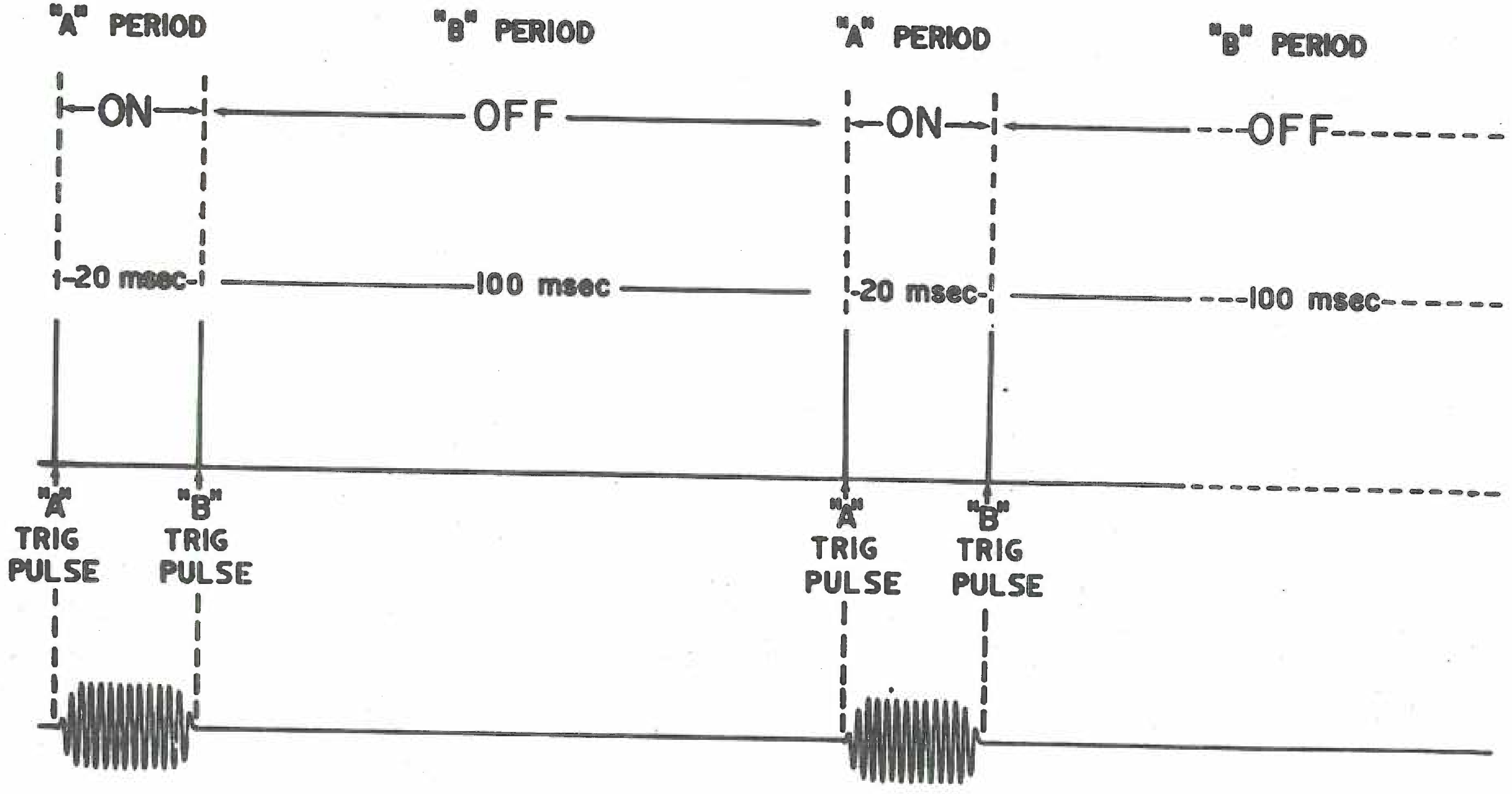
## V. Processing of Single Unit Data

Data processing equipment was arranged so that spike information could be handled in either an on-line or off-line fashion. For both analyses, spike trains were converted into trains of pulses corresponding to the occurrence in time of each spike in a data run. In the on-line system, these pulses were fed into logic-controlled counters which computed the frequency of discharge per unit of time. After every ten stimuli, the accumulated spike counts were transferred to a printer which provided a paper tape print-out of the number of spikes which occurred during either the stimulus-on or the stimulus-off periods. Off-line, the pulses corresponding to spike action potentials were stored using a punch-tape system controlled by an additional programmable logic system. The punch-tape tabulation of spike data was then processed by a programmable calculating system (Wang, model 720).

All data counts were registered in terms of the number of spikes occurring in ten trials. A single trial consisted of a 20 msec tone burst followed by a 100 msec quiet interval. As illustrated in Figure 6, for convenience, the tone burst interval will be called the "A" period and the tone-free interval the "B" period. The total duration of one trial was A plus B, or 120 msec; the stimulus repetition rate was 8.33 tone bursts per second; and accumulated 10-trial spike counts were printed out every 1.2 seconds. Thus during any 60-second period, whether TEST, SPONTANEOUS, LOAD or RECOVERY, there were 50 successive print-outs of accumulated spike counts, each such print-out including an A total and a B total. These accumulated totals represented, respectively, the number of spikes occurring during 200 msec (20 msec of A x 10 trials) of driven activity and 1,000 msec (100 msec of B x 10 trials) of non-driven activity. It is interesting to note that the B measures were not equivalent to measures of "true" spontaneous activity, for the B periods always exhibited lower spike counts than did equal intervals during periods of sustained freedom from stimulation. In order to obtain discharge rates expressed as spikes per second, A counts were multiplied by five (spikes per 200 msec x 5 = spikes per second). No correction was required to obtain the rate

FIGURE 6.

A schematic representation of stimulus parameters. For convenience, the stimulus-on interval is referred to as the "A" period while the stimulus-free interval is referred to as the "B" period. The A period corresponds to the presentation of a 20 msec tone burst. The total duration of one test trial was A plus B or 120 msec. Stimulus repetition rate was thus, 8.3/second.


"A" PERIOD
"B" PERIOD
"A" PERIOD
"B" PERIOD
ON
OFF
ON
OFF
20 msec
100 msec
20 msec
100 msec
"A" TRIG PULSE
"B" TRIG PULSE
"A" TRIG PULSE
"B" TRIG PULSE

in spikes per second from the B totals.

A. On-Line Data Reduction

The right side of Figure 4 illustrated the on-line processing and reduction system. Since it was desirable to obtain a preliminary on-line indication of fiber discharge rate to tone burst stimuli during the TEST CF and RECOVERY TEST CF conditions (in the first case, to determine a control mean rate of spike discharge per second, and in the second case, to evaluate recovery of the fiber spike rate before exposing it to further acoustic overload); spike data were processed by means of an on-line system that provided a printed paper tape tabulation of fiber spike discharge totals per unit of time. The on-line system included two specially modified electronic counters (Hewlett-Packard, model 5212-A), a two-channel digital printer (Hewlett-Packard, model 562-A), and transistorized programming modules (Massey Dickinson). The system operated in the following manner.

The spike data were fed into a level-detector module of the solid-state logic system, which generated a pulse whenever the trigger level was exceeded. The level at which spike occurrences were registered was continuously monitored by a second oscilloscope (Tektronix, model 564) fitted with a dual-channel amplifier (Tektronix, type 3A72). The top channel of the oscilloscope displayed the output pulses of the trigger while the bottom channel displayed the corresponding neural spikes. The output pulses of the level detector were led to the two electronic counters. One counter tabulated spikes during the A periods; the other counter computed the number of spikes during the B periods. The "start" and "stop" signals (which were synchronized to the time-base generator's A and B periods) for the counters were provided by the logic equipment.

Following a start-count command delivered by a logic module, the counters accumulated and displayed their appropriate pulses coming from the trigger module until a stop-count command was received. After ten stimulus presentations, the counters ceased to accept inputs from the trigger, transferred the accumulated spike counts to the buffer storage of the digital printer and the printer printed out the total (channel 1 displayed A counts and channel 2 displayed B counts). Once the information had been stored in the printer, the counters automatically reset to zero and in 2 msec were ready to accept the next start-count commands.

To provide an accuracy check on the reliability of the operation of the counting circuit, a standard 1.0 kHz signal, substituted for the incoming raw spike data, was fed through the level detector module and the resulting output pulses were counted and printed at the beginning of each experiment.

In order to determine if a particular fiber had returned to its pre-exposure stimulus-driven discharge rate following a LOAD condition, an average was computed from ten A values chosen at random from the printed paper tape tabulations of the pre-overload TEST period. Similarly, ten post-overload A values were randomly chosen from a RECOVERY TEST CF series and their average computed. As a working criterion, mean discharge rate following overload had to return to within 10% of the control rate before the fiber was considered to have recovered.

## B. Off-Line Data Reduction

A block diagram of the off-line data processing and reduction system is shown in Figure 7. The major difference between the on-line and off-line processing systems was that the counter-printer equipment used in the former analysis was replaced by a paper-punch system in off-line processing. The system operated in the following manner.

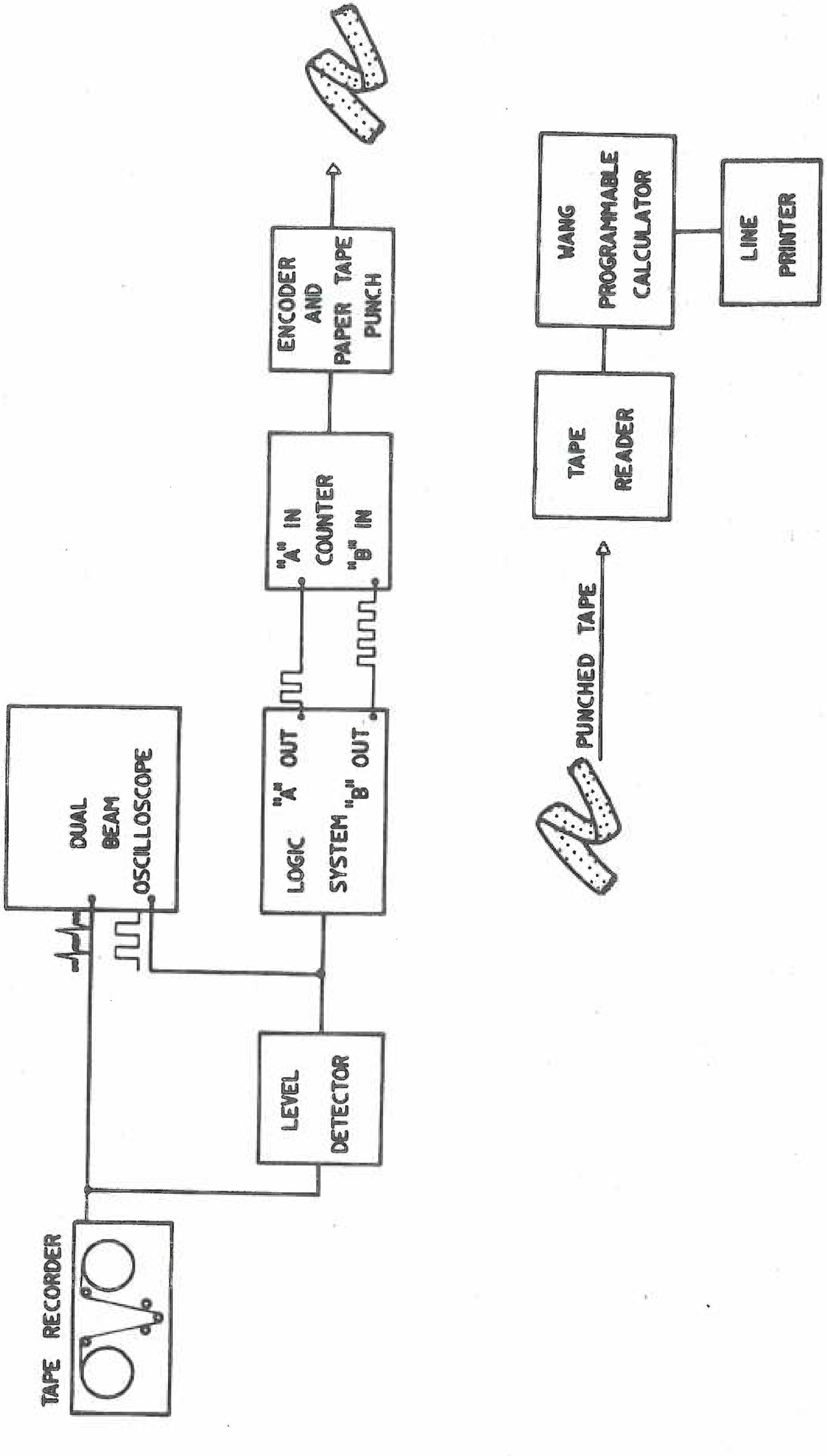
The tape recorder output from the spike data channel was connected to a level detector module adjusted to trigger on the positive-going portion of the fiber action potential for each spike that reached a given threshold level. The trigger supplied pulses to a counter module for each spike discharge. An end-of-count command transferred the contents of the counter to storage thus freeing the counter to accept incoming signals within 30 $\mu$-seconds. The stored spike total was then punched out on paper tape.

To insure that the spike data was counted in the correct time interval (i.e., A vs. B periods), the synchronizing pulses, recorded on a second channel of the magnetic tape, were fed into a second level detector which provided pulses to the counter of the logic system controlling the paper tape-punch equipment. At the end of a block of ten stimulus presentations, a print command was delivered to the counter and the total number of A and B spikes which occurred during that 1.2 second time interval was punched out on paper tape.

All computations and statistical analyses were performed on the programmable calculating system (Wang, model 720). The off-line plotting was accomplished with the calculator's line-printer (Wang, model 721). For the purpose of graphic display, the data for all

FIGURE 7.

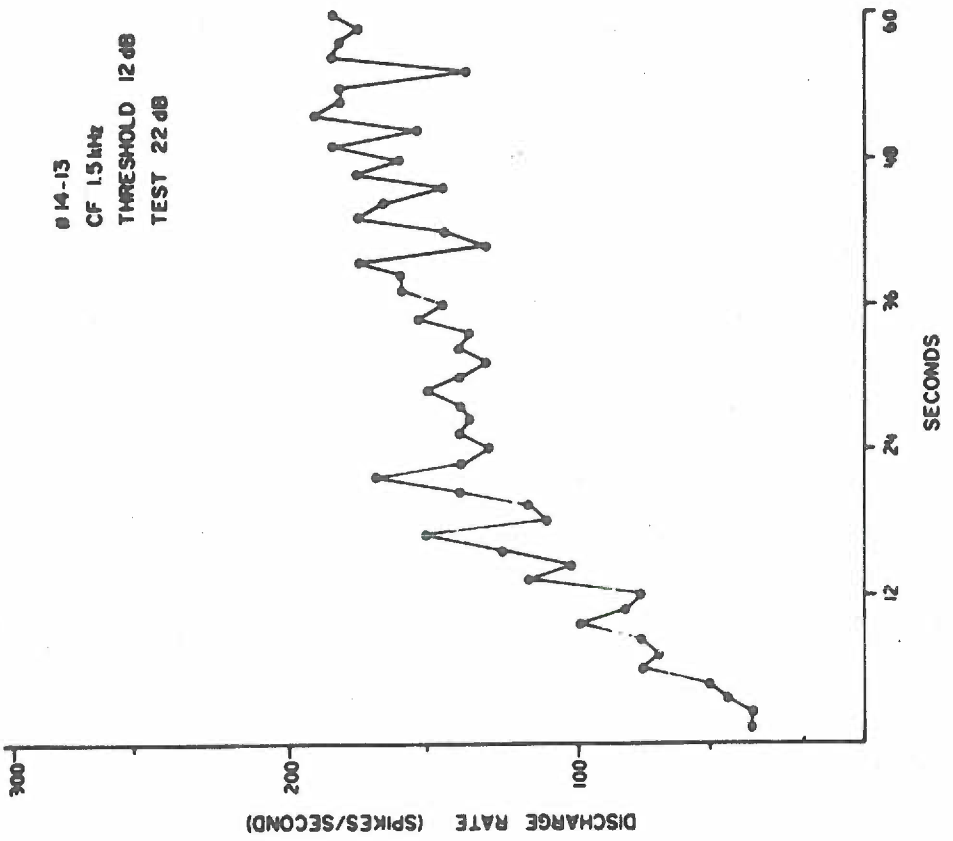
Block diagram of off-line data reduction and analysis system. Pulses corresponding to spike action potentials are stored on punch tapes, which were then processed by the programmable calculating system.


TAPE RECORDER
LEVEL DETECTOR
DUAL BEAM OSCILLOSCOPE
LOGIC SYSTEM
"A" OUT
"B" OUT
"A" IN
COUNTER
"B" IN
ENCODER AND PAPER TAPE PUNCH
PUNCHED TAPE
TAPE READER
WANG PROGRAMMABLE CALCULATOR
LINE PRINTER

conditions were "smoothed" by a running-average technique in which each spike count was replaced with the average of itself and its two neighbors, as in Figure 8. The first and last points in any 50-count period are unaveraged. Individual points are joined by straight lines. For statistical computations, only the raw, unsmoothed spike counts were used.

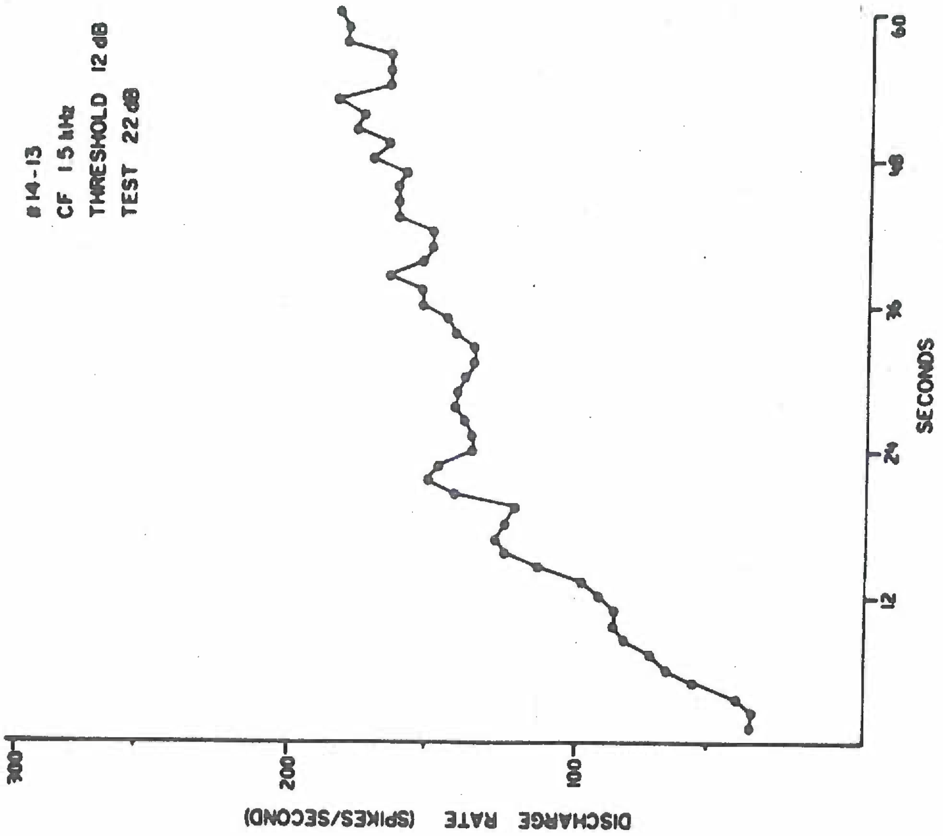
FIGURE 8.

An example of the smoothing procedure applied to the rate-time curves. The abscissa of each graph represents the 1-minute time period in seconds (the example chosen was taken from a RECOVERY record). The ordinate shows the discharge rate in response to the CF test stimuli. Each point on the graph represents the sum of 10 stimulus presentations. The graph in (b) represents the same data as in (a), except that each point has been replaced by the mean of itself and its two nearest neighbors. The first and last points are unaveraged. Cat and unit number, fiber CF and threshold, and test level of CF tone burst stimuli are indicated in upper right-hand corner for this curve and all succeeding rate-time curves.



# 14-13
CF 1.5 kHz
THRESHOLD 12 dB
TEST 22 dB
DISCHARGE RATE (SPIKES/SECOND)
300
200
100
12
24
36
48
60
SECONDS

a



# 14-13
CF 1.5 kHz
THRESHOLD 12 dB
TEST 22 dB
DISCHARGE RATE (SPIKES/SECOND)
300
200
100
12
24
36
48
60
SECONDS

b

# RESULTS

A total of 25 cats was used in the present research. Of these, 11 were used to develop and refine the surgical preparation, the acoustical procedures, and the special overload protocol described in the METHODS section. The remaining 14 cats yielded observations on a total of 198 single cochlear nerve fibers. While many more than these were isolated, this is the number of fibers "held" long enough to permit determination of the characteristic frequency.

In the data to be presented below, the number of units upon which a given generalization or conclusion was based is indicated by an accompanying statement of the sample size. When data from an individual fiber are presented for illustration, the fiber is identified by the cat number and unit number. For example, the fiber in Figure 8 was recorded from Cat 75-15 and was the thirteenth unit isolated from the nerve.

## I. Recording Events

When the micropipet was inserted into that portion of the cochlear nerve which was inside the internal acoustic meatus, spike discharges were recorded only with monophasically positive waveforms such as are illustrated by the spike train in Figure 9a. Such discharges have been studied in detail previously and may be presumed to be characteristic of cochlear nerve fibers (Kiang et al., 1965).

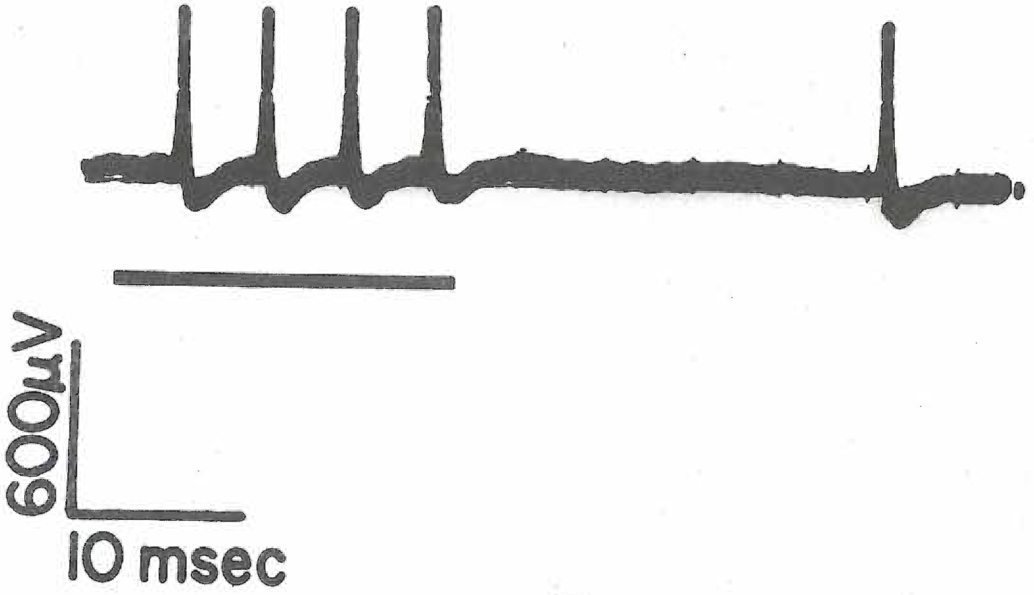
As the micropipet first contacted a fiber, perhaps penetrating the myelin sheath to touch the membrane (Tasaki, 1952b) the spikes were large. Discharges were at times initially over 1 mV in amplitude but usually decreased over the recording period to approximately 100 to

FIGURE 9.

Typical spike potentials observed in single units of the cochlear nerve.

(a) Oscilloscope tracing of the response of a single nerve fiber in the cat cochlear nerve to a tone burst (represented by horizontal bar) at the CF (1.9 kHz). The intensity of the tone burst was 10 dB above threshold for the fiber. Upward deflection represents positivity at the electrode relative to the indifferent electrode.

(b) Oscilloscope tracing of sample spike train of spontaneous activity for one unit. The unusually large amplitude of the unit activity led to over-driving at the first stage of amplification which resulted in the evident peak clipping seen here.



**a**

**b**

200 μV. The noise level was generally on the order of 5 μV. Although the responses from a single nerve fiber were not easily isolated for extended periods of time, "contact times" of 10 to 20 minutes were not uncommon and one of the units in the present investigation was held for 140 minutes. Figure 10 illustrates the distribution of contact times for fibers held longer than two minutes.

