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#### RESEARCH OBJECTIVES AND SUMMARY OF RESEARCH

The principal activities of the Communications Biophysics Group tend to combine electrophysiological and behavioral experiments with machine data processing and analytical methods. Our major objective is to obtain a better understanding of sensory communication — in particular, of hearing. But in addition to our major research interests, we have found it profitable to apply our tools and methods selectively to other organisms and other systems as suggested below.

The group continues close cooperation with the Eaton-Peabody Laboratory of Auditory Physiology at the Massachusetts Eye and Ear Infirmary. This laboratory is operated cooperatively by M.I.T. and the Eye and Ear Infirmary. The cooperative arrangements include joint appointments of scientific staff. Some of the projects described below (Sec. A) will actually be carried out at the Eaton-Peabody Laboratory by staff members and students of the Communications Biophysics Group.

Our research program can be divided into five or six major areas. The programs for each area are discussed individually in the following subsections.

#### A. Research on the Peripheral Auditory System

Our studies of the auditory system in the recent past have ranged from the acoustic properties of the external ear to the electrical activity recorded at the cortex. The principal projects of current and future interest are the following.

1. During the past few years, we have measured the transfer function of the middle ear by making direct visual measurements of the displacement of the ossicles. This technique is quite tedious and also relatively insensitive. We propose to develop a more convenient and precise method of measurement before extending our studies of the middle ear. A technique for using a small Mossbauer source of narrow spectrum gamma rays placed on the vibrating component seems promising. After developing a convenient system for making measurements, we plan to obtain a more accurate transfer function for the cat's middle ear over a wider frequency range than we have obtained previously. Also, we would extend our measurements to other conditions (e.g., with the incudo-stapedial joint interrupted) in order to determine a unique circuit model for the middle ear that can be tested at the element level.

2. An experimental program has been started in which responses to acoustic stimuli from single cells in the superior olive of anesthetized cats are recorded and the locations of the cells are determined anatomically. The aim is to determine whether various categories of physiological behavior can be correlated with certain nuclei, regions, or cell types within the complex. One conclusion that can be drawn from the data at hand, is that relatively few active cells are found in the accessory superior olive, and none of those active cells that have been found responds in the manner described by earlier workers.

3. Techniques have been developed for recording intracochlear potentials with micropipette electrodes and for locating electrode tracks histologically in the cat. These techniques have been used to study the responses to sound within the cochlear scalae as in the immediate vicinity of the Organ of Corti. We expect to devote considerable effort to these experiments in the coming year with the aim of obtaining a more complete description of the cochlear potentials and more precise hypotheses about the mechanisms involved in producing them.

4. The effects of electrical stimulation of the efferent crossed olivocochlear bundle (OCB) on firings of single auditory-nerve fibers in anesthetized cats have been studied. A number of results have been summarized in a Ph.D. thesis submitted by M. L. Wiederhold to the Department of Electrical Engineering, M.I.T., in September 1967. This work will continue; in the future, emphasis will be placed on the time course of the inhibition produced by long trains of electric OCB stimulation. An attempt will

also be made to clarify the effects of crossed OCB stimulation on the "spontaneous" activity of auditory-nerve fibers. A comparison of the effects produced by stimulation of the crossed and uncrossed olivocochlear bundles is also planned.

5. The study of extracellular unit potentials in the auditory cortex of the cat will continue. In general it appears that auditory cortical neurons are more responsive to complex stimuli and less responsive to simple ones. The main objective of this work will be to provide as much information as possible about the kinds of acoustic stimulation that are effective in evoking responses in these cortical cells.

N. Y. S. Kiang, W. T. Peake, W. M. Siebert,

T. F. Weiss, M. L. Wiederhold

#### B. Neuroelectric Correlates of Conditioning

During the past year, our search for neuroelectric correlates of conditioning has followed a somewhat different approach from that of previous years in which the emphasis was primarily on evoked potentials in the primary afferent pathways. Although the analysis of sensory evoked potentials has continued, our primary concern in this endeavour has been the clarification of "state" related changes in evoked responses, particularly at the cortical level. On the other hand, the response, or motor, side of the system has assumed much more importance in studies aimed directly at the conditioning problem.

1. A systematic study of the eyelid reflex has been initiated because this relatively simple reflex has properties that promise to make it quite useful in the study of neural processes underlying conditioning. Some progress has been made in delineating the neural pathways and activity involved in the unconditioned reflex in the rat, although much remains to be done in this regard. We have also developed a method for measuring the eyeblink without impeding movement of the rat's head, but a pressing problem is the development of a system whose output is linearly related to evelid position and movement. In studies recently initiated, we are attempting to gain control of the eyelid response through both classical and operant conditioning procedures and to measure the neural activity in the motor nucleus of the VIIth Nerve under these conditions. Habituation of the unconditioned reflex to corneal stimulation is also under study, with our initial interest again being in the activity of motoneurons serving the orbicularis oculi muscle. Another aspect of this program includes the study of single cells in the Spinal Nucleus of the Vth Nerve which respond to corneal stimulation. Briefly, our program is directed toward as full an understanding of the unconditioned eyelid reflex as we can achieve while we press concurrently for techniques whereby we can control it, measure it, and record the underlying neural activity.