## II. General Characteristics of Sample of Cochlear Nerve Fibers

### A. Discharge Characteristics

### (1) Driven Activity

The selective frequency sensitivity of individual units in the various nerves studied in these experiments is shown in Figure 11. The distribution of CF for the cochlear nerve fibers ranges from 0.2 to above 20 kHz. If tone bursts at the fiber CF are delivered regularly, spikes whose occurrences are more or less time-locked to the delivery of the stimuli can be detected. Figure 9a illustrates a sample spike train from a single cochlear nerve fiber in response to a suprathreshold tone burst at its CF.

Discharge rate to CF tone bursts can vary considerably between fibers. Figure 12 indicates the driven rates for fibers of the present investigation when stimulated by CF tones at 10-15 dB above threshold. The distribution of rates elicited by CF tones for 61 fibers had a median value of 220 spikes/second, with a range of 44 to 315 spikes/second. As shown by others (Kiang et al., 1965; Kiang, 1968), discharge characteristics, both driven and spontaneous, were not discernibly related to the CF.

FIGURE 10.

Distribution of durations for which units were "held". Data are from 189 fibers in 17 cats. Filled circles correspond to units included in the statistical analysis of the overload effects. The graph does not show fibers held for periods of time shorter than 3 minutes (this was the approximate time required for measurement of CF and few records were kept for fibers lost before CF was established).

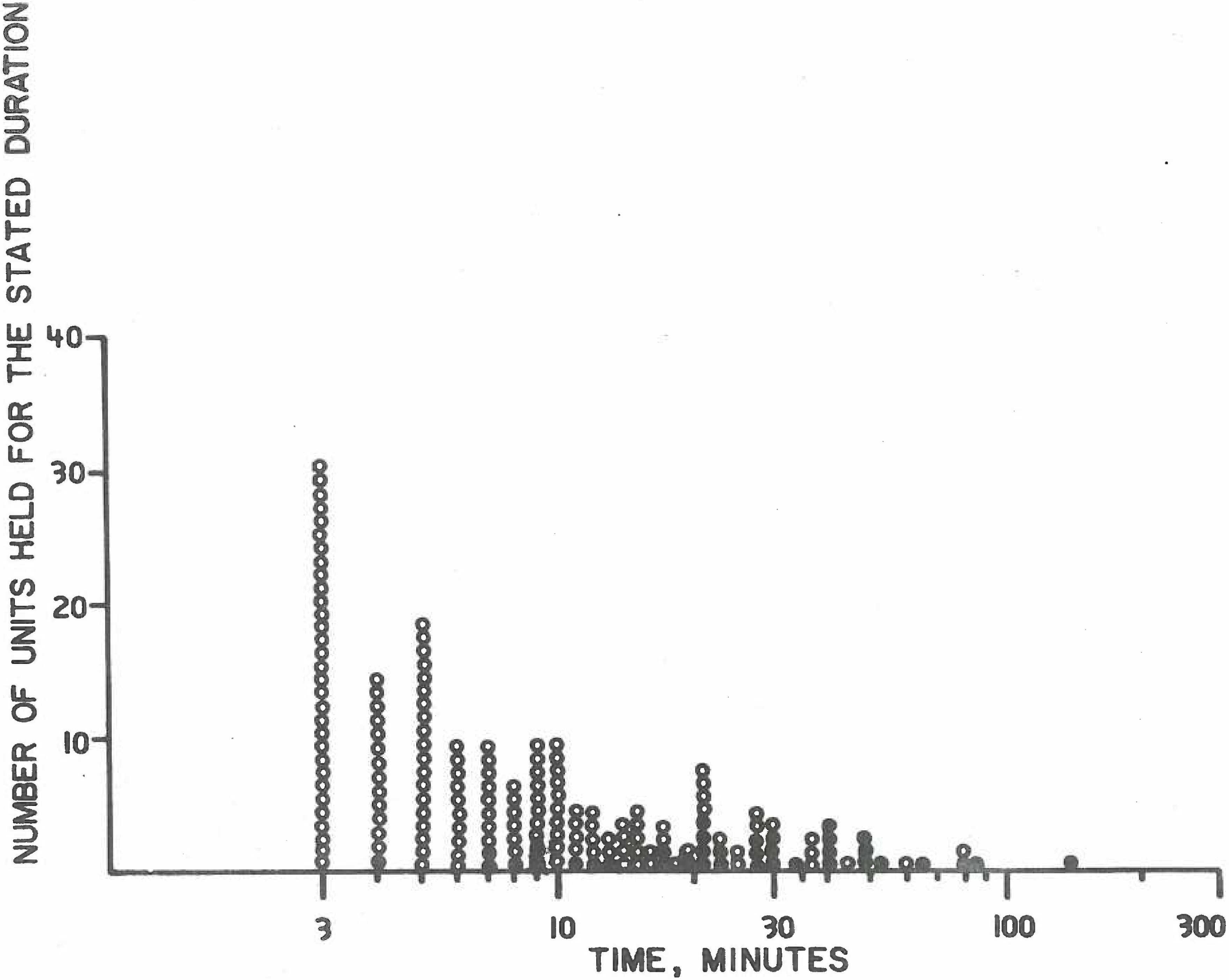

NUMBER OF UNITS HELD FOR THE STATED DURATION
40
30
20
10
3
10
30
100
300
TIME, MINUTES

FIGURE 11.

Distribution of fiber CFs. Data are from 198 fibers in 17 cats. The shaded area represents those units included in the statistical analysis of the overload effect. The output capabilities of the 1-inch microphone fall off rapidly above 20 kHz, thus few fibers with CFs above 20 kHz were identified. In every cat, some fibers were isolated whose CF could not be determined. It is probable that such fibers had CFs above 20 kHz and that the acoustic system was not capable of reaching their thresholds.

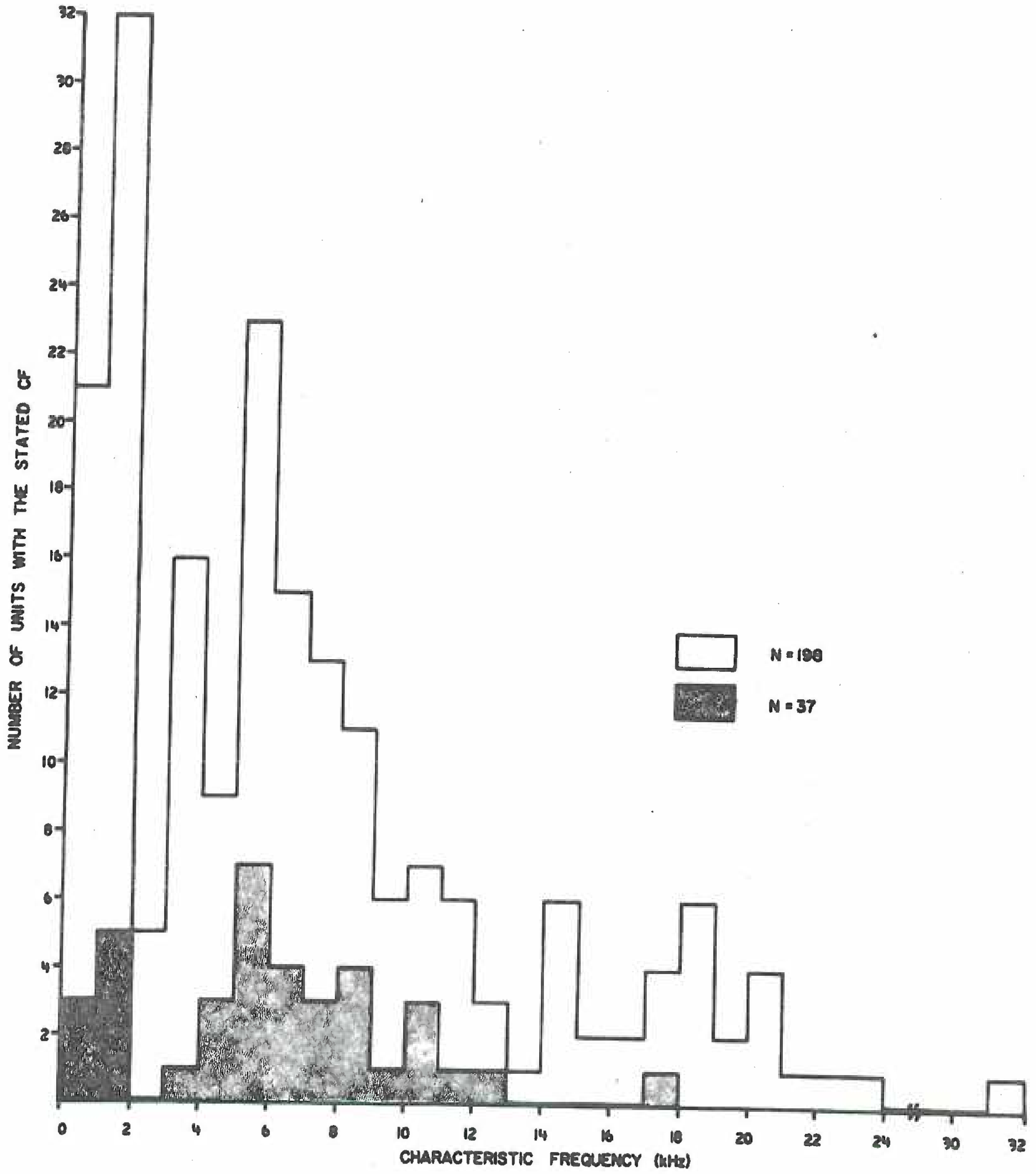

NUMBER OF UNITS WITH THE STATED CF
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
18
20
22
24
30
32
CHARACTERISTIC FREQUENCY (kHz)
N = 198
N = 37

FIGURE 12.

Driven discharge rates in response to stimulation at the CF. Data are from a representative group of 58 fibers obtained in 8 cats. Stimulus level was 10-15 dB above fiber threshold. A tendency toward a bimodal distribution is evident, with one mode around 80-120 spikes/second and the other around 200-240 spikes/second. These discharge rates are consistent with data in other reports describing single fibers of the cat's cochlear nerve (Kiang et al., 1965).

FIGURE 13.

Distribution of spontaneous discharge rates. Data are from a representative group of 61 fibers in 8 cats. Again, there is a multimodal distribution, with the first mode between 0-10 spikes/second and the larger, less sharply-peaked mode around 40-100 spikes/second.

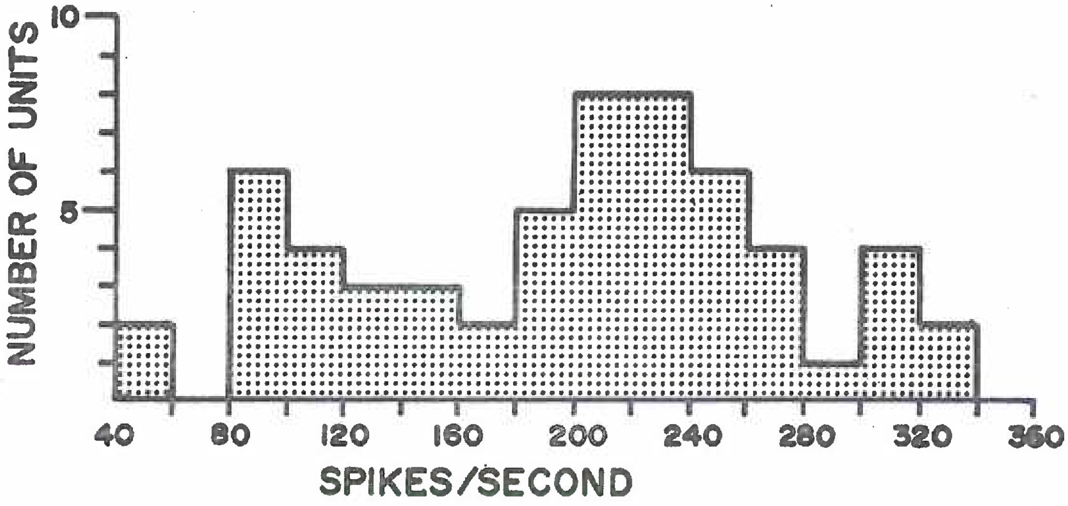


FIGURE 12

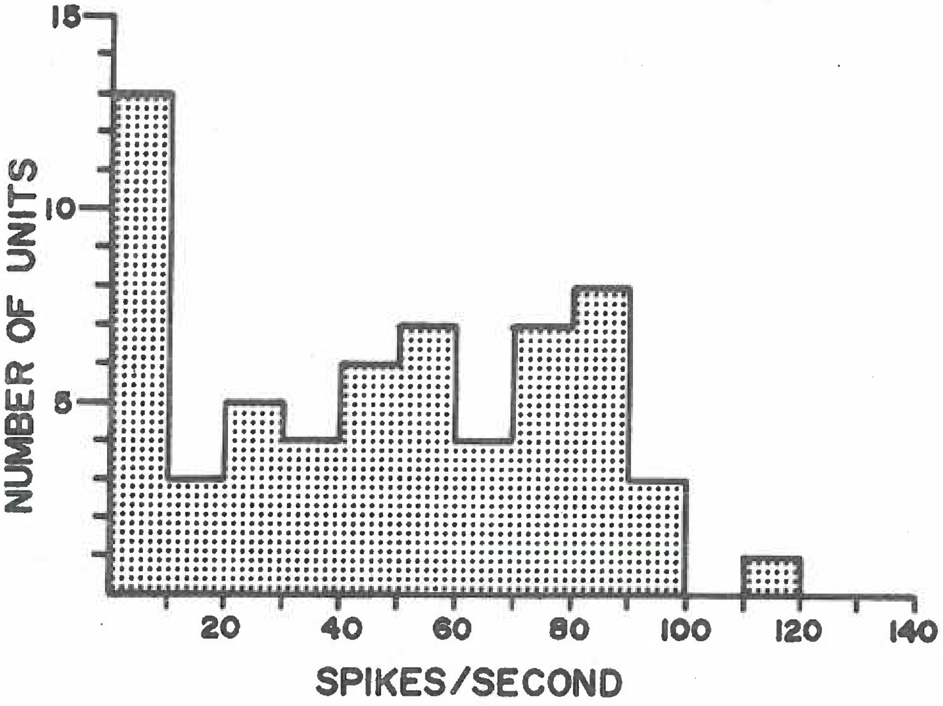


FIGURE 13

(2) Spontaneous Activity

In the absence of any apparent acoustic stimuli, most cochlear nerve fibers exhibit spontaneous activity (Kiang et al., 1965). Figure 9b illustrated sample spontaneous discharges from a single nerve fiber. As reported by many others (Tasaki, 1954; Kiang et al., 1962, 1965; Nomoto et al., 1964; Rose et al., 1971; Evans, 1972) great variability of individual spontaneous rates within a population of fibers occurs. In this study, mean spontaneous rates which varied from virtually zero to as high as 115 spikes/second were observed. For any one fiber, this mean rate remained relatively constant over the entire monitoring period. A sample of spontaneous activity was routinely taken for each fiber soon after it was isolated, and at regular one-minute intervals following acoustic overload. There was usually no major change of spontaneous activity during the time of observation, thus indicating that units were not in general damaged during the recording session.

A histogram of the mean spontaneous rates for 61 cochlear nerve fibers, recorded under quiet conditions in the experimental set-up, is shown in Figure 13. Although there was considerable spread in mean frequency of discharge, the distribution of spontaneous rates was multimodal, with nearly half of the fibers demonstrating spontaneous rates of less than 50 spikes/second. In fact, approximately 21% had spontaneous rates of less than 10 spikes/second.

It was observed that the rate of spontaneous discharge for a given nerve fiber was not correlated with either its CF or threshold; however, there was a positive correlation between mean spontaneous rate and driven rate (the latter measured using CF tone bursts at 10-15 dB above fiber threshold). That is, as Figure 14 shows, the driven rate was an increasing function of spontaneous rate. A similar relation for cat cochlear nerve fibers has been reported previously (Sachs et al., 1974).

### B. Threshold

Using the 20 msec tone bursts described earlier, thresholds for responses at the CF were readily obtained. A histogram of the thresholds for 72 typical nerve fibers is shown in Figure 15. Besides the existence of a considerable range of thresholds across nerve fibers, there was also great variation in the threshold of nerve fibers at any given CF even in the same animal. Figure 16 shows some plots of threshold versus CF. The thresholds for single units in the cochlear nerve followed in general the form of the cochlear potential 1 μV isopotential curves (measured from the round window), but were obviously much closer to absolute hearing thresholds.

Although there was a wide range of fiber thresholds at any given CF, it is clear that the threshold also depended somewhat on the fiber's CF. As Figure 16 shows, for CFs between 0.2 and 0.6 kHz, the thresholds ranged from -1 to +43 dB SPL, with a mean of approximately +21 dB SPL. On the other hand, for CFs between 1.0 and 10.0 kHz, the threshold for the majority of fibers was in the range of -26 to +20 dB SPL with a mean of 0 dB SPL.

## III. Major Experimental Results

Data in this section are presented in the form of rate-time functions (discharge rate vs. time during a given experimental condition).

FIGURE 14.

Correlation between spontaneous discharge rate and mean driven discharge rate. Data are derived from 57 representative units. Driven rates were determined in response to CF test bursts at 10-15 dB above fiber threshold. Filled circles correspond to fibers included in the statistical analysis of overload effects. The Pearson product-moment correlation is given in the lower-right portion of the figure. As would be expected, there was a positive correlation between spontaneous and driven discharge rates.

FIGURE 15.

Response thresholds for CF stimuli. Data are from 72 units in 6 cats. The shaded portion of the histogram represents fibers included in the statistical analysis of overload effects. Threshold was determined using an audio-visual criterion as described in the text. Such a criterion yields thresholds from 5-20 dB less sensitive than those obtained in computer-assisted determinations (Kiang et al., 1965). Thus if allowance is made for a 5-20 dB increase in sensitivity which could be measured with more sensitive techniques, the majority of fibers in this sample would show thresholds close to or below the 0 dB level (0.0002 μbar).