2. Our earlier studies of evoked potentials during aversive conditioning indicated that the observed changes in evoked activity under such procedures were related to a general change in the "state" of the organism. We have pursued the study of state-related changes in acoustically evoked potentials in two ways: first, by examining changes in cortical evoked potentials during natural sleep and waking, and second, through the manipulation of those potentials by a variety of pharmcological agents. Data on hand from the sleep experiments point to several possible sources of the confusion in the published record of such studies. We hope to present within the coming year a reasonably detailed picture of the changes in cortical evoked potentials during sleep and waking, and to provide additional information pertinent to the analysis of the complex waveforms of cortical responses in unanesthetized animals.

R. D. Hall

#### C. Other Neurophysiological Research

In addition to the programmatic research described above, work in our laboratory

has also included and will continue to include a number of other studies of the nervous system. These are often of a kind that we feel will profit from our general interest in analytical and computer techniques, and they serve to enrich our intellectual environment by exposing both students and senior personnel to a variety of problems and techniques in the study of the nervous system. Current projects, some of which will continue, include the following.

1. A study of the neural circuitry in the abdomen of the crayfish has several aims: (a) to identify the role that the stretch receptor plays in the behavior of the organism, (b) to quantify the various intrasegmental and intersegmental feedback relations that are known to exist, (c) to delineate some of the synaptic relationships in the abdominal ganglion, and (d) to examine the effects of activity in higher nervous structures on cells in that ganglion.

2. Recent studies of somatic evoked potentials recorded from the human scalp will be extended to include an investigation of acoustically evoked potentials. The emphasis will again be on relating the scalp potentials to parameters of the stimulus.

3. During the past year, the capabilities for performing sucrose-gap, voltageclamp experiments on single lobster axons were developed. Furthermore, a hybrid analog-digital computer facility has been programmed to solve the Hodgkin-Huxley equations which appear to represent the voltage-current characteristics of a patch of nerve membrane. These two experimental-theoretical capabilities will be used in continuing studies of nerve membrane.

4. The experimental study of unit activity in the optic nerve of the ground squirrel, a mammal with an all cone retina, has been directed toward an understanding of chromatic adaptation. The study of retinal activity will continue, along with the development of a model for information processing in the retina that will take into account adaptation phenomena.

5. Among projects completed this year are a study of respiratory units in the medulla of the cat, an investigation of firing patterns of cells in cat cerebellar cortex to acoustic stimulation, and a study of the response patterns to gustatory stimuli in the glossopharyngeal nerve, also in the cat.

W. A. Rosenblith, R. W. Henry

#### D. Psychophysics

#### 1. Binaural Hearing

Our research on binaural hearing during the past year has been concerned primarily with just-noticeable differences (JND's) in interaural time delay and interaural amplitude ratio for tones.<sup>1</sup> We have begun to develop a new quantitative model of binaural processing in which the firing patterns in the auditory nerve are regarded as inputs to a black-box central processor, and have performed preliminary experiments on discrimination of interaural time and amplitude for a 500-Hz tone. Measurements were made of the interaural time and interaural amplitude JND's as functions of interaural time, interaural amplitude, and over-all level. The results were found to be consistent with data on time-intensity trading and with the predictions of the new model for the interaural amplitude JND, but to be inconsistent with the predictions of the new model for the interaural time JND and with the prediction of the equalization and cancellation model that relates interaural time JND's to interaural amplitude JND's.

We have also completed our analysis of a previous experiment on binaural unmasking, which was concerned with the effect of noise bandwidth, and have prepared the results for publication.<sup>2</sup>

Our principal effort in this area during the coming year will be to develop the new

model of binaural processing, extend our experimental results on JND's for tones, and explore JND's for other types of stimuli.

#### 2. Magnitude Estimation and Absolute Identification

Using certain concepts of signal-detection theory, we have begun to develop a model of magnitude estimation (ME) and absolute identification (AI) for unidimensional stimulus sets. According to this model, AI performance should be predictable from ME performance, and conversely. In order to test this model, preliminary experiments have been performed in which the stimulus set consists of tones differing only in intensity, and the subjects are required to do ME in some tests and AI in others. Although only a portion of the data from these experiments has been analyzed, it appears that the performances in the two tasks are related as expected. In particular, the confusions that arise in AI can, on the average, be predicted from a knowledge of the dispersion of the responses in ME for the same set of stimuli.