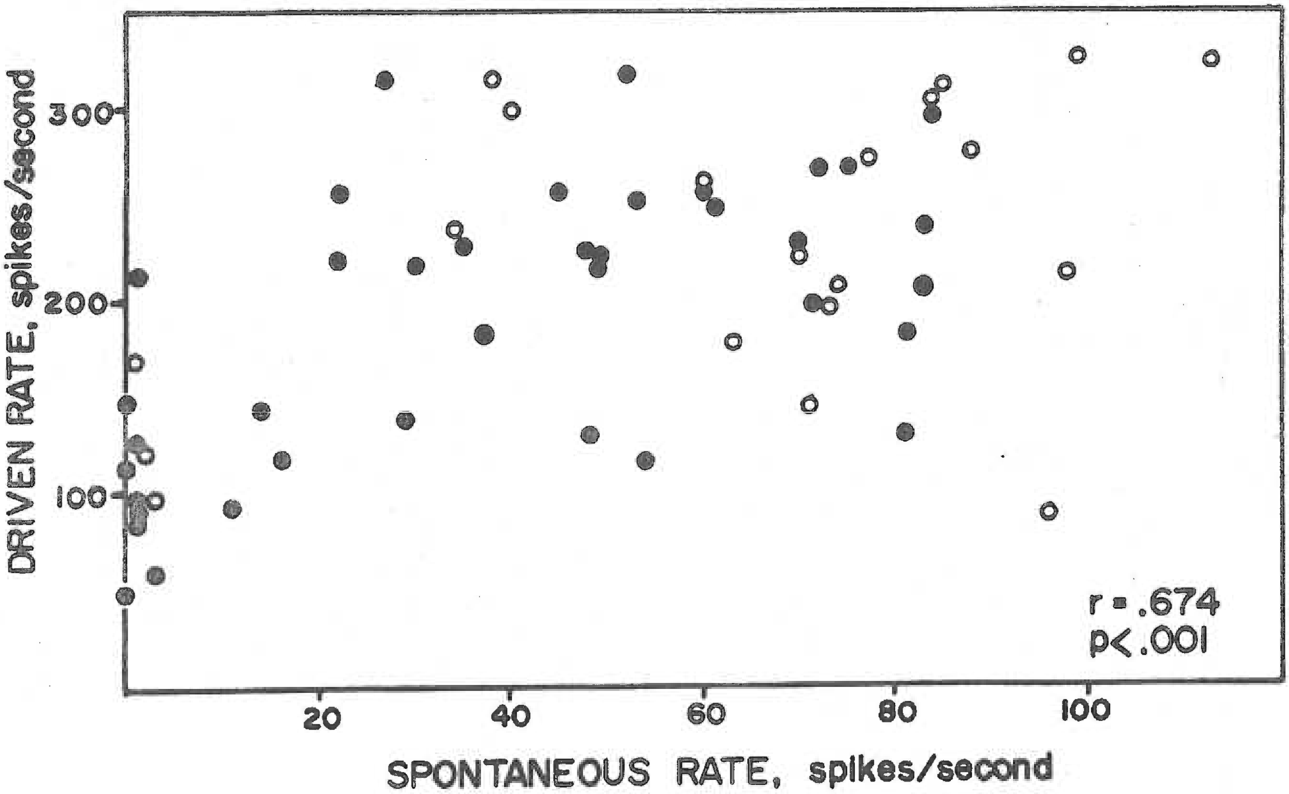


FIGURE 14

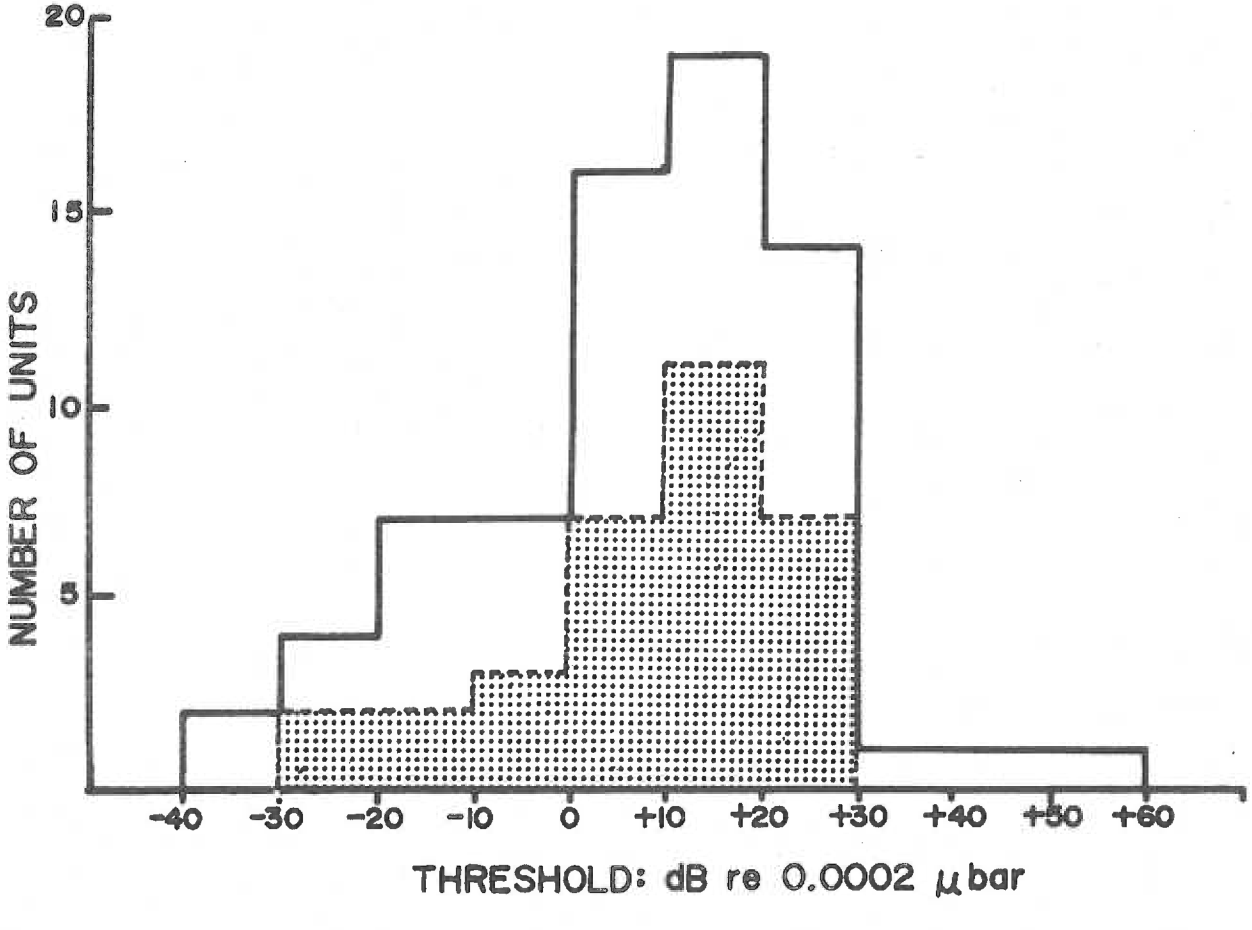
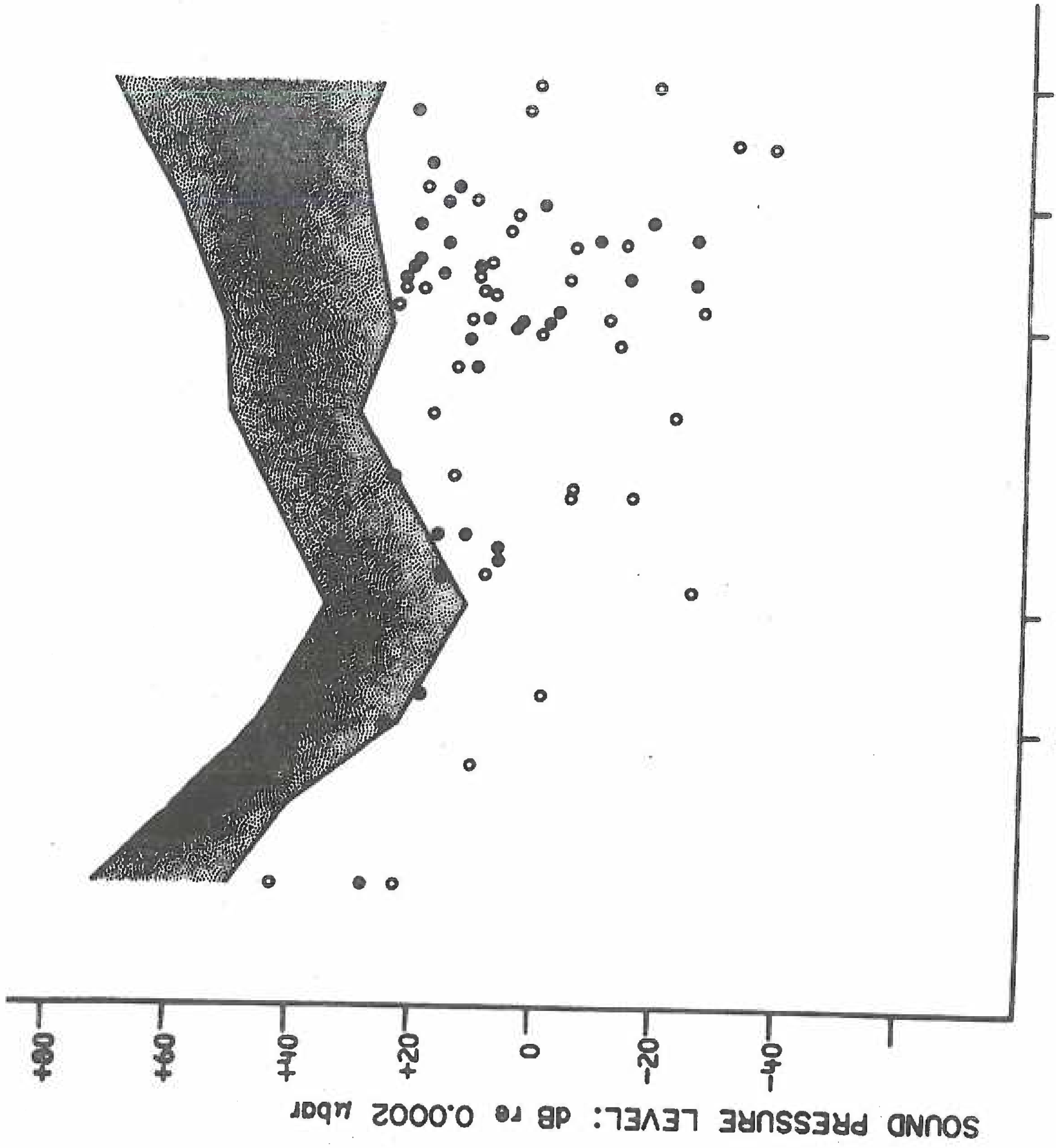


FIGURE 15

FIGURE 16.

Fiber thresholds plotted as a function of CF. Each point plots the threshold at the CF as a function of CF for a single cochlear nerve fiber. The stimuli were the standard 20 msec tone bursts with 1.5 msec rise-fall times presented at a repetition rate of 8.3/second. Filled circles correspond to fibers included in the statistical analysis of overload effects. The shaded area represents the range of cochlear-potential frequency functions (1μV isopotential curves) obtained from 11 of the cats used in the present experiments. The single unit data are from 72 representative fibers in 5 of these cats.


SOUND PRESSURE LEVEL: dB re 0.0002 µbar
+80
+60
+40
+20
0
-20
-40
CHARACTERISTIC FREQUENCY (kHz)
.5
1
5
10
20

The response measure utilized in this study, i.e., the number of discharges occurring during tone bursts of 20 msec duration, repeated 8.3 times every second (every 120 msec), appeared to be stable from one measurement to another. The repeatability of results that were obtained with this response measure is illustrated in Figure 17 in which rate of spike discharge per second is plotted as a function of time during the one-minute test period. Two sets of measurements, separated by 15 minutes, were made. Figure 17 presents discharge rates during the A periods (stimulus on), the B periods (stimulus off), and the intervals of quiet when true measures of "spontaneous" activity could be obtained. The rates obtained under these three conditions showed little or no change in these and other similar control observations.

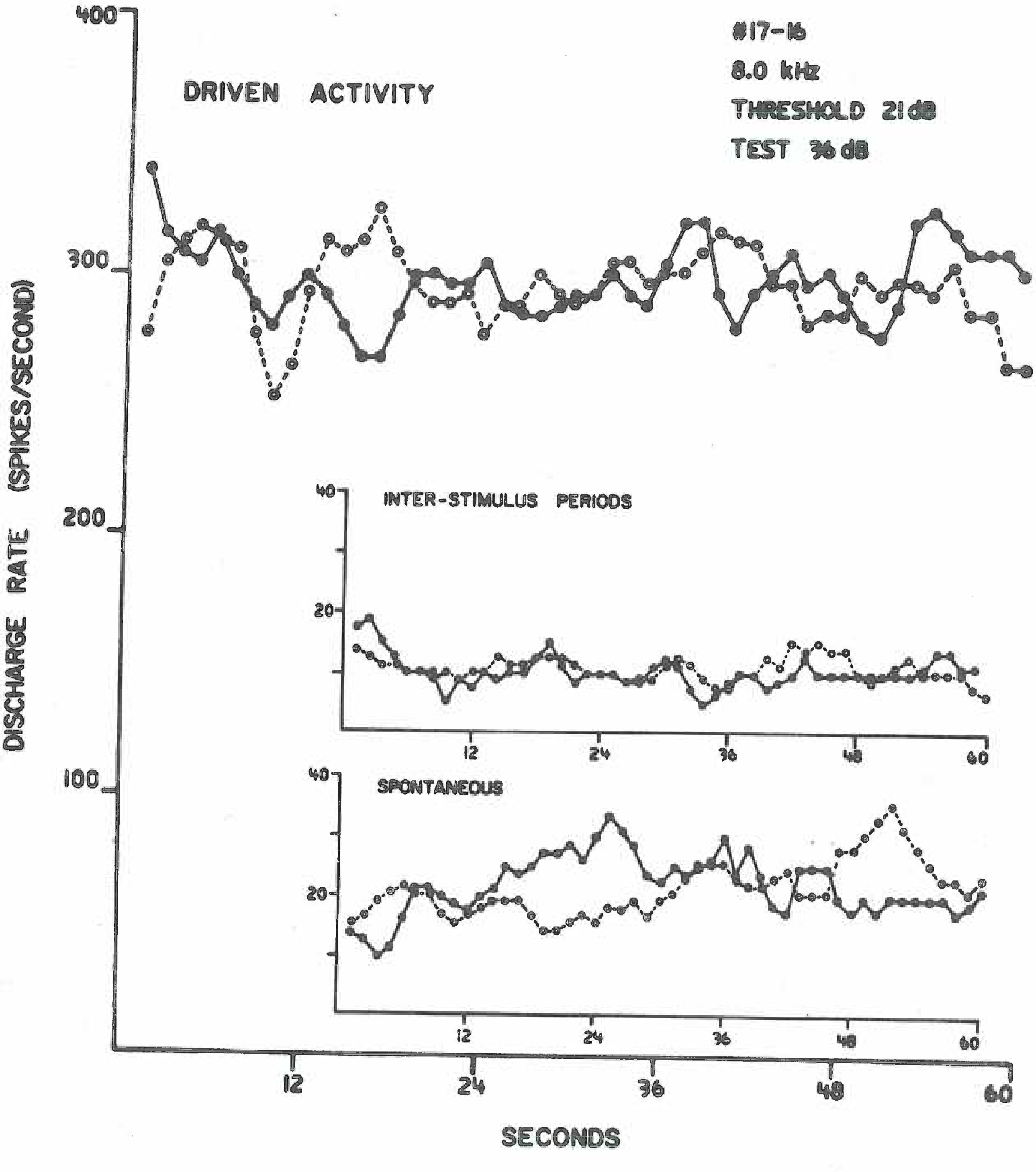
To illustrate a particular effect of an experimental condition, two different types of data will be presented. One type consists of individual rate-time functions for a given unit. The other type consists of mean data in which discharge rates for all fibers in any one experimental group were combined at each point in time. A rate-time curve was then plotted which represents the average discharge rate for a particular group of fibers throughout the time period of interest (for example, during one of the one-minute RECOVERY test periods).

## A. Discharge Rate Evoked by Acoustic Overload Stimuli

Examples of the decline in discharge rate during the prolonged LOAD stimulus are shown for the six experimental groups in Figure 18. Because discharge rates among different fibers varied considerably, for a given fiber the discharge rate at each point in time during the LOAD interval was divided by that fiber's discharge rate measured during the

FIGURE 17.

Reliability over time of the rate-time functions for a single fiber. The driven activity shown here was elicited by standard CF test stimuli. The two curves in the larger graph compare responses during the first TEST CF period (solid line) and driven activity of the same unit measured 15 minutes later (dashed line). No overload stimuli were presented during the period over which this unit was recorded. Lower graphs show interstimulus and spontaneous activity compared similarly. Solid lines represent initial measurements, while dashed lines correspond to the later measurements.


DRIVEN ACTIVITY
#17-16
8.0 kHz
THRESHOLD 21 dB
TEST 36 dB
INTER-STIMULUS PERIODS
SPONTANEOUS
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
40
20
12
24
36
48
60
SECONDS

last 10 seconds of the pre-exposure TEST CF period. These ratios were then expressed as percentage values. The group curves of Figure 18 represent the medians of the percentage values for all fibers in a particular experimental condition.

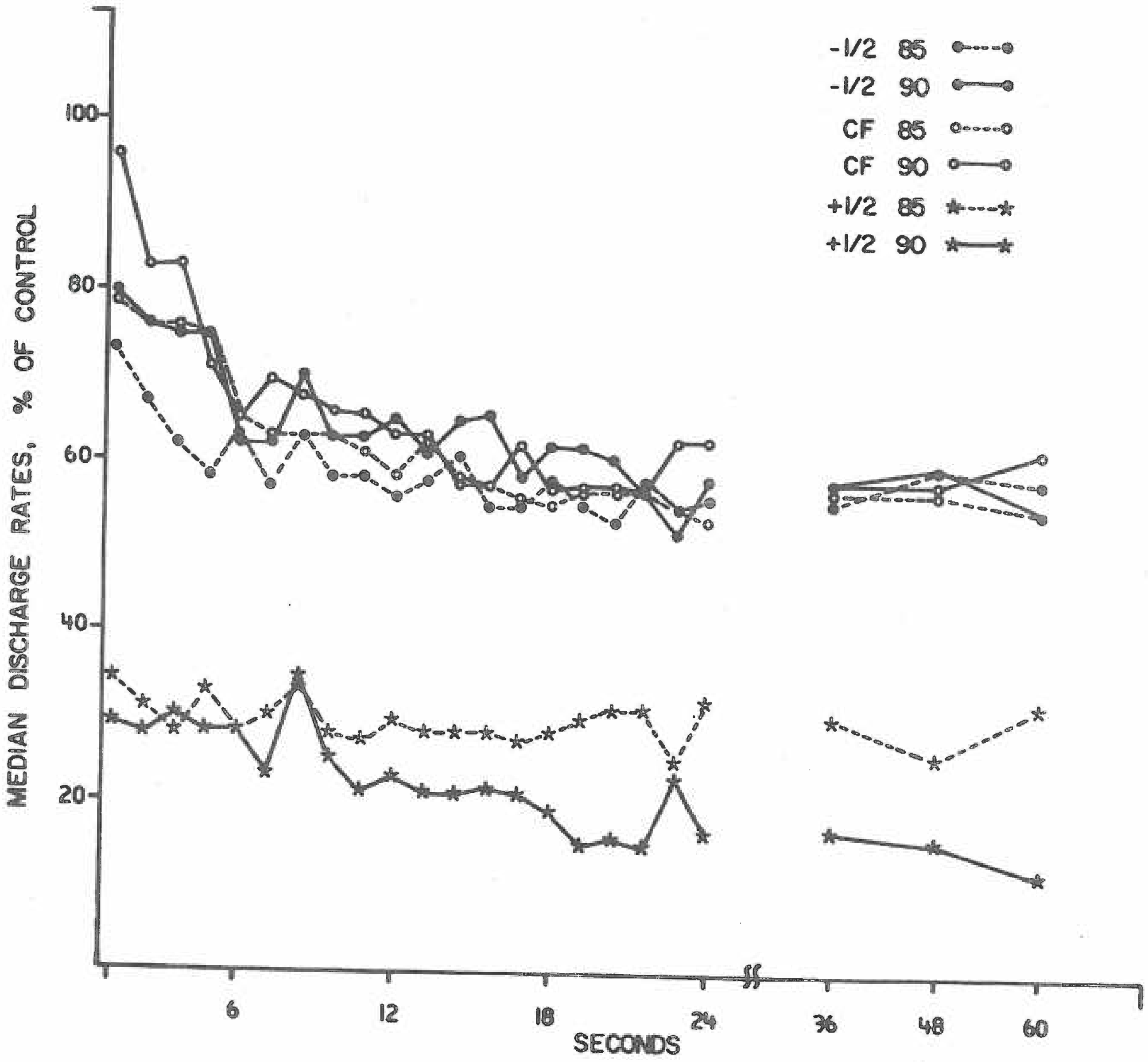
Figure 18 reveals the temporal development of response decrements introduced by the exposure tone. In each group, data are plotted for the first 24 seconds of the one-minute LOAD period, and thereafter, are plotted only at the 36th, 48th and 60th seconds.

A similar pattern of decline was seen in the two CF and -1/2 OCT groups. During the first 6 seconds following onset of overstimulation, the discharge rate decreased very rapidly. At least 90% of the total decline was completed during this time. As stimulation was prolonged, a further slow decline followed and in many fibers persisted to the end of the exposure period. However, as reported previously (Kiang et al., 1965; Young & Sachs, 1973), the discharge rate during the sustained stimulus was never observed to decline to or pass below the fiber's spontaneous rate. The $CF_{90}$ group appeared to show a higher level of discharge upon onset of the LOAD tone, although this difference was not statistically significant (t-test).

As illustrated in Figure 18, while the CF and -1/2 OCT exposures behaved very similarly throughout the LOAD period, these groups were very different from the two +1/2 OCT groups. Although a slight trend towards a decrement in discharge rate can be detected, the two overload frequencies above the CF produced little effect on the discharge rate of a fiber. In fact, even at these high stimulus levels, +1/2 OCT stimulation elicited only about 30% of the discharge rate

FIGURE 18.

Perstimulatory decline in discharge rate during acoustic overload. The median normalized discharge rates (defined in the text) for the six experimental groups are plotted. Stimulus frequencies and levels are given in the legend as are the symbols indicating each experimental group. Data for the first 24 seconds of the overload period and for the 36th, 48th and 60th seconds are shown. Discharge rate was computed in successive 1.2 second bins.



-1/2 85
-1/2 90
CF 85
CF 90
+1/2 85
+1/2 90
MEDIAN DISCHARGE RATES, % OF CONTROL
100
80
60
40
20
6
12
18
24
36
48
60
SECONDS

measured during the TEST CF period.

In Figure 19, individual examples of the decline in discharge rate during the sustained stimulation period are shown for eight cochlear nerve fibers from the CF and -1/2 OCT groups. Fiber discharge rates during the continuous exposure tone are plotted between 0 and 60 seconds on the abscissa.

When individual curves from the CF and -1/2 OCT groups were examined in this way, a tendency for overload time courses to separate into two general patterns could be seen. Figure 19a shows an example of LOAD curves which are roughly "exponential" in shape, that is, there was a rapid decay in discharge rate followed by a more gradual decline to the end of the exposure period. In contrast to this exponential type of decrease, a number of fibers showed the type of decreasing function illustrated in Figure 19b. No particular shape characterized such curves, apart from the fact that all exhibited a slow decline in discharge rate.

Although there was considerable variability within the various groups, it was obvious that the exponential type of overload pattern was more prevalent in the $CF_{85}$ exposure condition than in either the $CF_{90}$ or -1/2 $OCT_{85}$ groups. Furthermore, for the -1/2 $OCT_{90}$ exposure group, the majority of fibers exhibited the rather amorphous, gradually declining type of time course.

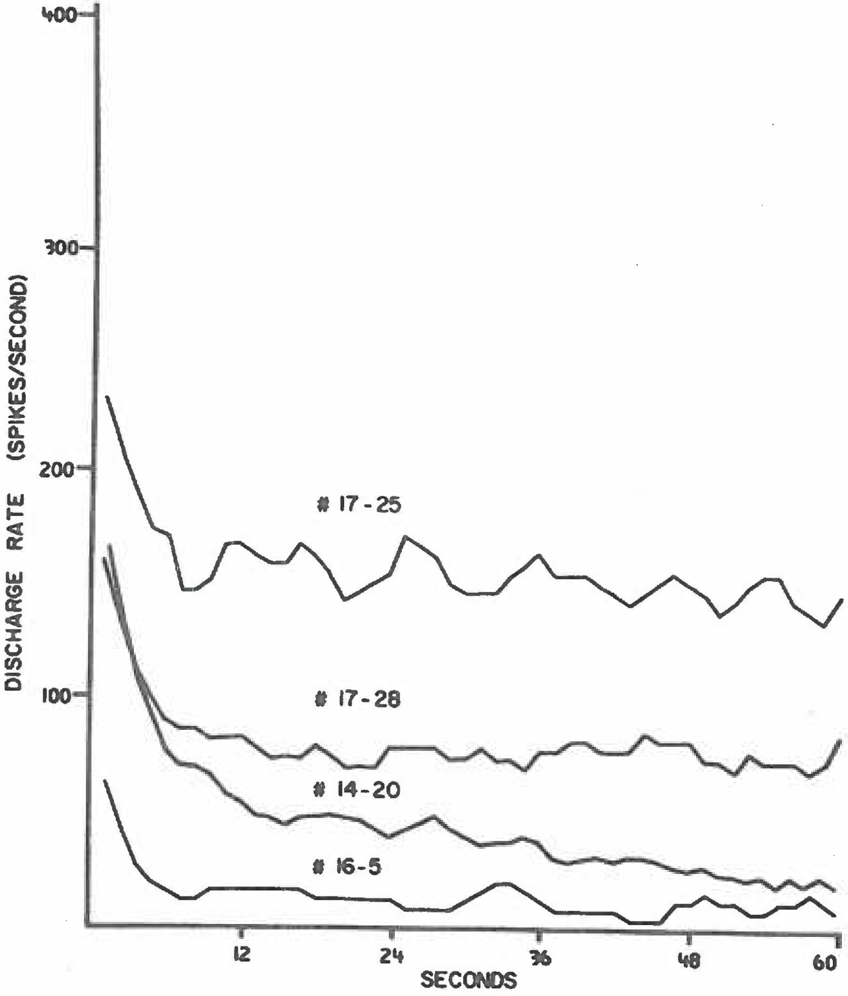
It was of interest to consider to what extent the decline in discharge rate seen in the exposure period was related to the individual characteristics of a fiber, i.e., CF, threshold, spontaneous and driven discharge rates. No correlation between the time course of

FIGURE 19.

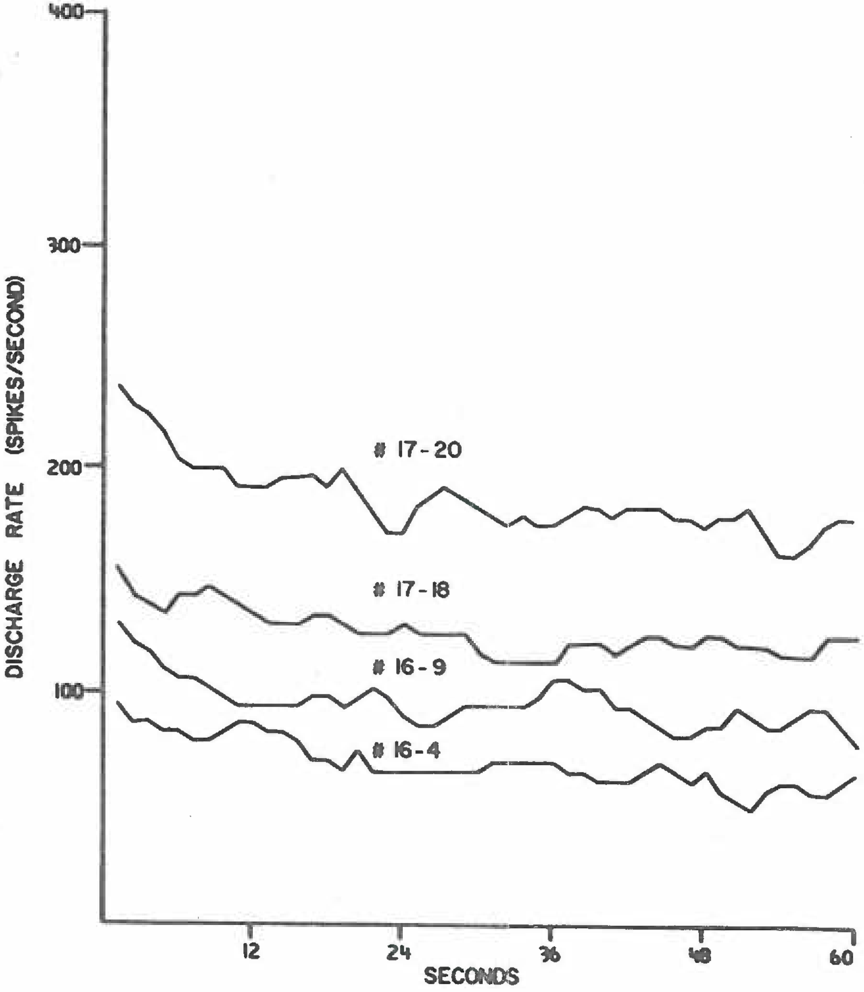
Two different patterns of perstimulatory decline in discharge rate.

(a) the "exponential" type of decline in firing rate for four fibers from the CF and -1/2 OCT exposure groups. The frequencies and levels of the overload stimuli were as follows: Fibers #17-25 (CF=6.4 kHz) and #16-5 (CF=17.1 kHz) were -1/2 $OCT_{90}$ and -1/2 $OCT_{85}$, respectively; Fibers #17-28 (CF=7.3 kHz) and #14-20 (CF=8.0 kHz) were $CF_{90}$ and $CF_{85}$, respectively.

(b) The "gradual" type of decline in firing rate for four CF and -1/2 OCT fibers. The frequencies and levels of the overload stimuli were as follows: Fibers #17-20 (CF=6.6 kHz) and #16-4 (CF=9.1 kHz) were -1/2 $OCT_{90}$ and -1/2 $OCT_{85}$, respectively; while Fibers #17-18 (CF=0.5 kHz) and #16-9 (CF=5.0 kHz) were $CF_{90}$ and $CF_{85}$, respectively.


400
300
200
100
DISCHARGE RATE (SPIKES/SECOND)
# 17-25
# 17-28
# 14-20
# 16-5
12
24
36
48
60
SECONDS

**a**


400
300
200
100
DISCHARGE RATE (SPIKES/SECOND)
# 17-20
# 17-18
# 16-9
# 16-4
12
24
36
48
60
SECONDS

**b**

response decrement and any of these parameters was evident, however.

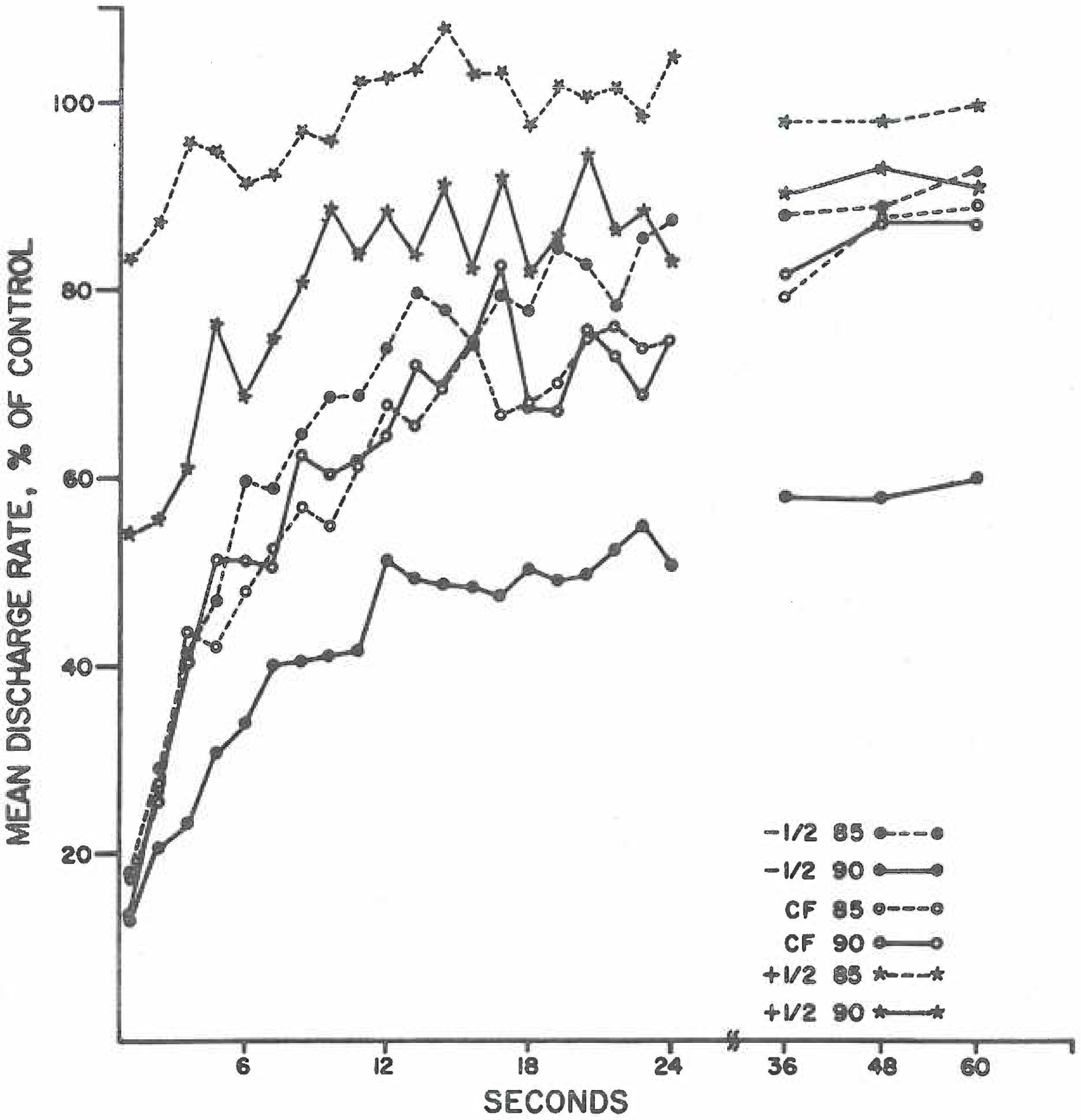
### B. Extent of Depression of Discharge Rate Following Overstimulation: Over-All Comparisons

Following exposure to a LOAD tone, the stimulus-evoked discharge rate of cochlear nerve fibers was depressed. Although recovery to pre-exposure discharge rates can be described as monotonically increasing (except for random fluctuations), both the frequency and intensity of the exposure tone exerted significant effects upon the response rate of cochlear nerve fibers. The principal finding was that the fiber responses were significantly more depressed following -1/2 $OCT_{90}$ exposure. Figure 20 shows rate-time functions for tone bursts at fiber CFs following the various acoustic overload conditions. The percentage values here were computed in the same manner as described in section A above. For all conditions, discharge rate recovered rapidly over the first 7-8 seconds. At this point, there was a noticeable bend in the rate-time curves, and recovery to the control discharge rate displayed a more gradual, although steady, time course.

Notable differences can be seen between the curves for the different overstimulation frequencies. Figure 20 reveals that the overload frequency which produced the greatest reduction in fiber response rate was the one-half octave below the characteristic frequency at 90 dB; while the two +1/2 OCT groups produced the least decrement in discharge rate. For the experimental groups that showed the greatest effect of the sound exposure, the -1/2 $OCT_{90}$ group demonstrated the slowest time course of recovery. Two major differences between the -1/2 $OCT_{90}$

FIGURE 20.

Recovery of discharge rate following sound exposure. The mean normalized response rates (defined in the text) of the six experimental groups are plotted as a function of time in seconds during the initial post-exposure RECOVERY period. Overload frequencies and levels are given in the legend as are the symbols corresponding to each experimental group. Data are shown for the first 24 seconds and the 36th, 48th and 60th seconds following the overload period. Discharge rate was computed in successive 1.2 second bins. The reduction in discharge rate of the -1/2 $OCT_{90}$ group is considerably greater than that for the other experimental groups. The $CF_{90}$, -1/2 $OCT_{85}$, and $CF_{85}$ groups all show very similar mean recovery curves. The +1/2 OCT groups show little effect of sound exposure.


MEAN DISCHARGE RATE, % OF CONTROL
100
80
60
40
20
6
12
18
24
36
48
60
SECONDS
−1/2 85
−1/2 90
CF 85
CF 90
+1/2 85
+1/2 90

curve and the curves of the other conditions can be seen in this regard. First the initial onset of recovery discharge rate was not as rapid as seen in the other groups; and, secondly, although recovery continued, it was considerably more gradual than seen in the other conditions.

There was considerable variability among individual fibers within any one experimental group. Figure 21 illustrates the extreme cases for each group, and indicates that part of this variability was due to the random variation in firing rate to be expected from any single fiber, while part was due to individual differences in the time course of recovery. As will become apparent in the next section dealing with individual recovery functions, the differences between recovery time courses were substantial.

The mean discharge rates during the first 24 seconds for the three overload frequencies at the two overload intensities, are plotted in Figure 22a. This figure reveals that regardless of intensity level, the -1/2 OCT exposure produced substantially more reduction in response rate than the +1/2 OCT overload condition. In contrast to this finding, there was no apparent difference between -1/2 OCT and CF at the 85 dB level, while it appears that at 90 dB, the -1/2 OCT exposure produced slightly more decrement in discharge rate than overstimulation at the CF. The overall significance of these findings was tested in a three factor analysis

FIGURE 21.

Variability among individual fibers within the six experimental groups. The shaded area is representative of the extreme ranges. The individual curves in each graph represent smoothed rate-time functions for selected fibers from each group. These curves were selected as examples of the wide range observed during recovery. The graphs indicate both types of variability seen in the recovery data: that due to random variation in firing rate to be expected from any single fiber, and that due to individual differences in time course of recovery.

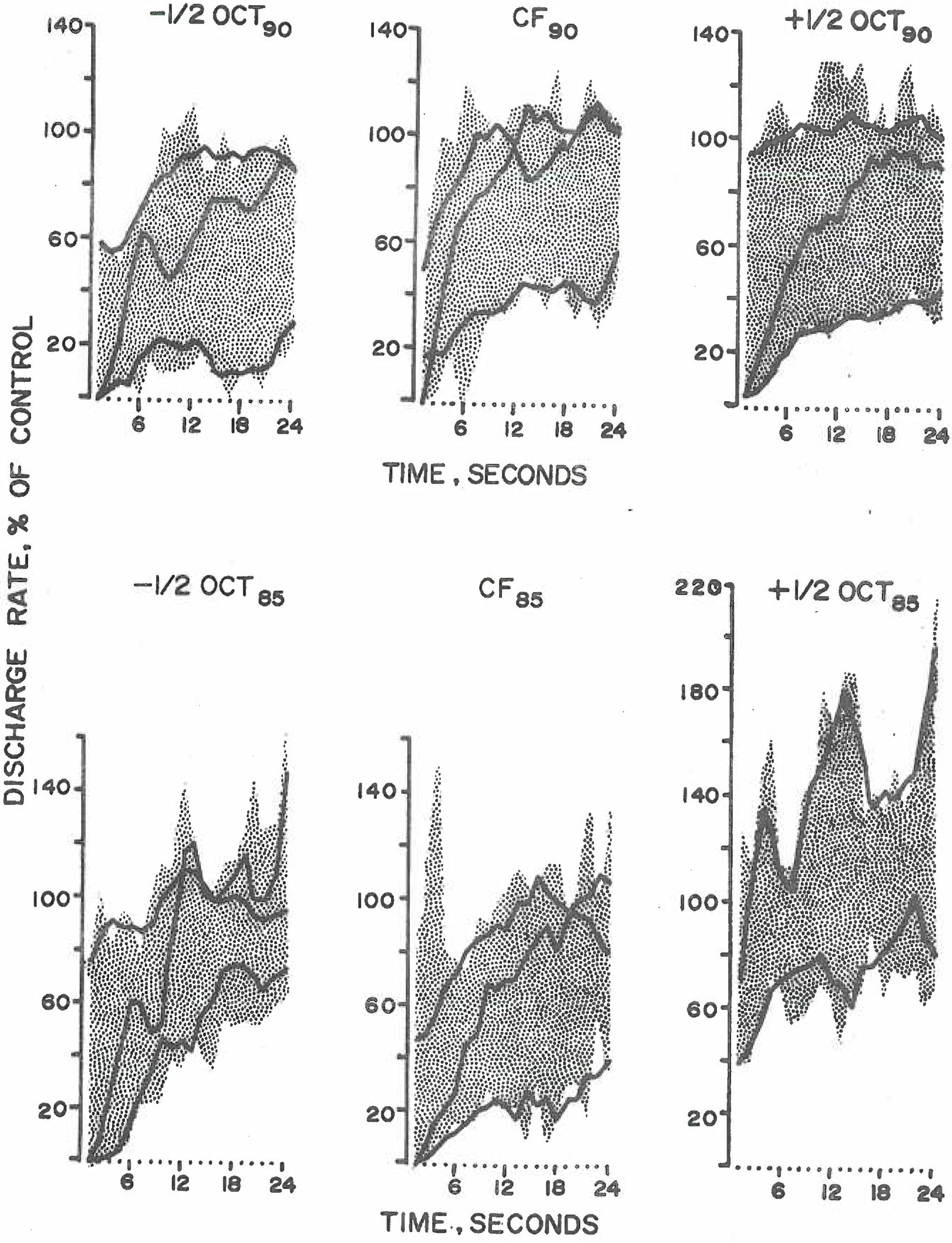
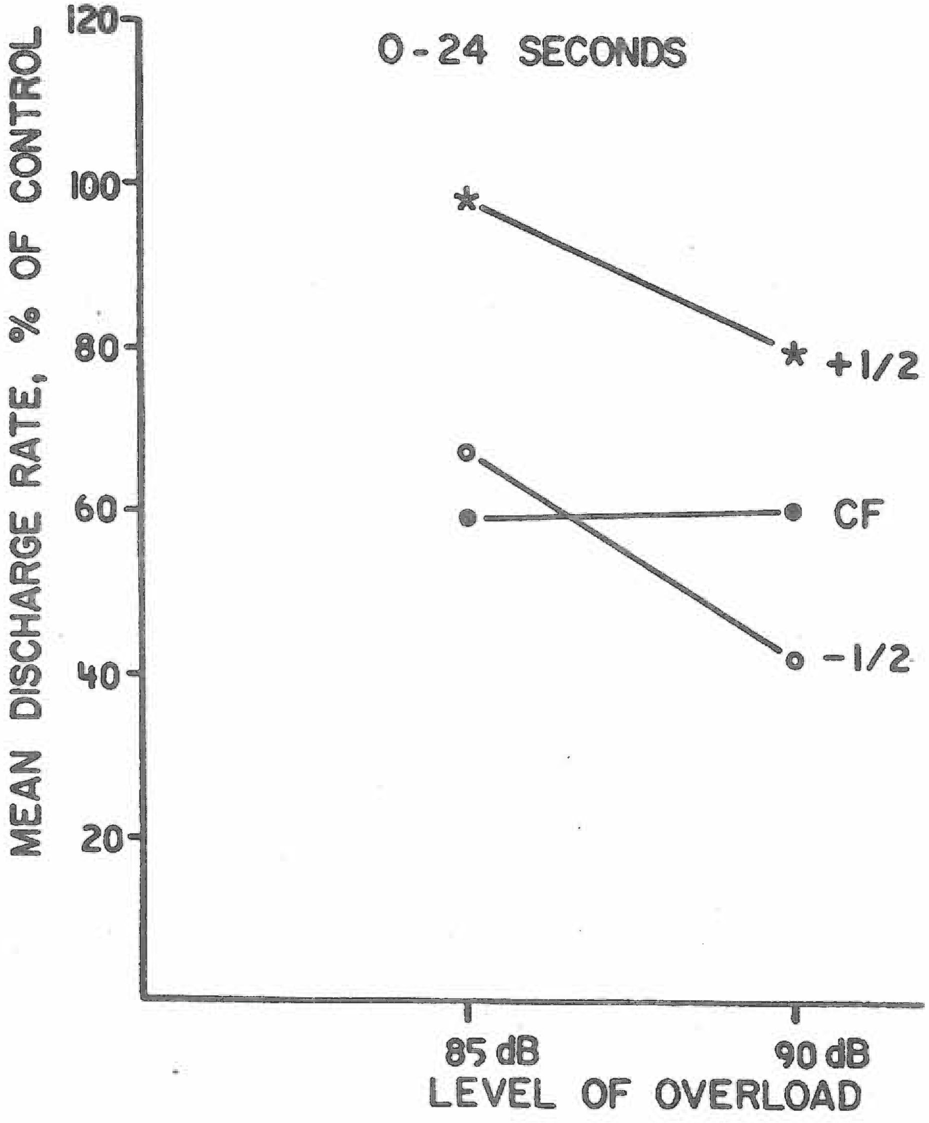

−1/2 OCT$_{90}$
CF$_{90}$
+1/2 OCT$_{90}$
−1/2 OCT$_{85}$
CF$_{85}$
+1/2 OCT$_{85}$
DISCHARGE RATE, % OF CONTROL
TIME, SECONDS
TIME, SECONDS
220
180
140
100
60
20
6
12
18
24

FIGURE 22.

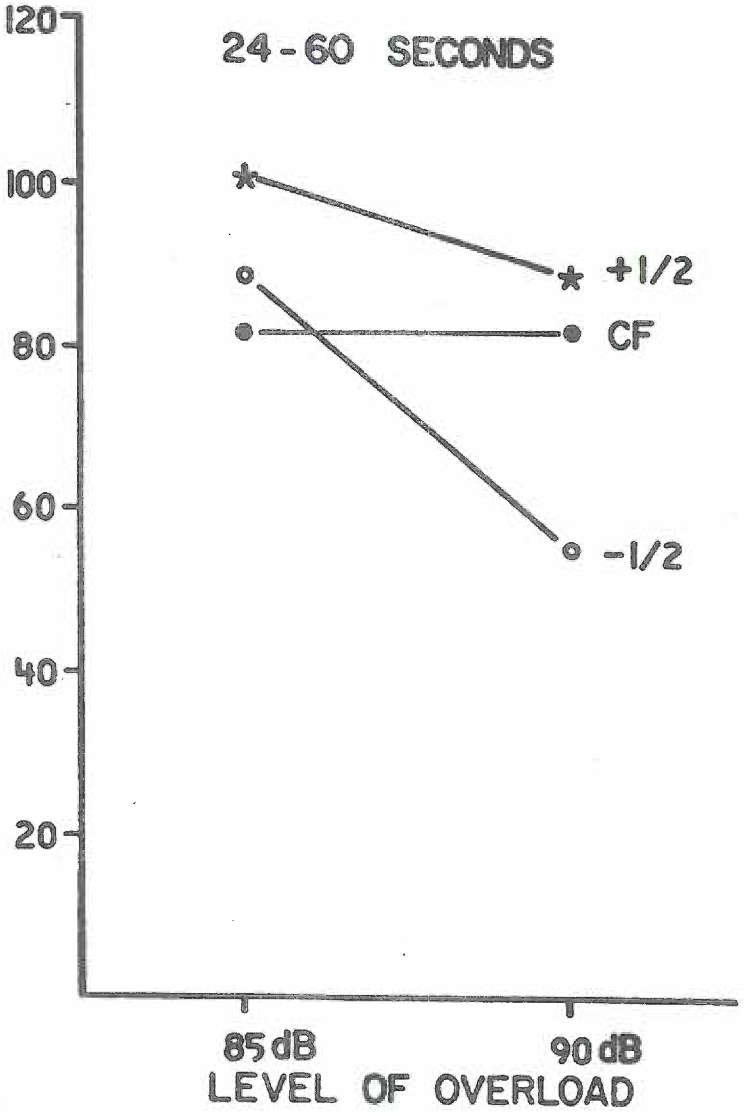
Summary of the effects of overload frequency and intensity upon the magnitude of response depression. Mean percentage remaining of control discharge rate is plotted vs. level of sound exposure for the six experimental groups.

(a) During the initial 24 seconds of RECOVERY.

(b) During the last 36 seconds of the first RECOVERY period. The fact that a statistically significant interaction between frequency and level of exposure stimulus was obtained is evident in the crossing of the lines for the CF and -1/2 OCT groups (24-60 seconds).


MEAN DISCHARGE RATE, % OF CONTROL
120
100
80
60
40
20
0-24 SECONDS
+1/2
CF
-1/2
85 dB
90 dB
LEVEL OF OVERLOAD

a


120
100
80
60
40
20
24-60 SECONDS
+1/2
CF
-1/2
85 dB
90 dB
LEVEL OF OVERLOAD

b

of variance (2 x 3 x 20)[1] carried out on the percentage discharge scores following exposure. This analysis showed the following significant effects: (1) an effect of intensity (F=11.5, df=1/64, $p < .01$) demonstrating that the 90 dB intensity level produced a greater decrement in firing rate; (2) an effect of frequency (F=23.9, df=2/64, $p < .01$) indicating that the amount of reduction in discharge rate differed for the three overload frequency conditions; (3) an effect of recovery time (F=46.3, df=19/1216, $p < .01$) reflecting the overall return toward the pre-exposure control rates; and finally, (4) a significant frequency x recovery-time interaction (F=2.6, df=38/1216, $p < .01$), indicating that the response rates of the experimental groups (-1/2 OCT, CF, +1/2 OCT) diverged over the initial seconds of the post-exposure period.

In order to determine if the apparent difference between the -1/2 $OCT_{90}$ overload and either the $CF_{90}$ or +1/2 $OCT_{90}$ exposures was significant, all possible pairs of means at this level were tested using the Newman-Keuls procedure. These tests revealed a significant difference between the -1/2 $OCT_{90}$ and the +1/2 $OCT_{90}$ groups; however, the difference between overload at the $CF_{90}$ and the -1/2 $OCT_{90}$ did not quite meet the criterion ($p < .05$) for statistical significance.

Figure 22b shows the effect of overload stimuli on the later portions of the RECOVERY period (24-60 seconds) and reveals that the differences between the -1/2 $OCT_{90}$ and the CF, +1/2 OCT, and -1/2 $OCT_{85}$

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[1] Factor 1: overload level (85 dB vs. 90 dB); Factor 2: overload frequency (-1/2 OCT vs. CF vs. +1/2 OCT); Factor 3: time (the 20 successive measurement points, spaced 1.2 seconds apart, which corresponded to the first 24 seconds of the RECOVERY interval). The analysis was designed for repeated measures on Factor 3.

groups were somewhat greater during the last 36 seconds than in the first 24 seconds. The percentage discharge scores of the six experimental groups were compared using a 2 x 3 x 4 analysis of variance[1]. This test established that during the last 36 seconds of the RECOVERY period, not only was there a significant difference between response decrements produced by 90 dB vs. 85 dB tones ($F=11.1$, $df=1/64$, $p<.01$), but also between the reduction in discharge rate produced by the three overload frequency conditions ($F=7.3$, $df=2/64$, $p<.01$). Further comparison of the means of the three frequency groups at the 90 dB intensity level, using a Newman-Keuls test of the differences between group means, revealed that $-1/2$ $\text{OCT}_{90}$ overload stimuli produced significantly more reduction in firing rate than either the $\text{CF}_{90}$ or $+1/2$ $\text{OCT}_{90}$ exposure stimuli. Once again there was a significant main effect due to recovery time ($F=7.7$, $df=3/192$, $p<.01$) indicating that the mean discharge rate increased during the last 36 seconds of the first post-exposure period. A significant interaction between intensity level and frequency of exposure stimuli ($F=3.7$, $df=2/64$, $p<.05$) reflected the fact that the -1/2 OCT exposure produced a greater decrement in firing rate at the 90 dB level than it did at the 85 dB level. A significant overload frequency x recovery time interaction established that the rate of change of discharge rate during the last 36 seconds of the initial RECOVERY period, differed for the three overload frequency conditions depending on the intensity of overload.

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[1] Factor 1: overload level (85 dB vs. 90 dB); Factor 2: overload frequency (-1/2 OCT vs. CF vs. +1/2 OCT); Factor 3: time (24th, 36th, 48th and 60th seconds of the RECOVERY period). A repeated measures design was used for Factor 3.

In summary then, the basic form of the reduction in discharge rate produced by -1/2 $OCT_{90}$ exposure consisted of a progressive increase in the magnitude of the difference between this group and the other overload conditions, and this relationship was established during the first 24 seconds of RECOVERY. By the end of the first 60 seconds of the post-exposure period, the -1/2 $OCT_{90}$ group demonstrated a significantly more depressed firing rate than fibers in the other overload groups.

C. Extent of Depression of Discharge Rate Following Overstimulation: Individual Comparisons.

(1) -1/2 OCT Exposures

Figure 20 summarized the changes in rate-time functions for all experimental groups over the initial RECOVERY TEST CF period. The effects observed in fibers overstimulated with frequencies one-half octave below the CF are now examined. The two corresponding curves in Figure 20 represent data from 14 fibers in the 85 dB group with CFs ranging from 1.5-17.1 kHz and from 10 fibers in the 90 dB group with CFs in the range of 0.6-10.2 kHz. It is clear from this figure that although both intensity groups generally followed a similar time course of recovery, i.e., a monotonically increasing function, recovery for fibers in the 90 dB group was considerably slower than that for 85 dB fibers.

At the onset of the RECOVERY period, response rate for the -1/2 $OCT_{85}$ group was reduced to 18% of the pre-exposure firing level. However, within one minute of overload, the response rate was approximately 90% of the control value. On the other hand, for the -1/2 $OCT_{90}$

condition, the initial response rate was 13% of the pre-exposure rate and by the end of the first minute of recovery, barely 50% of the normal discharge rate had recovered.

These trends seen in the -1/2 OCT group are further illustrated in Figure 23 which shows samples of individual rate-time functions. Although individual fibers demonstrated considerable individual variability, two general patterns of time course for recovery to pre-exposure discharge rates are revealed in the separate panels of this figure. Figure 23a shows an example of "fast" recovery to pre-exposure discharge rate for fiber 17-13 in the -1/2 $OCT_{85}$ condition. This fiber's discharge rate in response to the post-exposure test bursts showed an initial firing rate of 0%. After ten seconds of recovery, the response rate increased to 75% of its pre-exposure rate. Within 20 seconds after termination of the overload period, the fiber recovered to its mean control discharge level of 199 spikes/second. A similar fast recovery time course for fiber 16-8, also from the 85 dB overload condition but having a lower mean discharge rate of 138 spikes/second is illustrated in Figure 23b. Figure 23c shows that fiber 11-2 from the 90 dB group also demonstrated the fast recovery effect. The initial discharge rate at the beginning of recovery was 8% of its pre-exposure rate, but within 8 seconds it had recovered to its mean control rate of 173 spikes/second.

In contrast to the fast recovery demonstrated in Figures 23a, b, and c, Figures 23d and e illustrate a much slower time course of recovery for two other fibers in the -1/2 $OCT_{85}$ and 90 dB groups. For fiber 14-14 overstimulated at the 85 dB level, the initial discharge rate at the beginning of recovery was 10% of its pre-exposure value. Within 13 seconds of cessation of the overload tone, it had recovered to only 50% of its control rate. Indeed, by the end of the first post-exposure period, the fiber's response rate had only returned to the 75% firing level.