In another series of experiments (which, also, have not yet been completely analyzed), we have examined the use of ME and AI for determining detection performance. We have compared sensitivity indices (d's) and receiver operating characteristics (ROC's) obtained with ME, AI, confidence ratings, and "yes-no" binary responses. The results appear to be roughly the same for all methods, and the efficiency of the various methods for obtaining ROC's appears to increase in the following order: binary responses, confidence ratings, AI, ME.

During the coming year, we hope to complete the analysis of our preliminary data and to prepare the results for publication. Then we intend to explore in detail the range of stimulus sets over which ME and AI are equivalent, the way in which ME and AI performance depends on various properties of the stimulus set, and, more generally, the extent to which performance in ME, AI, discrimination, and detection can be interpreted within the context of a single, unified theory.

3. Short-Term Memory for Sounds

Another topic that we are studying concerns the degradation of performance that occurs when interfering stimuli or tasks are inserted among the primary stimuli of a discrimination experiment. Preliminary theoretical work has been initiated and the first in a series of experiments is now being performed. The primary task in this experiment involves the discrimination of tone-pulse intensity, and attention is being given to the effects of time decay, interference imposed by extraneous stimuli, and interference imposed by extraneous tasks. Eventually, we hope to develop a general model that will enable us to integrate the results of these experiments with those on magnitude estimation and absolute identification.

4. Figural Aftereffects in Vision

Preliminary work has been completed on a model that is intended to account for the displacement of contours in the visual field caused by previously presented contours (figural aftereffects). A computer program has been developed to represent the model, and preliminary runs have produced results that are qualitatively consistent with observed phenomena in perceptual experiments. Future research will be aimed at adjusting the parameters of the model to obtain quantitative agreement.

#### 5. Bilocal Cutaneous Unmasking

In an experiment performed in 1965, we explored the extent to which a phenomenon analogous to binaural unmasking occurs when the signal and noise are presented through two vibrating probes (rather than earphones) and applied to two patches of skin (rather than the two ears).<sup>3</sup> Certain of the results were found to contradict previous results

from other laboratories. During the next few months, we intend to examine these contradictions more closely and to complete an article on this work for publication.

#### 6. JND's in Frequency Ratio

In an experiment performed in 1966, we attempted to measure the JND in frequency

ratio for tones.<sup>4</sup> Unfortunately, it was discovered at the end of the experiment that, because of subtle learning effects and inadequate facilities, the cues used for discrimination might not have been confined solely to ratio cues. We now intend to repeat this experiment and to eliminate this uncertainty.

## 7. Selective Attention and Binaural Message Competition

Recent work has suggested the application of signal-detection theory to the analysis of the selective mechanisms that operate when a listener receives different messages in his two ears.<sup>5</sup> Experiments are planned to measure changes in the detectability of a rejected message in the presence of an accepted one. Different proportions of target to nontarget signals will be used in an attempt to obtain receiver operating characteristics for subjects under different conditions of message competition.

#### 8. Sensitivity to Details of Noise Waveforms

It is often assumed that a significant factor in the variability of a subject's responses in experiments involving noise signals is the randomness of the noise. If this were the case, listeners should be capable of determining whether or not repeated noise bursts are identical or merely statistically identical. During the coming year, we hope to perform an experiment to test this capability.

#### 9. Hearing Defects

In addition to the research projects already listed, we intend to consider the feasibility of initiating a program to study hearing defects. The primary purpose of this research would be to increase our understanding of the auditory system, rather than to contribute directly to clinical diagnostics. The number of subjects to be studied would be small and they would be selected on the basis of their willingness to participate in long series of experiments, their observational talent, the advice of members of the medical profession about how such experiments might influence a subject's health, and the degree to which psychophysical analysis of a particular hearing defect appears to be a fruitful venture for the development of auditory theory.

#### 10. Laboratory Facilities

Considerable effort is being spent to improve our laboratory facilities for psychophysical research. The objectives of this effort are to provide: (a) transducers and signal-generating equipment that are flexible, easy to use, and of high quality; (b) a general-purpose, computer-aided facility that is suitable for performing experiments involving complex stimulus sets, complex response sets, modification of the stimulus sequence on the basis of past responses, measurements of temporal aspects of the subject's responses, and monitoring of the stimulı; (c) another facility that is suitable for performing simple experiments, increases our capacity for handling the increasing number of personnel who are interested in psychophysical research, and is independent of the computer-aided facility (so that simple and complex experiments can be run concurrently and simple experiments can be run while the computer is being used for purposes other than psychophysical research). The pursuit of these objectives will continue during the coming year.