Figure 23e illustrates a typical example of "slow"recovery for fiber 14-8 in the -1/2 $OCT_{90}$ group. Initially, the fiber's discharge rate was 23% of the pre-exposure rate, and by the end of the first minute of RECOVERY, it had only returned to 40% of the control firing level of 192 spikes/second.

The extent to which changes in response rate due to exposure were related to the individual characteristics of a fiber was also investigated. Table I summarizes the relevant correlations. It was observed

| Correlations | rho Values<br>-1/2 $OCT_{90}$ | <br>-1/2 $OCT_{85}$ |
|---|---|---|
| CF vs. % Discharge Level Remaining Following Overload | -.64* | .4 |
| Threshold vs. % Discharge Level Remaining Following Overload | .68* | -.45 |
| Mean Pre-exposure Driven Rate vs. % Discharge Level Remaining Following Overload | -.32 | -.41 |
| Spontaneous Rate vs. % Discharge Level Remaining Following Overload | -.07 | -.11 |

*$p < .05$

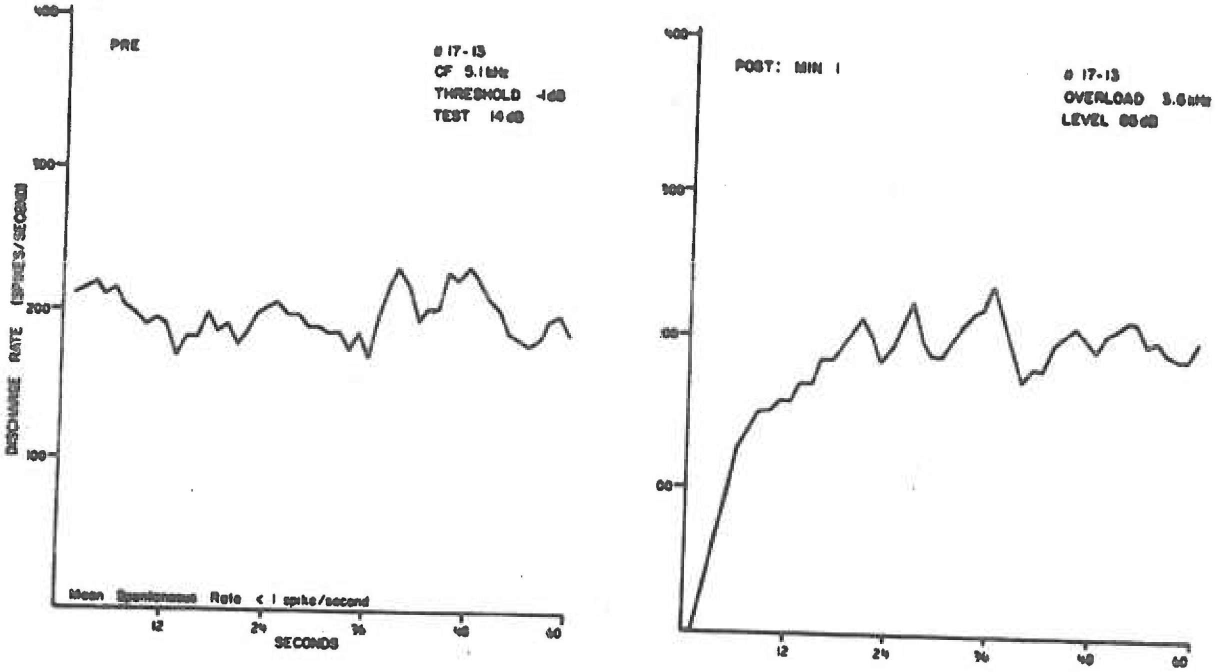
TABLE I
Spearman rank-order correlations between individual characteristics of fibers and percentage of response rate remaining following -1/2 OCT exposure.

that for the 1/2 $OCT_{90}$ group, there was a correlation of the threshold of a nerve fiber with the percentage discharge rate remaining following

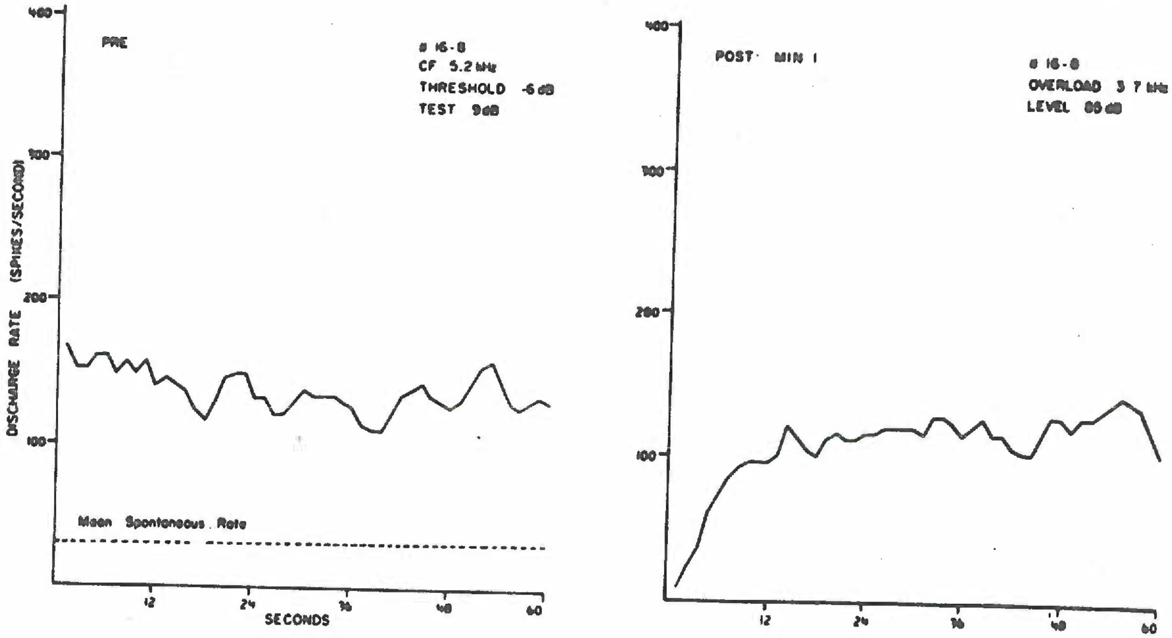
FIGURE 23.

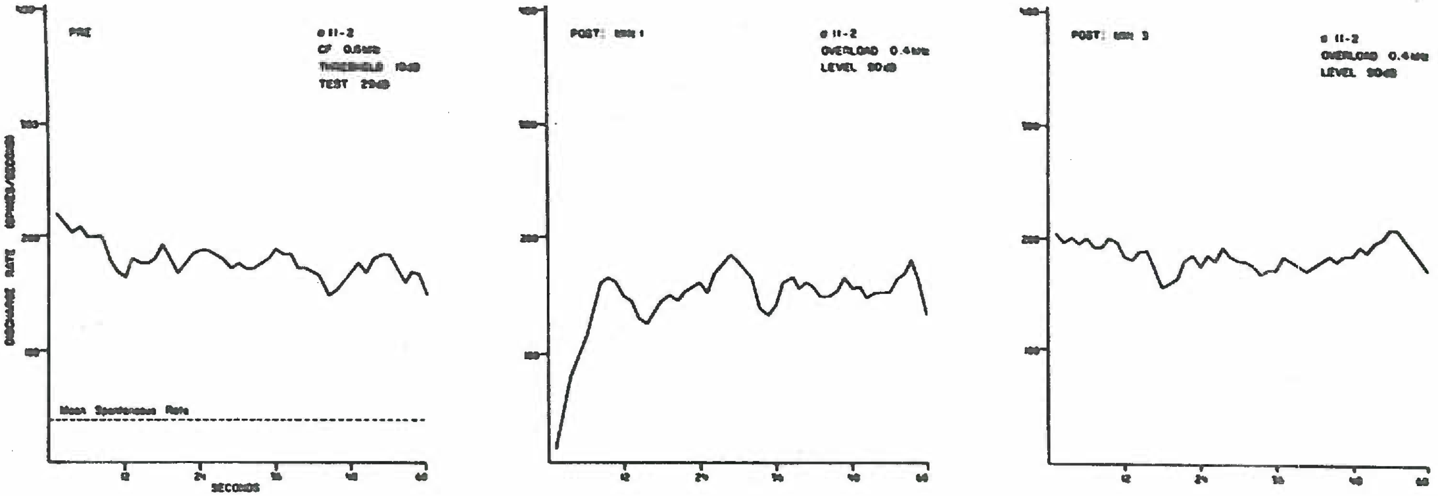
Individual recovery curves for fibers exposed to -1/2 OCT acoustic overload. The pre-exposure rate-time function is shown to the left of each group of curves relating to any one unit and overload. The average level of pre-exposure spontaneous activity is represented by the dashed line in the lower half of each pre-exposure graph. Overload frequency and intensity are indicated in the upper right-hand corner of the post-exposure graphs. The individual fibers are as follows: (a) #17-13, a fiber with a high driven rate, exposed to -1/2 $OCT_{85}$ and demonstrating a "fast" recovery curve (described in the text); (b) #16-8, a fiber with a low driven rate, exposed to -1/2 $OCT_{85}$ and demonstrating a fast recovery curve; (c) #11-2 exposed to -1/2 $OCT_{90}$ and demonstrating a fast recovery curve; (d) #14-14 exposed to -1/2 $OCT_{85}$ and showing a "slow" recovery curve; and, (e) #14-8 exposed to -1/2 $OCT_{90}$ and showing a slow recovery curve. Parts (d) and (e) show only the PRE and the first POST interval in the standard 60-second recovery graph. Because the slow recovery fibers would require many successive 1-minute graphs to show their recovery curves, the recovery functions in (d) and (e) have been abbreviated by plotting discharge rates in 12-second blocks (small scale divisions). The numbers under the 5-block segments indicate the corresponding time in minutes. Thus, the segments labelled "PRE" and "1" in the abbreviated, long-term graphs summarize the same data as shown in more detail in the two expanded, 60-second graphs given first.

**a**

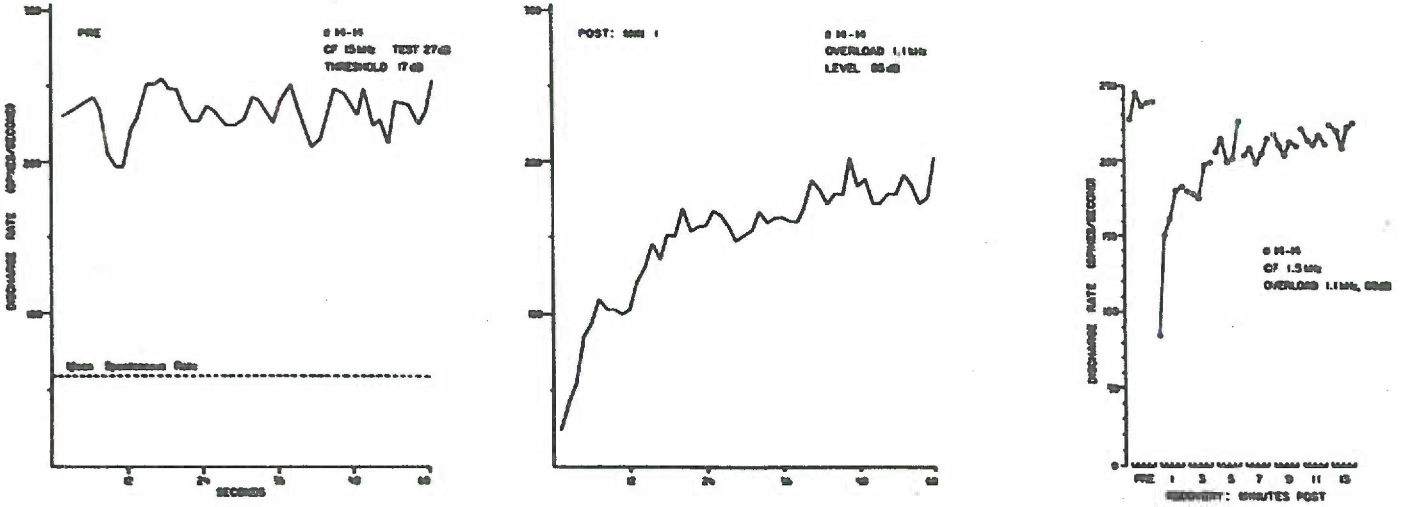

PRE
# 17-13
CF 5.1 kHz
THRESHOLD -1 dB
TEST 14 dB
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
Mean Spontaneous Rate < 1 spike/second
12
24
36
48
60
SECONDS
POST: MIN 1
# 17-13
OVERLOAD 3.6 kHz
LEVEL 85 dB
400
300
200
100
12
24
36
48
60

**b**

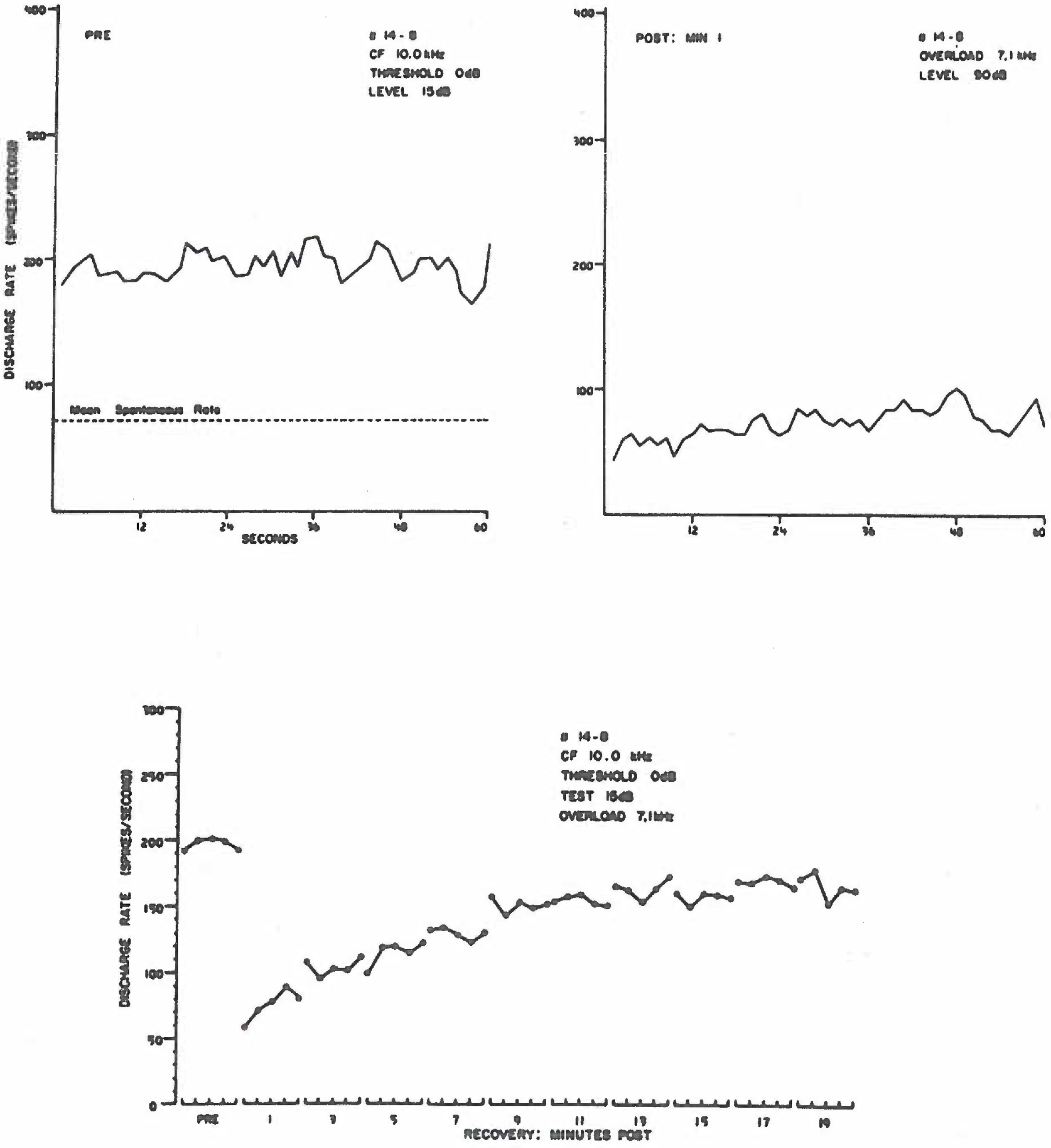

PRE
# 16-8
CF 5.2 kHz
THRESHOLD -6 dB
TEST 9 dB
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST MIN 1
# 16-8
OVERLOAD 3.7 kHz
LEVEL 85 dB
400
300
200
100
12
24
36
48
60


400
300
200
100
DISCHARGE RATE (SPIKES/SECOND)
PRE
# 11-2
CF 0.6kHz
THRESHOLD 10dB
TEST 29dB
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 11-2
OVERLOAD 0.4kHz
LEVEL 90dB
POST: MIN 3
# 11-2
OVERLOAD 0.4kHz
LEVEL 90dB

c


300
200
100
DISCHARGE RATE (SPIKES/SECOND)
PRE
# 14-14
CF 15kHz TEST 27dB
THRESHOLD 17dB
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-14
OVERLOAD 1.1kHz
LEVEL 86dB
250
200
150
100
50
0
# 14-14
CF 1.5kHz
OVERLOAD 1.1kHz, 86dB
PRE
1
3
5
7
9
11
13
RECOVERY: MINUTES POST

d


PRE
# 14-8
CF 10.0 kHz
THRESHOLD 0dB
LEVEL 15dB
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-8
OVERLOAD 7.1 kHz
LEVEL 90dB
400
300
200
100
12
24
36
48
60
# 14-8
CF 10.0 kHz
THRESHOLD 0dB
TEST 15dB
OVERLOAD 7.1kHz
DISCHARGE RATE (SPIKES/SECOND)
300
250
200
150
100
50
0
PRE
1
3
5
7
9
11
13
15
17
19
RECOVERY: MINUTES POST

e

exposure; i.e., the higher the threshold, the greater the percentage of response rate remaining. In addition, it was also observed for the -1/2 $OCT_{90}$ group, that percentage of response rate remaining was a decreasing function of CF. That is, fibers with low CFs showed the greatest percentage of discharge rate remaining following exposure.

(2) CF Exposures

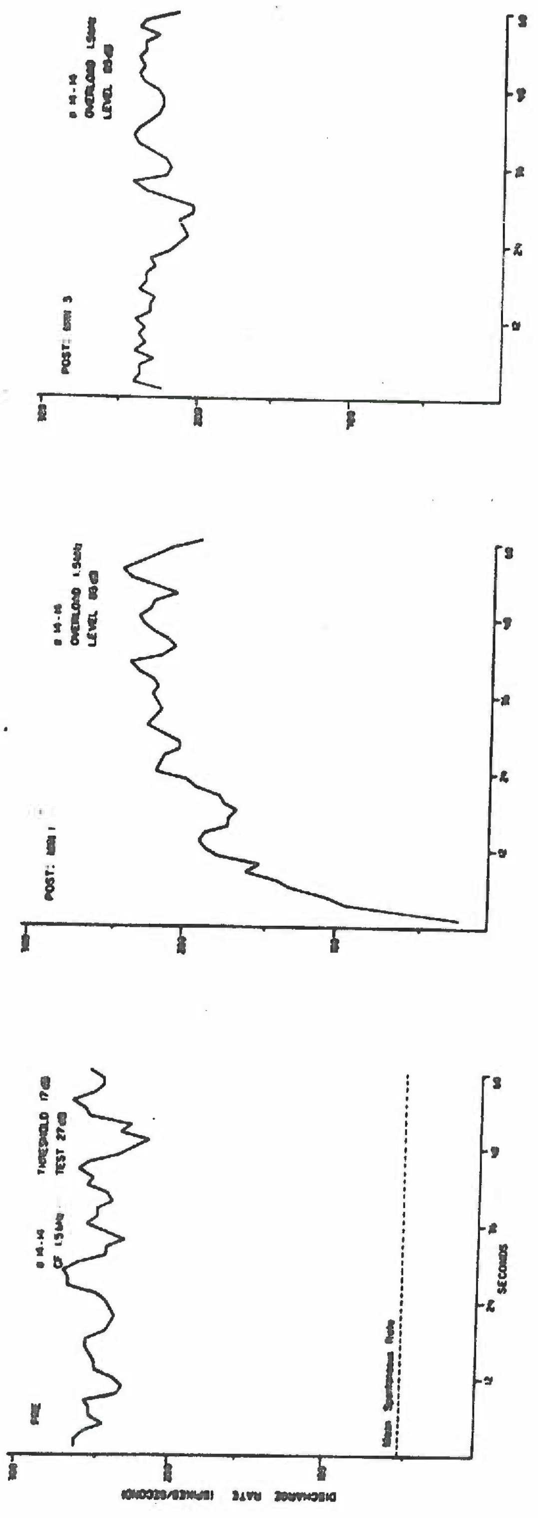
Rate-time functions of fibers exposed to frequencies at the CF are shown in Figure 20. These data were obtained from 14 fibers with CFs ranging from 1.5-17.1 kHz in the 85 dB intensity group and from 10 fibers in the 90 dB group with CFs in the range of 0.5-10.2 kHz. The general features shown by the -1/2 $OCT_{85}$ group were also apparent for the CF groups: although initially reduced to 13% and 17% of the pre-exposure firing level for the 90 dB and 85 dB conditions respectively, within one minute after overstimulation, the percentage reduction in response rate recovered to within approximately 85% of the normal driven rate for these fibers.

When individual fibers from the two CF groups were examined, again, there was a general tendency for the recovery time courses to separate into two groups. As seen in the -1/2 OCT groups, the time course for recovery in some fibers was longer than that for others. Data illustrating the "fast" type of recovery in two fibers, fiber 14-14 from the $CF_{85}$ condition and fiber 17-28 from the $CF_{90}$ group, are illustrated in Figure 24a and b.

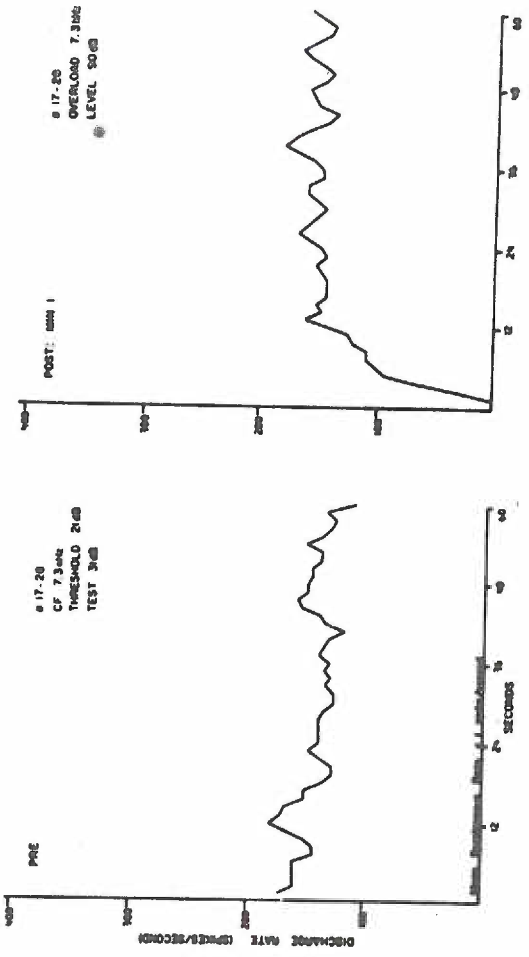
In contrast to these fast recoveries, Figure 24c and d illustrate a slower time course of recovery for two fibers in the $CF_{85}$ (14-20) and $CF_{90}$ (14-12) conditions. The discharge rate of these fibers had

FIGURE 24.

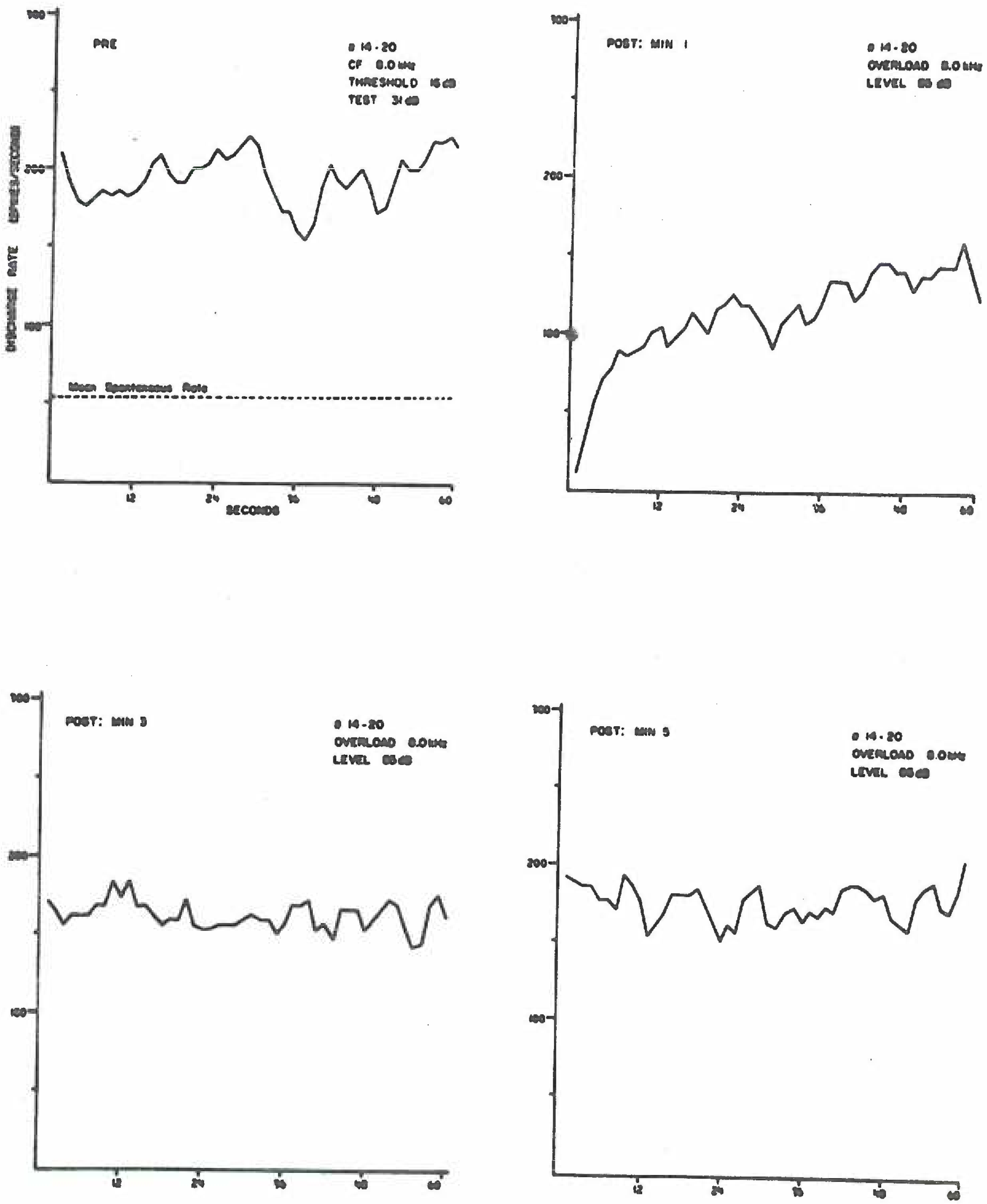
Individual recovery curves for fibers exposed to CF acoustic overload. The data are plotted in the same way as described in Figure 22. The individual fibers are as follows: (a) #14-14 exposed to $CF_{85}$ and showing a fast recovery curve; (b) #17-28 exposed to $CF_{90}$ and demonstrating a fast recovery curve; (c) #14-20 exposed to $CF_{85}$ and showing a slow recovery curve; and, (d) #14-12 exposed to $CF_{90}$ and demonstrating a slow recovery curve. Dotted line in the first post-exposure period (POST: Min 1) of #14-12 represents an interval in which a gain change in the amplifier interfered temporarily with counting of unit spikes.


PRE
# 14-14
CF 1.5 kHz
THRESHOLD 17 dB
TEST 27 dB
Mean Spontaneous Rate
DISCHARGE RATE (SPIKES/SECOND)
300
200
100
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-14
OVERLOAD 1.5 kHz
LEVEL 93 dB
POST: MIN 3

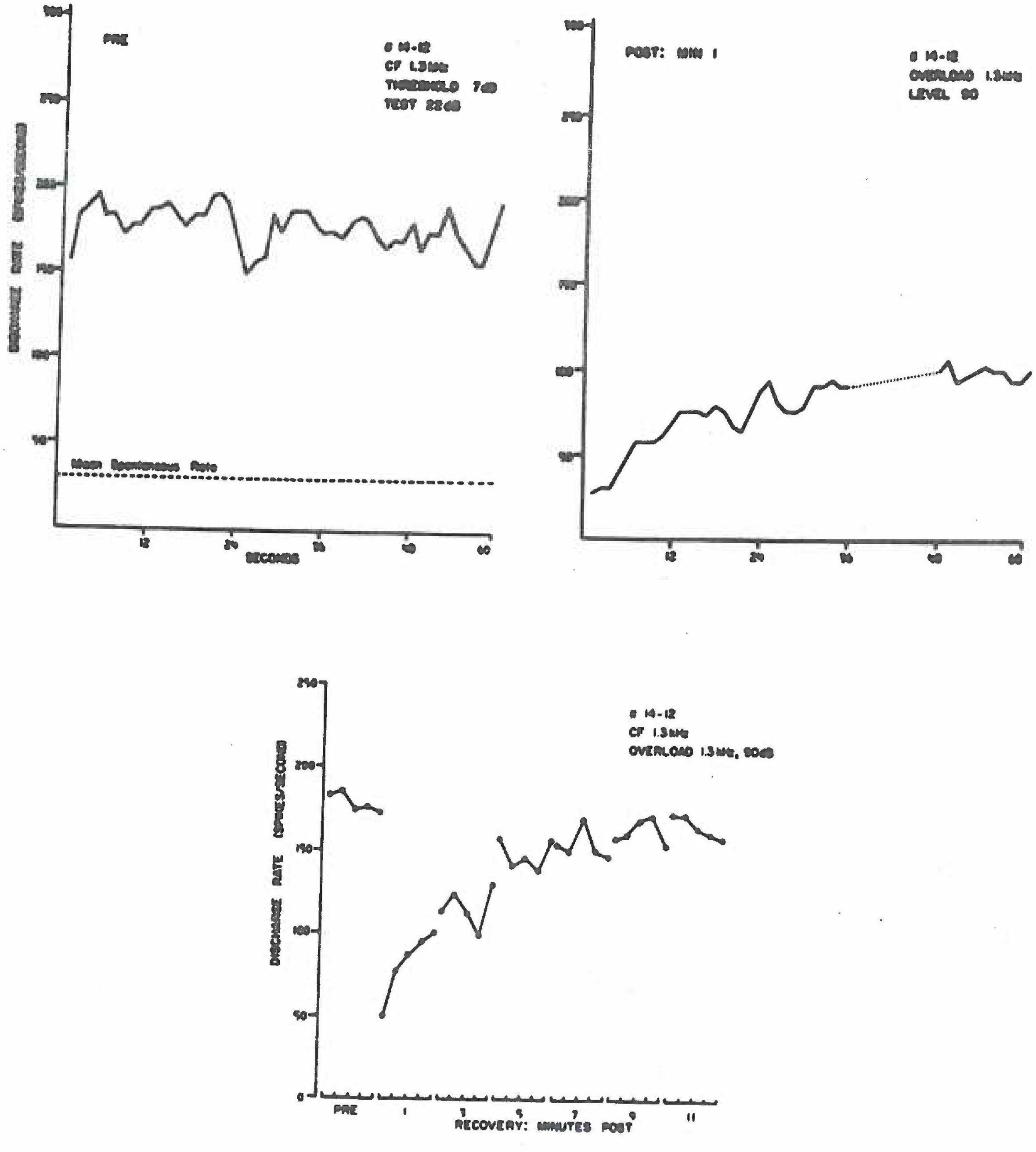
a


PRE
# 17-20
CF 7.3 kHz
THRESHOLD 21 dB
TEST 31 dB
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
12
24
36
48
60
SECONDS
POST: MIN 1
# 17-20
OVERLOAD 7.3 kHz
LEVEL 90 dB

b


PRE
# 14-20
CF 8.0 kHz
THRESHOLD 16 dB
TEST 31 dB
DISCHARGE RATE (SPIKES/SECOND)
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-20
OVERLOAD 8.0 kHz
LEVEL 85 dB
300
200
100
12
24
36
48
60
POST: MIN 3
# 14-20
OVERLOAD 8.0 kHz
LEVEL 85 dB
300
200
100
12
24
36
48
60
POST: MIN 5
# 14-20
OVERLOAD 8.0 kHz
LEVEL 85 dB
300
200
100
12
24
36
48
60

C


PRE
# 14-12
CF 1.3 kHz
THRESHOLD 7dB
TEST 22dB
300
250
200
150
100
50
DISCHARGE RATE (SPIKES/SECOND)
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-12
OVERLOAD 1.3 kHz
LEVEL 90
300
250
200
150
100
50
12
24
36
48
60
250
200
150
100
50
0
# 14-12
CF 1.3 kHz
OVERLOAD 1.3 kHz, 90dB
DISCHARGE RATE (SPIKES/SECOND)
PRE
1
3
5
7
9
11
RECOVERY: MINUTES POST

d

returned only to the 50-70% firing level by the end of the first post-exposure period.

The relationship between fundamental fiber parameters (CF, threshold, spontaneous and driven rates) and the percentage of response rate remaining following overload is presented in Table II. As found earlier for the -1/2 $OCT_{90}$ group, it was observed that for the $CF_{90}$ group, the higher the fiber threshold, the greater the percentage of firing rate remaining. Furthermore, correlations of driven discharge rate with percentage of response rate remaining revealed that for the $CF_{90}$ group, the lower the driven discharge rate, the higher the percentage of response rate remaining following exposure. Finally, it was observed for the $CF_{85}$ overload group that percentage discharge rate remaining was a decreasing function of CF. That is, following

| Correlations | rho Values | |
|---|---|---|
| | $CF_{90}$ | $CF_{85}$ |
| CF vs. % Discharge Level Remaining Following Overload | -.15 | -.6* |
| Threshold vs. % Discharge Level Remaining Following Overload | .90** | -.05 |
| Mean Pre-exposure Driven Rate vs. % Discharge Level Remaining Following Overload | -.56* | .40 |
| Spontaneous Rate vs. % Discharge Level Remaining Following Overload | -.18 | .09 |

* $p < .05$
** $p < .01$

TABLE II
Spearman rank-order correlations between individual characteristics of fibers and percentage of response rate remaining following CF exposure.

overload, there was a higher percentage of discharge rate remaining for fibers with low frequency CFs.

(3) +1/2 OCT Exposures

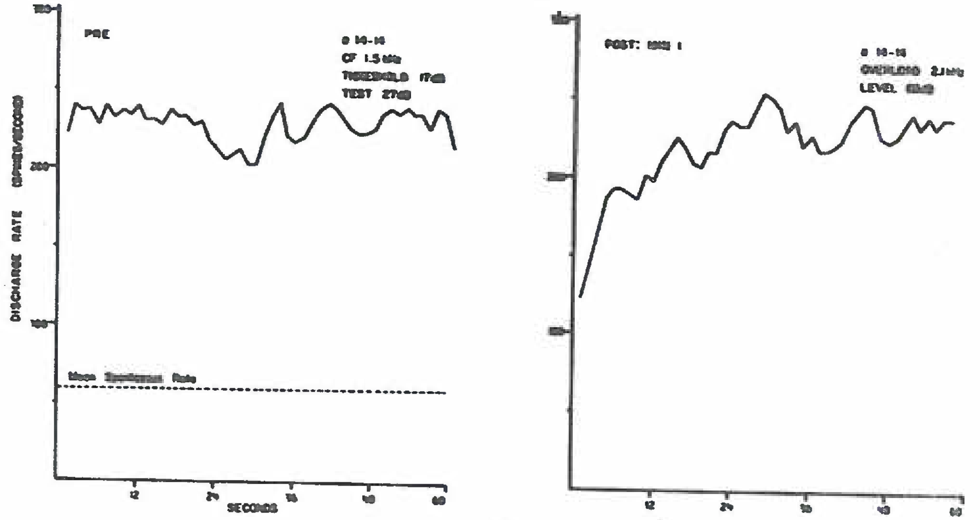
Again, referring back to Figure 20, there are two curves representing the +1/2 OCT exposure groups. These curves represent data from 14 fibers with CFs ranging from 1.5-8.9 kHz for the 85 dB group, and 8 fibers with CFs ranging from 0.6-11.0 kHz in the 90 dB intensity group. Figure 20 indicates clearly that for overload frequencies one-half octave above the fiber CF, the rate-time functions were much less affected by acoustic overload than those for both the CF and -1/2 OCT LOAD groups.

Figure 20 shows that the +1/2 $\text{OCT}_{90}$ exposure produced a greater response decrement than did the +1/2 $\text{OCT}_{85}$ group (the 85 dB group returned to its pre-exposure firing level within 10 seconds after the LOAD period while the +1/2 $\text{OCT}_{90}$ group attained only 85-90% of the control discharge rate within one minute after exposure). However, this difference was not great. The majority of the +1/2 $\text{OCT}_{90}$ fibers recovered to within one standard deviation of their control discharge rates 35 seconds after the beginning of the RECOVERY period.

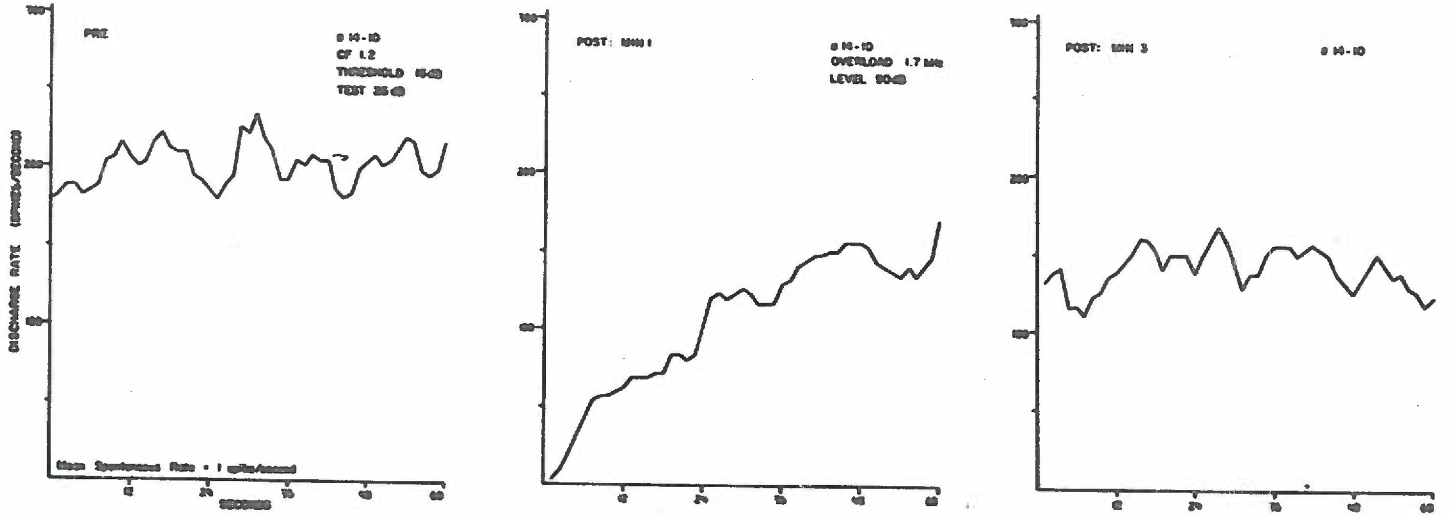
Figure 25 shows response rate versus time plots of six fibers in the +1/2 OCT group. These examples show that although the overall effect of stimulating at frequencies above the CF was slight or nonexistent, some systematic trends related to fiber CF were observed. In Figure 25a, fiber 14-14 (CF=1.5 kHz) of the 85 dB group displayed a fairly substantial effect; a similar effect could be seen in Figure 25b for fiber 14-10 (CF=1.2 kHz) of the 90 dB group. Fiber 14-17, an intermediate CF (5.5 kHz) fiber stimulated at 85 dB, showed a slight effect

FIGURE 25.

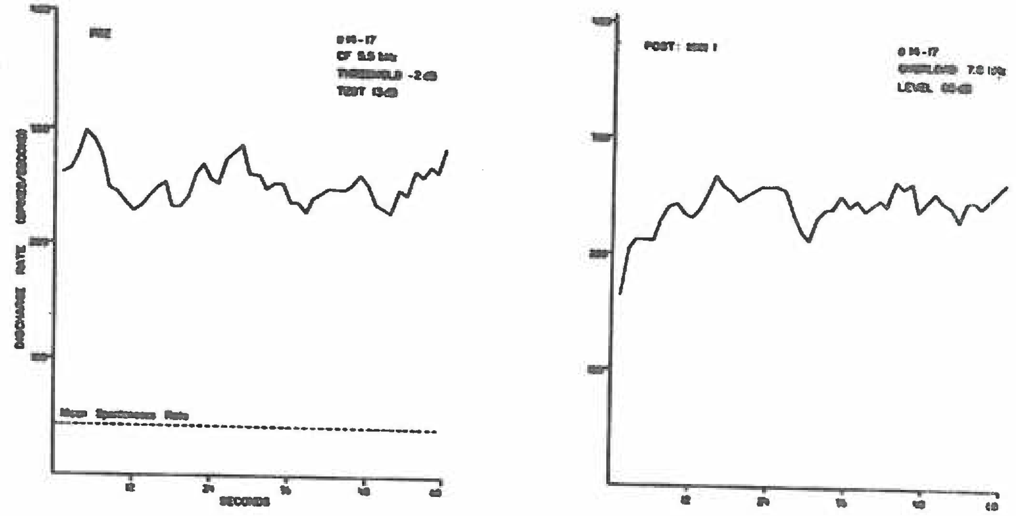
Individual recovery curves for fibers exposed to +1/2 OCT acoustic overload. Data are plotted as described in Figure 22. The individual fibers are as follows: (a) #14-14 exposed to +1/2 $OCT_{85}$; this fiber had a low CF and showed a relatively large effect; (b) #14-10 exposed to +1/2 $OCT_{90}$; the CF was low, and the effect was again large; (c) #14-17 exposed to +1/2 $OCT_{85}$, the CF was intermediate, and little effect was demonstrated; (d) #12-5 exposed to +1/2 $OCT_{90}$; again, the CF was intermediate, and little or no effect is observed; (e) #14-20 exposed to +1/2 $OCT_{85}$; this fiber had a high CF and appeared to be unaffected by the overload; and, (f) #14-6 exposed to +1/2 $OCT_{90}$; this was another high-CF fiber showing no effect of the overload.


PRE
# 14-14
CF 1.5 kHz
THRESHOLD 17dB
TEST 27dB
DISCHARGE RATE (SPIKES/SECOND)
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-14
OVERLOAD 2.1 kHz
LEVEL

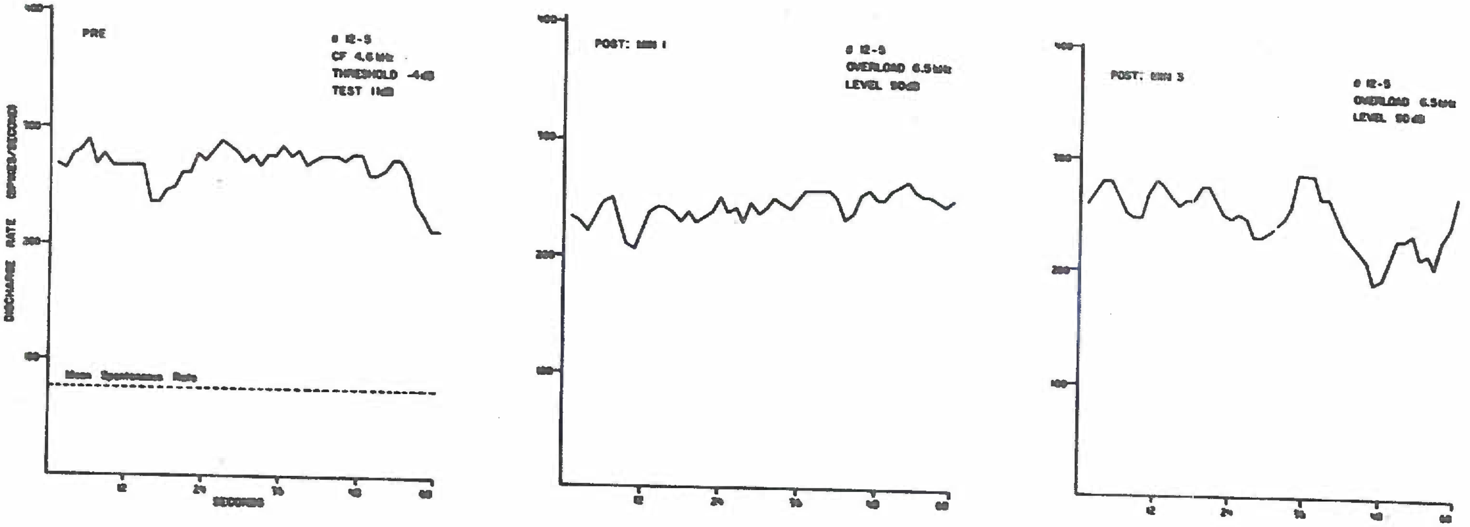
a


PRE
# 14-10
CF 1.2
THRESHOLD
TEST 26 dB
DISCHARGE RATE (SPIKES/SECOND)
300
200
100
Mean Spontaneous Rate = 1 spike/second
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-10
OVERLOAD 1.7 kHz
LEVEL 90dB
POST: MIN 3
# 14-10

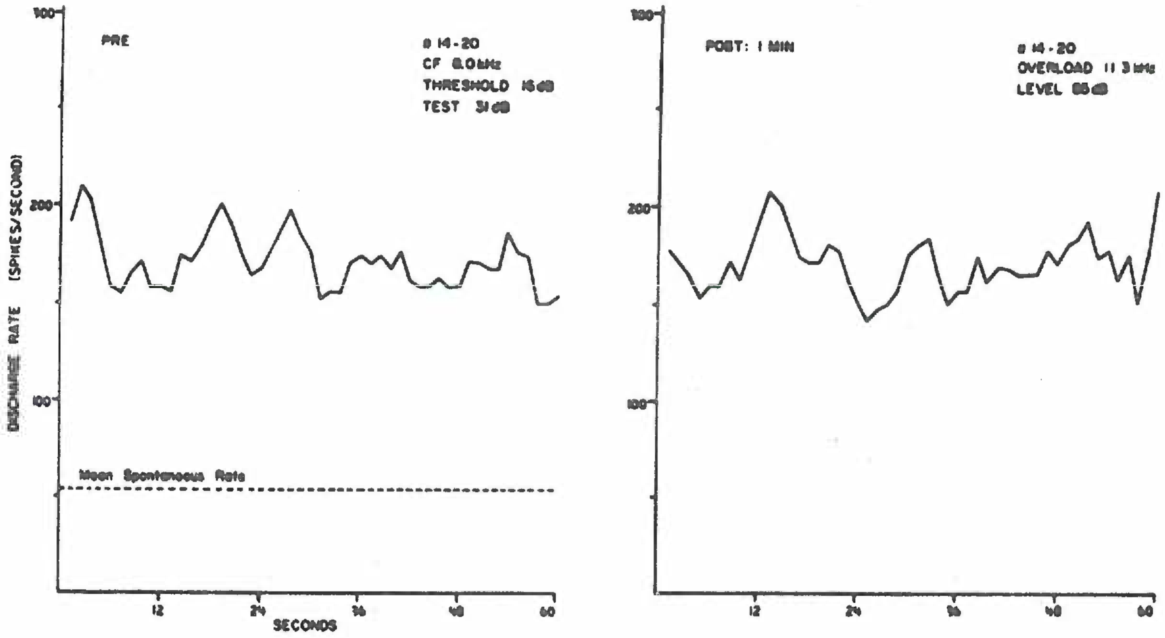
b


PRE
# 14-17
CF 5.5 kHz
THRESHOLD -2 dB
TEST 13 dB
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-17
OVERLOAD 7.0 kHz
LEVEL 90 dB

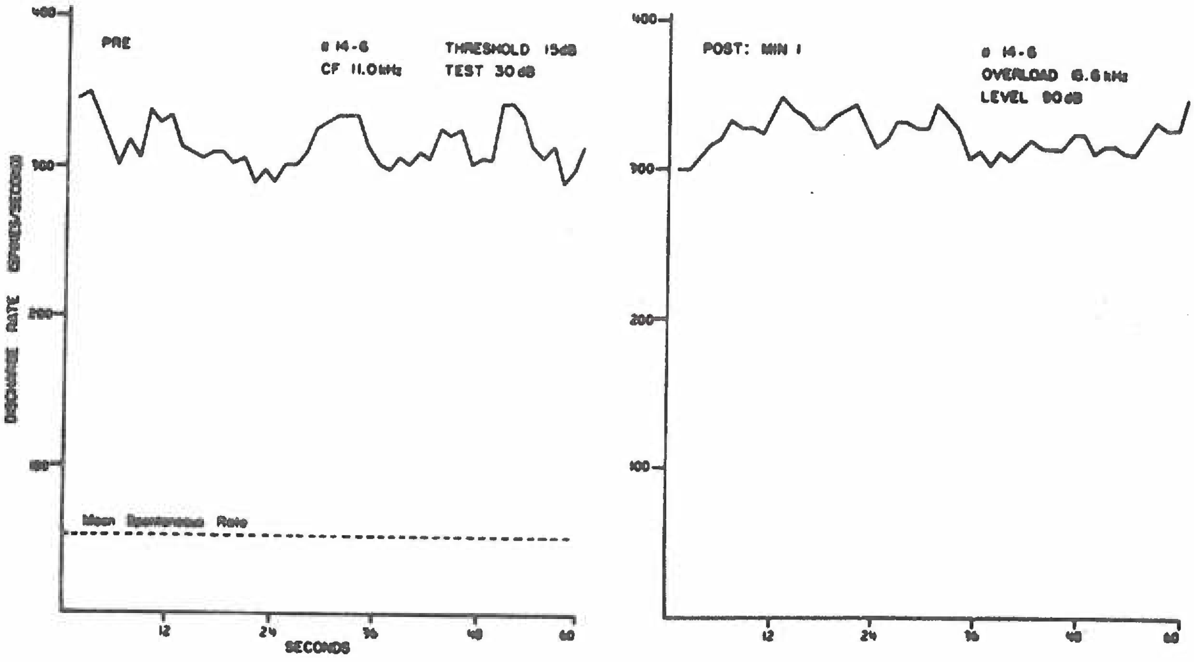
c


PRE
# 12-5
CF 4.6 kHz
THRESHOLD -4 dB
TEST 11 dB
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 12-5
OVERLOAD 6.5 kHz
LEVEL 90 dB
POST: MIN 3
# 12-5
OVERLOAD 6.5 kHz
LEVEL 90 dB

d


PRE
# 14-20
CF 8.0kHz
THRESHOLD 16dB
TEST 31dB
DISCHARGE RATE (SPIKES/SECOND)
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: 1 MIN
# 14-20
OVERLOAD 11.3kHz
LEVEL 85dB
300
200
100
12
24
36
48
60

e


PRE
# 14-6
CF 11.0kHz
THRESHOLD 15dB
TEST 30dB
DISCHARGE RATE (SPIKES/SECOND)
400
300
200
100
Mean Spontaneous Rate
12
24
36
48
60
SECONDS
POST: MIN 1
# 14-6
OVERLOAD 6.6kHz
LEVEL 90dB
400
300
200
100
12
24
36
48
60

f

of the +1/2 OCT overload (Figure 25c). In Figure 25d at the 90 dB intensity, fiber 12-5 with a CF of 4.6 kHz showed little effect of the prolonged exposure period. High frequency CF fibers showed no apparent effect of the +1/2 OCT exposure stimuli. Figures 25e and f illustrate data from fibers with CFs of 8.0 kHz and 11.0 kHz, respectively.

In summary, there was a tendency for fibers with low CFs to show a greater decrease in response rate than fibers with high CFs. Fibers with intermediate CFs (1.0-6.0 kHz) showed either a slight effect or, like the high frequency CF fibers, no effect whatsoever. Because of the smallness of the sample size this generalization must be viewed as tentative. Spearman rank-order correlations of changes in response rate with individual fiber characteristics failed to substantiate the CF-related effect discussed above. However, the trend described here was consistent with what is known about basilar membrane mechanics, as will be discussed more fully in the DISCUSSION section. Table III

| Correlations | rho Values | |
|---|---|---|
| | +1/2 OCT$_{90}$ | +1/2 OCT$_{85}$ |
| CF vs. % Discharge Level Remaining Following Overload | .31 | .25 |
| Threshold vs. % Discharge Level Remaining Following Overload | -.61 | .04 |
| Mean Pre-exposure Driven Rate vs. % Discharge Level Remaining Following Overload | .43 | .09 |
| Spontaneous Rate vs. % Discharge Level Remaining Following Overload | .83* | .05 |

*$p < .05$

TABLE III

Spearman rank-order correlations between individual characteristics of fibers and percentage of response rate remaining following +1/2 OCT exposure.

shows that the only significant correlation for the +1/2 OCT groups was that for the +1/2 $OCT_{90}$ condition, the higher the rate of spontaneous discharge, the greater percentage discharge rate remaining following acoustic overload.

D. Duration of Recovery

The duration of recovery of discharge rate for all overload conditions is illustrated in Figure 26. In order to compare fiber recovery rates between the various experimental groups, the following method of assessing recovery was used. Choice of a recovery measure was somewhat arbitrary in that single units could not be held indefinitely long, but could be expected to be measured on the average, for perhaps 10 to 20 minutes. Thus, some criterion for recovery was needed which could realistically be expected to be obtainable (for at least the moderate exposure levels) within approximately 10 to 20 minutes. Inspection of the recovery data indicated that a recovery criterion of 60%, for example, was too low to be useful as the majority of units recovered to at least 60% of control values within the first minute following the exposure. The final criterion adopted was that the fiber attain a discharge rate one standard deviation below its pre-exposure mean discharge rate. Using this criterion, recovery times were measured in seconds post-overload. As Table IV shows, some fibers especially in the -1/2 $OCT_{90}$ group, never reached the recovery criterion, even 20 minutes after cessation of the overload tone. For the purpose of statistical comparisons between groups, a time limit of 5 minutes was arbitrarily chosen as the maximum recovery value. Thus fibers which had still not recovered to control values within 5 minutes of exposure were nevertheless assigned a recovery score of 300 seconds.

| UNIT # | -1/2 $OCT_{90}$ TIME PRIOR TO RECOVERY | UNIT # | $CF_{90}$ TIME PRIOR TO RECOVERY |
|---|---|---|---|
| 17-15 | .2 min | 17-26 | 0 min |
| 11-2 | .4 | 17-15 | .2 |
| 12-5 | .8 | 17-18 | .2 |
| 17-24 | 7.0* | 17-28 | .2 |
| 17-26 | 7.6* | 17-13 | .6 |
| 14-11 | 9.0* | 11-2 | .8 |
| 17-20 | 15.0* | 12-5 | 2.0 |
| 14-8 | 19.0* | 14-5 | 2.0* |
| 14-5 | 21.0* | 14-8 | 4.0 |
| 17-25 | 33.0* | 14-12 | 6.4 |

* Unit lost after this time, complete recovery to pre-exposure discharge rates not observed.

TABLE IV

Recovery Times: Comparison of -1/2 $OCT_{90}$ vs. $CF_{90}$ Groups

The mean recovery times of the six experimental groups displayed in Figures 26 and 27 indicate that fibers in the -1/2 $OCT_{90}$ group exhibited recovery times which were far longer than those of fibers in the other overload conditions. The recovery scores of the overload groups were compared using a 2 x 3 analysis of variance[1]. This test established that 90 dB exposure produced significantly longer recovery times than did 85 dB overloads (F=6.7, df=1/63, $p < .05$). A significant effect of frequency of the overload was also evident (F=11.8, df=2/68, $p < .01$). Further analysis of the group means at the 90 dB exposure

---

[1] Factor 1: overload level (85 dB vs. 90 dB); Factor 2: overload frequency (-1/2 OCT vs. CF vs. +1/2 OCT).

FIGURE 26.

Mean duration of recovery time as a function of overload frequency and intensity. The solid bars are used to represent the groups exposed to 90 dB overloads. The groups exposed to 85 dB are represented by shaded bars.

FIGURE 27.

Summary of the effect of overload frequency and intensity upon recovery duration. Mean duration of recovery time in seconds is plotted vs. level of sound exposure for the six experimental groups. The statistically-significant interaction between exposure level and frequency is evident in the crossing of the -1/2 OCT and CF lines.

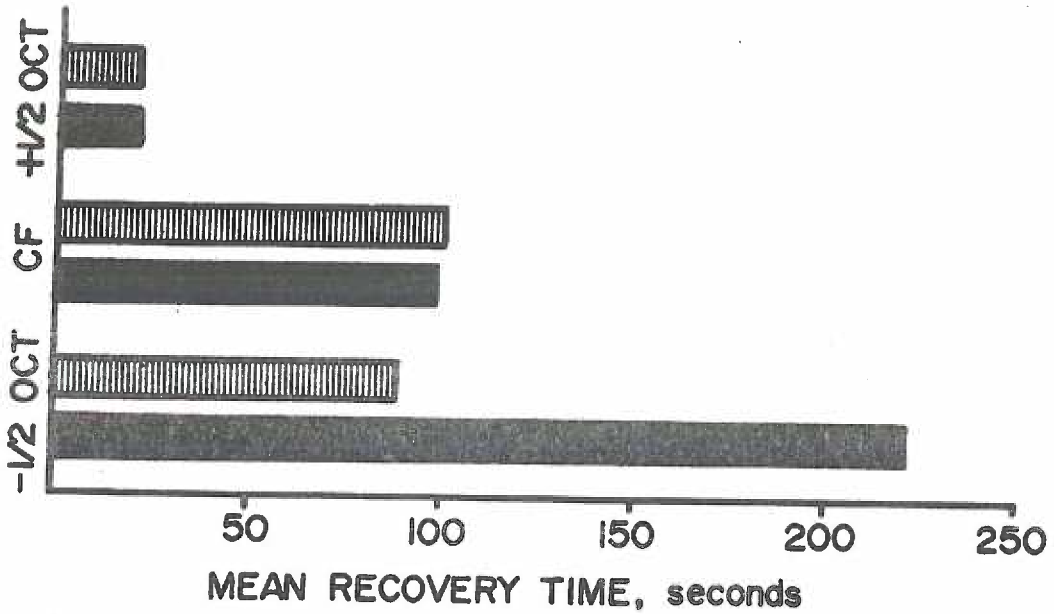


FIGURE 26

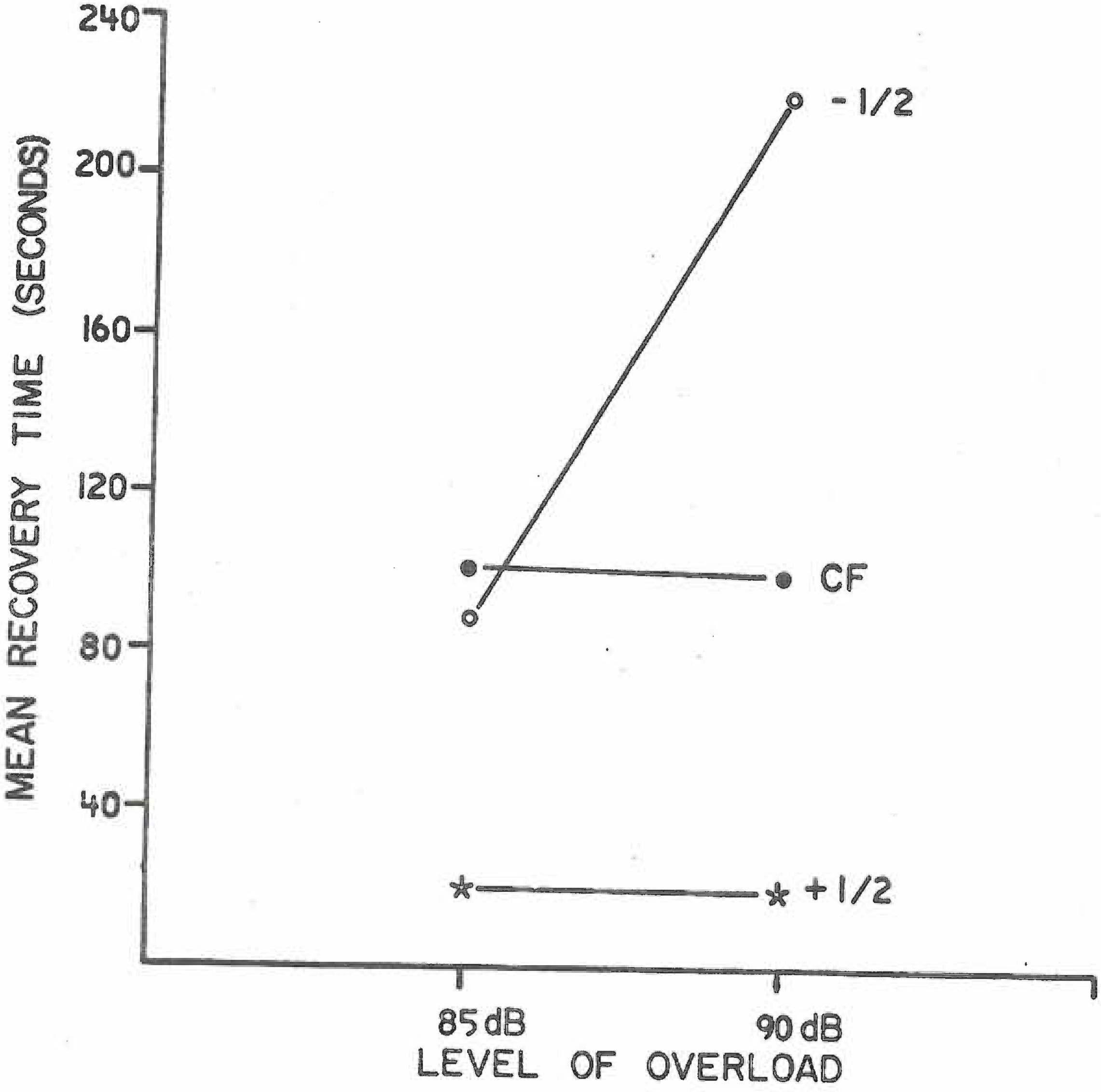


FIGURE 27

level using a Newman-Keuls test on differences between all pairs of means revealed that the -1/2 $OCT_{90}$ group showed significantly longer recovery times than either the $CF_{90}$ or +1/2 $OCT_{90}$ groups. The interaction between intensity and frequency of exposure was also significant ($F=4.2$, $df=2/63$, $p<.05$), indicating that the recovery times of the three frequency conditions (-1/2 OCT, CF, +1/2 OCT) differed as a function of overload intensity.

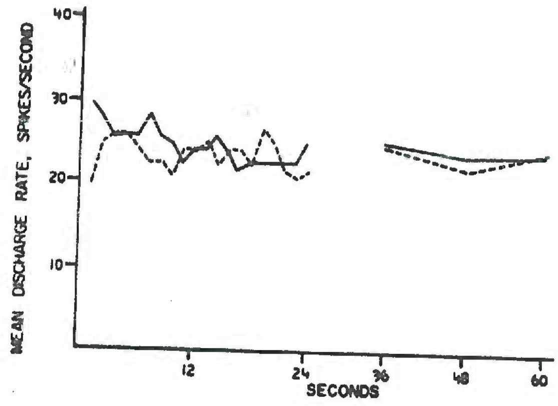
E. Discharge Rate During the Interstimulus Quiet Intervals: Changes Following Overstimulation

Following exposure to the overload stimulus, the interstimulus activity during the "B" periods showed a varied effect which was related to the frequency of the overload stimulus. As Figure 28a and b illustrate, the +1/2 OCT stimulation in general produced little apparent effect on the B period discharge rate. On the other hand, the -1/2 OCT and CF overloads both produced an initial decrement in the B discharge rates, as shown in Figures 28C through f. However, whereas fibers in the -1/2 $OCT_{85}$ and $CF_{85}$ groups tended to show a prompt return to pre-exposure rates of discharge, fibers in the -1/2 $OCT_{90}$ and $CF_{90}$ groups subsequently showed an increase to supernormal rates.

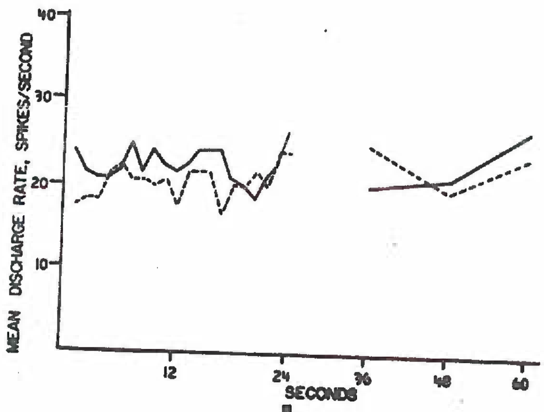
This increased discharge rate occurred between approximately the 4th and 22nd second following RECOVERY onset. For the $CF_{90}$ group (Figure 28d), the size of the increase was very small, little more than a suggestion of an increase. However, for the -1/2 $OCT_{90}$ group the increase in B activity was more pronounced, and it was therefore

FIGURE 28.

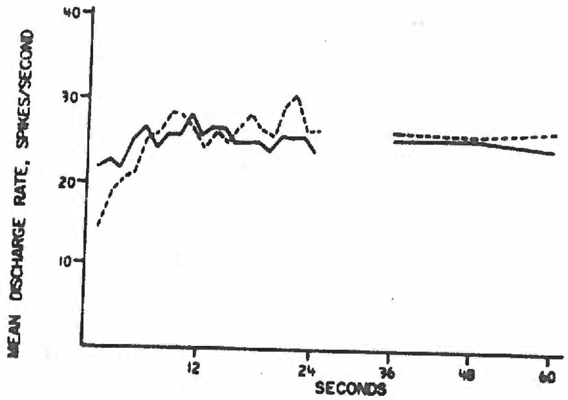
Effect of overload upon the discharge rate during the interstimulus interval ("B" periods). Each data point represents the mean group discharge rate for each moment in time. These data were obtained during quiet intervals between TEST CF stimuli: Solid lines illustrate the pre-exposure discharge rates, while dashed lines correspond to the post-exposure discharge rates. Data are plotted for the first 24 seconds of each of these intervals and for the 36th, 48th and 60th seconds. The experimental groups are as follows: (a) +1/2 $OCT_{85}$; (b) +1/2 $OCT_{90}$; (c) $CF_{85}$; (d) $CF_{90}$; (e) -1/2 $OCT_{85}$; and (f) -1/2 $OCT_{90}$. All groups show a more or less marked tendency toward depression in the first few seconds of RECOVERY. The $CF_{90}$ and -1/2 $OCT_{90}$ groups also appear to show a subsequent elevation in discharge rate.


40
30
20
10
MEAN DISCHARGE RATE, SPIKES/SECOND
12
24
36
48
60
SECONDS

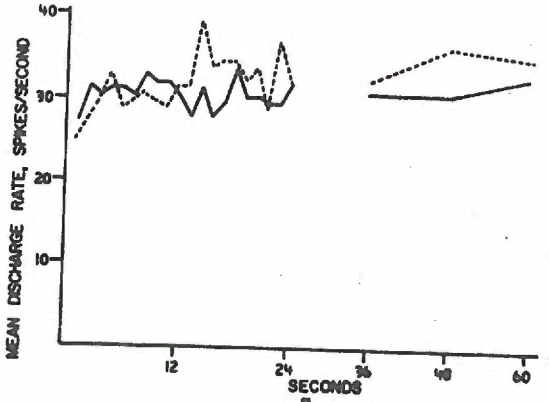
**a**


40
30
20
10
MEAN DISCHARGE RATE, SPIKES/SECOND
12
24
36
48
60
SECONDS

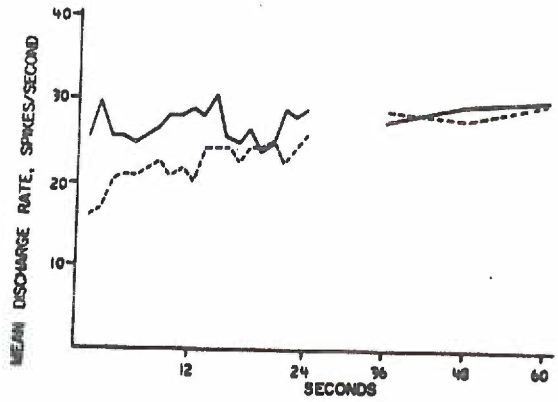
**b**


40
30
20
10
MEAN DISCHARGE RATE, SPIKES/SECOND
12
24
36
48
60
SECONDS

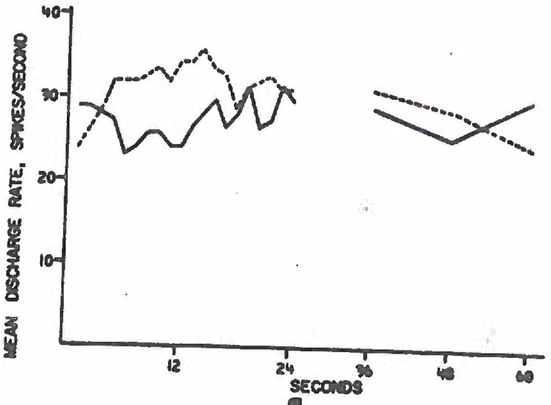
**c**


40
30
20
10
MEAN DISCHARGE RATE, SPIKES/SECOND
12
24
36
48
60
SECONDS

**d**


40
30
20
10
MEAN DISCHARGE RATE, SPIKES/SECOND
12
24
36
48
60
SECONDS

**e**


40
30
20
10
MEAN DISCHARGE RATE, SPIKES/SECOND
12
24
36
48
60
SECONDS

**f**

of interest to test whether this increase was statistically significant. The mean discharge rates during the post-exposure B periods (Figure 28 f) were compared to the corresponding pre-exposure values using a t-test on paired observations. The results of this test ($t=2.1$, $df=9$, $p < .05$) demonstrated that the discharge rate of B activity during the initial portion of RECOVERY (4-22 seconds) was significantly higher. In the DISCUSSION, implications of this result will be considered.

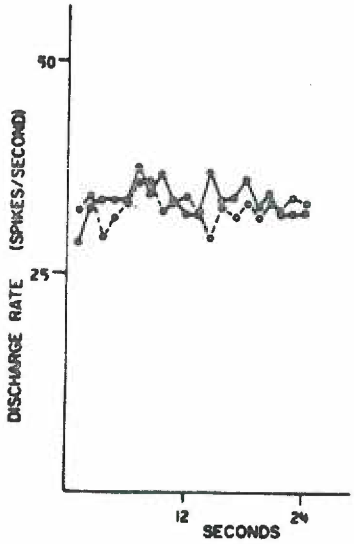
For all -1/2 $\mathrm{OCT}_{90}$ fibers, the change in B activity appeared to be independent of basic fiber parameters (CF, threshold, spontaneous and driven discharge rate).

## F. Recovery of Spontaneous Activity

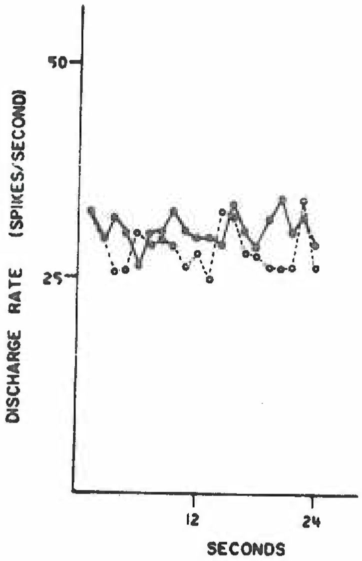
Unlike the case with driven and interstimulus activity, no effects of the acoustic overload stimulus upon the spontaneous rate of discharge were found in the present study. Figures 29a through f show a comparison of the mean discharge rate over the last 24 seconds of the pre-exposure TEST CF period with the first 24 seconds of the first post-exposure spontaneous period (following the standard one-minute post-exposure TEST CF interval) for the different overload conditions. It is clear that there were no differences between the pre-exposure and post-exposure spontaneous discharge rates for any of the experimental groups.

FIGURE 29.

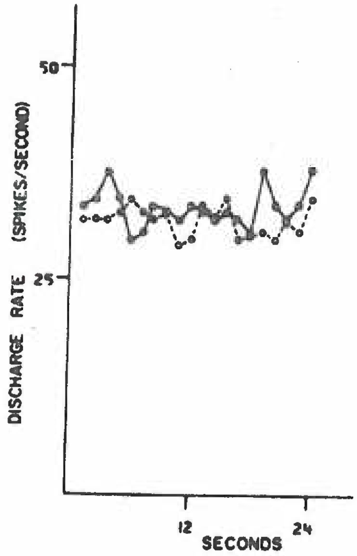
Spontaneous discharge rates before and after sound exposure for the six experimental groups. No acoustic stimuli were presented during the intervals in which the data were collected. Solid lines correspond to the pre-exposure spontaneous rates measured during the last 24 seconds of the PRE-LOAD SPONTANEOUS period. Dashed lines correspond to discharge rates measured during the first 24 seconds of the POST-LOAD SPONTANEOUS interval. The experimental groups are as follows: (a) +1/2 $OCT_{85}$; (b) +1/2 $OCT_{90}$; (c) $CF_{85}$; (d) $CF_{90}$; (e) -1/2 $OCT_{85}$; and (f) -1/2 $OCT_{90}$. These data were obtained following the standard 1-minute RECOVERY period immediately after the overload in which the CF test stimuli were presented every 120 msec. Probably because of the 1-minute delay, these data do not show immediate effects of the acoustic overload upon spontaneous activity; no effects of the overload upon spontaneous activity are evident.


50
25
DISCHARGE RATE (SPIKES/SECOND)
12
24
SECONDS

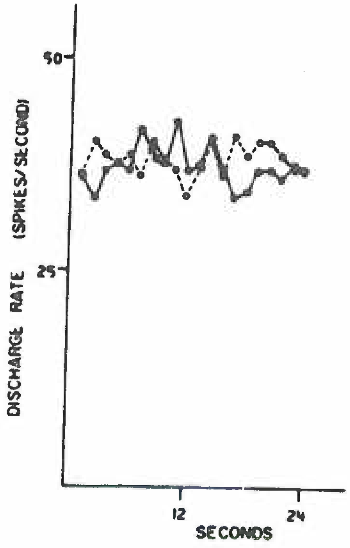
**a**


50
25
DISCHARGE RATE (SPIKES/SECOND)
12
24
SECONDS

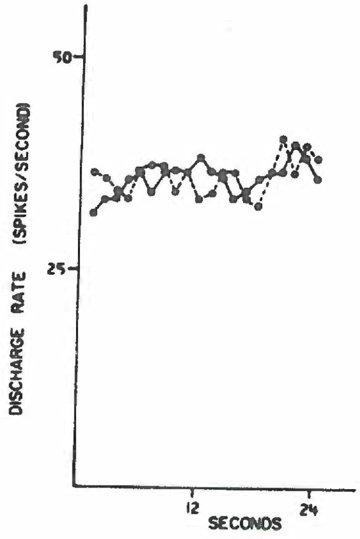
**b**


50
25
DISCHARGE RATE (SPIKES/SECOND)
12
24
SECONDS

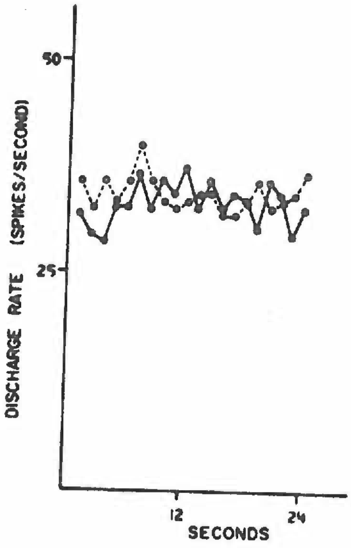
**c**


50
25
DISCHARGE RATE (SPIKES/SECOND)
12
24
SECONDS

**d**


50
25
DISCHARGE RATE (SPIKES/SECOND)
12
24
SECONDS

**e**


50
25
DISCHARGE RATE (SPIKES/SECOND)
12
24
SECONDS

**f**

# DISCUSSION

It appears, on the basis of the individual characteristics of cochlear nerve fibers described in the present report, that a sample of fibers was studied which was similar to those described by other investigators (for instance, Kiang et al., 1965; Young & Sachs, 1973). The characteristic frequencies of the fibers sampled ranged from 0.5 to 17.1 kHz, and spontaneous discharge rates varied from less than 1 spike/second to more than 100 spikes/second. In addition, the fiber thresholds reported here are representative of the range reported in the literature.

It must be clear that although the method of single unit analysis is not suited to direct exploration of the total basilar membrane area a given tonal stimulus involves, by varying stimulus frequency and intensity, the method can be used to identify those tones which are effective for an isolated nerve fiber. In this manner, the following observations of the effects of intense acoustic stimulation were obtained.

## I. Frequency-Dependent Effects

The principal finding of the present study was that, for exposure levels sufficiently intense (90 dB), stimulus frequencies one-half octave below a fiber's CF, rather than above or at the CF, produced the most severe reduction in fiber response rate. Such a result was predicted from the data of Mitchell (1973) on the AP of the cochlear nerve, and also from psychophysical studies of sound exposure in humans (Ward, 1963; Elliott & Fraser, 1970). This prediction stemmed from the observations that, following sound overload, both the AP and hearing were most depressed above the exposure frequency. Thus, fibers in the nerve which would be expected to be most depressed would be those whose CFs are above the frequency of the exposure stimulus. From this it follows that, for any given fiber, the most depressing overload would be at a frequency below its CF. This, then, was the primary hypothesis to be tested in the present research, and it appears to have been confirmed.

The time course of recovery following exposure at the half-octave below CF, for the 90 dB exposure group, was far longer than for any other exposure condition. Although the $CF_{85}$, $CF_{90}$, and -1/2 $OCT_{85}$ sound exposures also produced initial reductions in fiber response rates (and these were often substantial), there was a gradually-increasing difference over time between the recovery curves for these three exposure groups and the -1/2 $OCT_{90}$ overload group. Whereas the two CF groups and the -1/2 $OCT_{85}$ group showed in general a rapid return to pre-exposure response rates, the -1/2 $OCT_{90}$ fibers exhibited a more gradual return to control response levels. These data are consistent with some unpublished observations by Mitchell who used longer exposure durations (30 minutes) and a more intense exposure level (107 dB). In those observations, although recovery of AP amplitude at the overload frequency occurred within 3 hours of sound exposure, the AP amplitude at the half-octave above the overload frequency still had not recovered some 5 hours later. Comparisons of the "Times Prior To Recovery" which were given in Table IV indicate a similar difference between the $CF_{90}$ and the -1/2 $OCT_{90}$ groups in the present experiments. Thus, given a sufficiently intense exposure, the prediction that recovery would be longest after stimulation at one-half octave below a fiber's CF appears to have been confirmed.

Little or no reduction in discharge rate was found for exposure frequencies one-half octave above the CF. This result was anticipated on the basis of the shape of the tuning curves of single cochlear nerve fibers, which in general have very steep slopes as frequency increases above the CF. Thus, stimuli a half-octave above a fiber's CF would not be expected to be very effective, either for activating the fiber or for overloading it. While overload frequencies below about 4-6 kHz produced some brief reductions in the fiber responses following overload, higher exposure frequencies were almost completely without effect. Thus, the predicted ineffectiveness of exposures at one-half octave above the CF appears in general to have been demonstrated.

There appeared to be a systematic tendency for fibers with low frequency CFs to show a greater decrease in response rate, following exposure to the +1/2 OCT stimuli, than fibers with high-frequency CFs. This finding is consistent with the basilar membrane mechanical data of Békésy (1960) showing that low frequency tones activated almost the entire membrane, thus producing a broadly distributed membrane displacement. The present data showed that above about 5 kHz the effect of the +1/2 OCT overload stimuli abruptly decreased. This finding is consistent with Békésy's hypothesis that high-frequency tones activate very restricted, sharply-defined areas of the basilar membrane.

## II. Relation of the Results to the Half-Octave Shift Effect

Behavioral measurements of temporary shifts in hearing thresholds have demonstrated that the greatest changes in threshold following exposure to intense sounds occurred at frequencies higher than the exposure sound (typically, one-half octave above the exposure stimulus). The data of the current study supply additional evidence that as intensity is increased, the preferred frequency (i.e., that frequency---the CF at low stimulus intensities---which produces the maximum discharge rate) definitely shifts to a lower frequency. A trend of this sort had previously been identified in some of the reports dealing with single cochlear nerve fibers (Geisler et al., 1973; Rose et al., 1971). The present results thus confirm that the subjective phenomenon of the half-octave shift may be accounted for by changes in the firing rates of the primary afferent fibers of the cochlear nerve.

A number of mechanisms may be suggested as contributing to such changes. As previously discussed, recent mechanical measurements by Rhode (1971) indicated that with increases in intensity, a shift of the point of maximum basilar membrane displacement toward the base of the cochlea (high frequency end) occurred. This finding would certainly lend support to an hypothesis proposing a mechanical basis for the shift in frequency seen in psychophysical studies of sound over-exposure. If it is correct to assume that the driven rate of a fiber is controlled by basilar membrane displacement within a restricted region corresponding to the point of innervation, then the results of the present study can also be accounted for by the mechanical effects of increasing intensity. The present observations are also consistent with the assumption that it is at the point of maximum displacement of the basilar membrane that overload effects first become evident.

It does not seem probable that contractions of the middle ear muscles were responsible for the observed reductions in fiber responsiveness. Contraction of these muscles during the overload would have produced fluctuations in the level of the cochlear potential (Møller, 1963), and such fluctuations were never seen. Furthermore, the effects of the muscles upon sound transmission are negligible above 3-4 kHz (Wever & Vernon, 1955; Møller, 1965), while large reductions in fiber responses were seen to occur above these frequencies in many cases. It is also unlikely that the muscles show much activity in animals anesthetized with pentobarbital (Simmons, 1960).

Another possible mechanism of the post-exposure decrement in response rate which has been described is activation of the efferent fibers in the olivocochlear bundle. Activation of these fibers has been shown to inhibit the sound-induced discharge of cochlear nerve fibers (Fex, 1962; Wiederhold & Kiang, 1970). Such an activation during overload and a gradual decrease in responsiveness during recovery could explain the rapid decrease in response rate of afferent fibers during exposure and the post-exposure increase in discharge rate observed. However, several studies (Fex, 1962; Wiederhold & Kiang, 1970) have shown that efferent activation is maximal at stimulus onset and gradually decreases with time, thus demonstrating a time course of effect which is different from the observed monotonic reduction in fiber response rate. In addition, activation of efferent fibers by the 20 msec TEST CF stimuli during recovery thereby producing decreased response rates was unlikely since the latency of the response of these fibers to acoustic stimuli is approximately 20-40 msec. Thus the known characteristics of the inhibition of cochlear nerve fiber activity produced by the efferent fibers differ in several respects to the time course of overload effects described here.

It has commonly been held that increases in behavioral hearing thresholds which follow intense sound exposure are probably due to physiological changes at the neural (rather than receptor) level. One line of evidence supporting this contention was that the AC cochlear potentials, which were thought to represent receptor potentials (Davis, 1957; Dallos, 1973), appeared in the cat to be relatively unaffected by sound exposures up to at least 100 dB (Price, 1968). The observations of Mitchell (1973) indicated in guinea pigs that while AP potentials were severely depressed by sound pressure levels of 97-105 dB, the cochlear potentials remained unaffected. Observations of cochlear potentials which were made in the present study supported the conclusion that the cochlear potential in the cat was not reduced by the sound intensities used here (85 or 90 dB).

In contrast to the finding of no changes in receptor potentials, the present data demonstrated changes in both the driven and interstimulus interval neural activity. The fact that the cochlear potentials remained practically constant during the time in which the decreases in neural responding occurred suggests that the receptors were not responsible for those decreases.

A likely location for neural changes underlying acoustically-induced depression is the synapse between hair cell and nerve fiber. Synaptic effects of acoustic overload which might account for the neural changes could include such mechanisms as: changes in the amount of transmitter substance available; transient alterations in neural and non-neural structures; altered excitability of the post-synaptic membrane of the dendritic endings (Spoendlin, 1969; Elliott & Fraser, 1970). The possibility that the afferent fibers may temporarily lose their ability to produce propagated action potentials in response to a generator potential does not seem likely, for fibers in permanently damaged ears (whether acoustically damaged or drug-damaged) maintain normal responsiveness to electrical stimulation (Kiang et al., 1970; Kiang & Moxon, 1972).

## III. The Shape of the Recovery Curves

Although a few previous authors have measured discharge rate of single nerve fibers as a function of sound level for tonal stimuli, there is very little data available which is pertinent to the question of frequency-dependent effects following intense sound exposure. For example, Kiang et al. (1965), using continuous tones at fiber CF of approximately 70 dB, found that a transient reduction in spontaneous activity occurred immediately after the exposure period; a finding very similar to the short-term adaptation effects observed following stimulation with moderately intense tone burst stimuli (Kiang & Sachs, 1965; Kiang et al., 1965).

In the only exhaustive parametric study to date concerning the effects of sound exposure upon the responsiveness of single nerve fibers, Young and Sachs (1973) found that following exposure to steady tones at fiber CF, the discharge rate (both driven and spontaneous) was depressed for approximately 30 seconds. The form of the recovery functions (discharge rate plotted as a function of time) was well described by a simple exponential function. Although the general features of the recovery curves in the present study when plotted in linear coordinates resembled those of Young and Sachs (fast recovery at first, slower later), when the logarithm of discharge rate was plotted as a function of recovery time, the recovery curves in the present study were not linear. Thus it appears the recovery curves reported here were not of a simple exponential form.

Several important differences between the Young and Sachs study and the present investigation may account for this discrepancy. Their study was conducted using exposure stimuli only at fiber CF while the research presented here involved both CF and stimuli at other frequencies as well (one-half octave above and below CF). Furthermore, less intense exposure levels were used in their study than those used here (85-90 dB). In general, their highest level exposures were on the order of 80 dB. Thus, since in the current study, the CF recovery functions were not apparently exponential, it appears that the different findings concerning the time course of recovery were almost certainly a reflection of the difference in exposure sound level. In fact, in describing the dependence of recovery time on exposure level, these authors showed an example of a particular fiber (their Figure 7a) which was exposed to an unusually high overload level of 89 dB. It is interesting to note that rather than the usual simple exponential time course of recovery typical of fibers exposed to their moderate overload stimuli, this particular fiber showed a more gradual return to pre-exposure rates which resembled the recovery functions found in the present investigation.

## IV. Observations During the Overload Period

In view of the finding that at high levels of sound stimulation frequencies one-half octave below CF produce the greatest reduction in discharge rate, it is surprising that there appeared to be no relationship between the decline in fiber response rate during acoustic overload and the amount of reduction in fiber responding immediately following the overload. Although two prevalent patterns of overload time course could be identified ("exponential" vs. gradual overload curves), nevertheless, the monotonic decrease in discharge rate to an asymptotic level was qualitatively and quantitatively similar for both CF and -1/2 OCT experimental groups (see Figure 18). After the first second, each curve consisted of a rapid decay to an approximately asymptotic level which was slightly above the average spontaneous rate of discharge for each fiber. This finding is in agreement with those of Kiang et al. (1965) and Young and Sachs (1973) who found at lower sound intensities (70-80 dB) that discharge activity during continuous sound stimulation reached a steady level which was always above the rate of spontaneous activity.

Although there may be no necessary reason why discharge rate during the exposure period should be linearly related to percentage reduction of response rate during RECOVERY periods, one possible explanation may be that the 1.2 second time bins used to analyze the exposure interval were too long in duration to reveal subtle differences between the four experimental groups. The overload rate-time functions of Young and Sachs (1973) provide evidence to support this interpretation. Their curves, consisting of discharge rates averaged in the first 100 msec period of exposure and then in successive 600 msec time periods, showed a rapid decline in the first 700 msec of the exposure. It may well be that for fibers in the -1/2 $OCT_{90}$ group a similar decline in response rate occurred. However, because minus one-half octave stimuli had such a severe effect on these fibers (i.e., a high initial discharge rate that rapidly decreased), any fast decline which may have occurred was averaged out by the time the first 1.2 second measure was recorded.

## V. Additional Findings

The present observations indicated a rather surprising similarity between the effects of overload stimuli at $CF_{85}$, $CF_{90}$, and -1/2 $OCT_{85}$. In psychophysical studies of sound exposure (Ward, 1963; Elliott & Fraser, 1970), it has commonly been found that at low levels of sound stimulation (less than 50 dB), the maximum depressant effect was produced at the stimulation frequency, less at adjacent frequencies. As the sound level was increased (to approximately 60 dB), this no longer was true; instead, higher frequencies were sometimes more affected than lower. At around 85-90 dB the locus of maximum temporary threshold shift moved from the stimulus frequency to half an octave above. If sound intensity was further increased, behavioral findings indicated that the maximum loss gradually shifted upward, sometimes becoming as high as two octaves above the stimulating frequency, although it was more generally one-half to one octave above.

These observations suggest the possibility of a continuum such that at the 85 dB level the effects of $CF_{85}$ sound exposure were approximately equal to those of -1/2 $OCT_{85}$, but by 90 dB, the -1/2 OCT overload produced a greater reduction in fiber discharge rate. It is interesting to speculate that at 95 dB, the stimulating frequency which produces the maximum reduction in response rate may be even lower than the half-octave below fiber CF.

An unexpected finding was that the time course of recovery for activity during interstimulus intervals ("B" activity) was faster than that for stimulus-driven activity. In addition, after an initial depression immediately following the overload, the discharge rate in the interstimulus periods demonstrated a significant super-normal phase which lasted for approximately 18 seconds. Recovery of the non-driven activity thus was not monotonic. (Since the B activity corresponded to neural activity which occurred between test bursts and thus reflected short term adaptation effects produced by the stimuli (Kiang et al., 1965), it was not assumed to be equivalent to spontaneous activity measured during sustained quiet periods.)

A similar finding has been observed in parametric studies of the recovery from sound exposure of the whole nerve AP as well as in psychophysical studies of auditory adaptation. In the former studies, immediately following acoustic overload to intense tones above 100 dB, AP amplitude was depressed but within a few seconds there followed a period where AP was greater than its pre-exposure value (Hughes & Rosenblith, 1957). In the psychophysical studies, there was a period during recovery from sound exposure (usually 15-20 seconds following overload) in which an observer's auditory detection threshold was less than the pre-exposure value (Hirsh & Ward, 1952; Hirsh & Bilger, 1955; Noffsinger & Tillman, 1970).

At the level of single cochlear nerve fibers, there is some evidence from an early study that after intense sound exposures (the levels were unspecified), the spontaneous activity was first depressed and then accelerated (Galambos & Davis, 1943). However, more recent studies have not found spontaneous activity to behave in this way. These studies have demonstrated that following exposure to a steady tone, the spontaneous discharge rate was depressed (Kiang et al., 1965; Young & Sachs, 1973), and that recovery to pre-exposure rates was monotonically increasing (Young & Sachs, 1973). Again, this difference between recent studies and the present findings may be a reflection of the higher sound intensities used here. It should be noted that the present exposure levels, 85 and 90 dB, were more similar to those used in the psychophysical and whole nerve AP experiments than to those of the recent single unit investigations. In addition, as discussed above, it may be incorrect to assume that measurements of spontaneous acitvity taken during brief interstimulus periods are comparable to measurements of spontaneous activity made during sustained periods of quiet. Since the experimental protocol was designed to study the effects of sound exposure upon driven response rate rather than spontaneous activity as measured during prolonged quiet intervals, no immediate evaluation of the effects of acoustic overload upon spontaneous activity was possible. Thus, in the present study, no effect of sound exposure upon spontaneous activity was evident.

## VI. Limitations of Results

It is important to recall, as the individual recovery curves in the RESULTS section show, that for any one overload, considerable variations in individual recovery time courses were observed. These variations were evident even among fibers having similar CFs, thresholds, and discharge rates. Such variability serves to emphasize the notion that the cochlear nerve, like other portions of the nervous system, must transmit information in a probabilistic way. Despite such variability, it is remarkable that in a number of different cats and for fibers with CFs ranging over more than five octaves (0.5-17.1 kHz), with different thresholds, different firing rates, and with different asymptotic firing levels during the overload, the general features of the recovery curves were quite similar.

Given that individual fibers do possess widely varying characteristics and that the functional significance of these differences is but partially understood, it would be very desirable to have detailed comparisons of overload effects for a large number of fibers, with a wide range of CFs, thresholds, and so forth. Such correlations were attempted in the present study but they were severely limited by the sample size. The present data therefore are more suggestive than convincing of certain trends: There was some evidence that high threshold fibers in both the -1/2 $OCT_{90}$ and $CF_{90}$ groups demonstrated the least effect of the overload stimuli; there was also a suggestion that the effects of +1/2 OCT overloads were graded with respect to CF, the lower CF fibers showing the greatest amount of depression. Further study might well be addressed to these topics.

An unavoidable limitation in the use of sound exposure is that the physical characteristics of the middle ear impose a frequency-dependent effect on the amount of sound transmitted to the cochlea. That is, the middle ear is not a "flat" transmission system. For the cat, the frequency range for which the middle ear transmits sound most efficiently is above 1 kHz; that is, the sound pressure level of tones necessary to elicit responses either behaviorally or electrophysiologically is lowest above this frequency (Elliott, Stein, & Harrison, 1960). It is not surprising, therefore, that in the present experiments the average threshold for fibers with CFs of 5 kHz was approximately 20 dB lower than that for fibers with CFs of 1 kHz (Figure 16). In the single unit data presented here, the greatest percentage reductions in discharge rates were usually found for fibers with CFs above 1 kHz. These results suggest that the effective levels of stimulation reaching the cochlea were proportionately greater for frequencies above 1 kHz. It would be of interest to test this hypothesis by using a individual cat's middle ear characteristics (as estimated by the frequency function of the cochlear potential) to achieve more nearly equivalent exposure levels within the cochlea.

## VII. Limitations of the Conclusions

The assumption has been made that the discharge rate of a fiber is maximally influenced by basilar membrane displacements at only a single point of innervation; i.e., at the peak of maximum membrane displacement. Furthermore, it has also been assumed that the driven rate of a nerve fiber was related to the amplitude of membrane displacement. It should be remembered that since the relationship between basilar membrane displacement and the resulting neural discharge rate is largely unknown, the hypothesis concerning a mechanical explanation of the half-octave shift effect is at best only indirectly confirmed by the present study of cochlear nerve fibers.

In addition, it should be remembered that the present experiments were conducted on cats anesthetized with pentobarbital. It may be hazardous to draw inferences based on data from anesthetized animals concerning the role of the peripheral auditory system during acoustic overstimulation in a normal, waking organism.

Finally, it should be emphasized that the conclusions presented here are based on an experimental design in which sound exposures were chosen to be of relatively short duration and responsiveness of nerve fibers were tested with very brief tone bursts. It is not certain that the same or similar results would be obtained using different experimental variables; for instance, overload durations other than one minute, or test stimuli with different durations, repetition rates, or levels than those used here (20 msec, 8.3/second, 10-15 dB above fiber threshold).

Despite these limitations, the data presented here clearly demonstrated a frequency-dependent effect at the 90 dB level of sound exposure. These data suggest that further investigation utilizing higher exposure levels, with a broader range of frequencies around the CF, would be of value in understanding the effects of intense stimulation upon the ear.

## SUMMARY AND CONCLUSIONS

The effects of acoustic overstimulation were evaluated using various stimulation frequencies (at a given fiber's CF or at one-half octave above or below CF), and two exposure intensities (85 or 90 dB). The major results of the study can be summarized as follows:

(1) The most severe reduction in fiber response rate was produced by the -1/2 $OCT_{90}$ exposure. This effect was evident both in the extent of reduction in response rate following overload and in the time required for recovery to pre-exposure response levels.

(2) Less severe effects were found for the -1/2 $OCT_{85}$, $CF_{85}$, and $CF_{90}$ exposure conditions. These groups showed very similar recovery functions.

(3) Only slight effect on fiber responses was found for exposure stimuli at +1/2 OCT, whether at 85 or 90 dB. There appeared to be a slight tendency for fibers with lower CFs to exhibit greater depression of response rate.

(4) Perstimulatory declines in fiber discharge rate during the one-minute exposures were very similar for all -1/2 OCT and CF groups. There were no apparent differences in regard to the rapidity with which response decrement occurred, nor the final asymptotic discharge level reached. Perstimulatory declines for the +1/2 OCT groups were minimal.

(5) Discharge rates during the interstimulus intervals (100 msec quiet periods) exhibited non-monotonic recovery curves for the -1/2 $OCT_{90}$ overload condition. An initial brief depression (0-4 seconds) was followed by a super-normal phase (4-22 seconds) following the cessation of the exposure stimuli.

These observations suggest that there is an intensity level (at approximately 90 dB) at which the site of maximum stimulation no longer corresponds to the original CF, but instead, has moved toward the base of the cochlea; i.e., toward higher frequencies. This generalization is also consistent with the observations of basilar membrane displacement patterns at high intensities. The present results thus support the conclusion that the half-octave shift effect observed in both electrophysiological and psychophysical experiments may be accounted for by mechanically-induced changes in the discharge rate of single cochlear nerve fibers.

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