N. I. Durlach, N. P. Moray, W. M. Siebert, W. A. Rosenblith

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#### E. Methods of Processing Electrophysiological Data

Most of our work has been focused on the problem of characterizing electrophysiological data recorded from the intact human subject. Characterization includes the accumulation of baseline data and devising useful display techniques, as well as statistical analysis and the development of appropriate implementation schemes. Most of our effort has been applied to examining electroencephalographic data under a variety of behavioral conditions, including sleep. These data have been characterized in terms of time averages, even though it was known to be nonstationary. Recently, we have developed several methods that permit examination of the temporal structure of these data by displaying sequences of short-term statistics. Using these methods, we are, at present, undertaking a study of the effects of drugs on EEG sleep patterns. Because a three-dimensional display provides a perspective view of a considerable amount of data in rather compact form we think it may be quite useful in a clinical situation such as monitoring the depth of anesthesia during surgery. We also think it may be usefully applied as a monitor of physiological "state" for pilots or astronauts and are arranging with N.A.S.A. to process data recorded during a space flight. We hope that this work will not only contribute knowledge of the electrical activity of the nervous system but also result in clinically useful tools.

More recently, we have been concerned with the general problem of recording, processing, and displaying electrophysiological data from hospitalized patients. We are working on several cardiac monitor systems that include alarm features, automatic classification and counting of ectopic beats, and an inexpensive three-dimensional photographic display of several minutes of electrocardiogram.

S. K. Burns, W. A. Rosenblith

#### F. Cardiovascular System Studies

The aim of our work is the quantitative understanding of the cardiovascular control mechanism. In the past two years, we have studied that part of the carotid-sinus reflex which causes heart-rate changes following sudden alterations in the arterial blood pressure. We have recorded baroreceptor and cardiac vagal efferent activity in anesthetized dogs and cats, and obtained a preliminary description of how those nerve firings relate to blood pressure and heart rate.

At present, we are developing a physiological model to predict single-fiber baroreceptor nerve firing as a function of blood pressure. We are also testing descriptive

models, one relating multiple-fiber baroreceptor firing to blood pressure, the other one characterizing heart rate as a function of pressure. By studying the afferent and efferent impulses in the heart-rate reflex, we hope to gain at least a partial understanding of the functioning of the vasomotor center.

P. G. Katona

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# A. ECTOPIC BEAT DETECTOR

Cardiac arrhythmias are common manifestations of several disease entities, and may also be precipitated by drugs. Some arrhythmias may be quite detrimental to the over-all status of the patient, and some may be fatal. Since most arrhythmias are treatable at the present time by either pharmacologic or electric methods, early detection of arrhythmias is of prime importance.

Atrial and ventricular extrasystoles are thought to be indicants of cardiac irritability, and their frequency of occurrence may be modified by such disease processes as myocardial infarction, electrolyte imbalance, pulmonary embolism, hypoxia, thyrotoxicoses, myocarditis, valvular heart disease, heart surgery, and others. Ectopic activity is also modified by drugs such as digitalis, isoproterend, xylocaine, quinidine, and so forth. Cardiac irritability often appears to be slowly progressive and only after some hours or days may lead to a life-threatening arrhythmia such as a rapid supraventricular tachycardia, ventricular tachycardia or ventricular fibrillation. In its earliest stages, irritability may appear as only a rare atrial or ventricular premature contraction (1-5 per minute). Continuous monitoring of the frequency of such ectopic beats might reveal progression or regression of irritability, and thus serve as a valuable guide to early therapy. The question of whether dangerous arrhythmias such as ventricular tachycardia are the end result of a steady progression of irritability or occur without warning remains to be answered.

EKG rhythm strips or several minutes of observation of a monitor oscilloscope are unsatisfactory methods of sampling ectopic activity occurring at such slow rates. Much longer sampling periods are needed, and it seems that an automated method is desirable. A device has been designed and constructed which detects ectopic beats, identifies them as either atrial or ventricular extrasystoles, and counts them separately. The system, which is now undergoing clinical trials, is described briefly in this report.

1. Theory of Operation

Two measures are necessary in order to define and differentiate atrial premature contractions (APC's) and ventricular premature contractions (VPC's), namely the R-R interval and some measure of QRS wave shape. Many possible measures of wave shape might be used, and we have chosen arbitrarily the integral of the absolute value of the QRS complex over  $\Delta \tau$  seconds, beginning at the origin of the R-wave.  $\Delta \tau$  is adjustable, and at the present time we are using ~0.2 sec. Thus, the measure  $M_i$ , for the i<sup>th</sup> beat is defined as

$$M_{i} \stackrel{\Delta}{=} \int_{t=0}^{t=\Delta\tau} |v(t)| dt,$$

where v(t) represents the EKG, and t = 0 corresponds to the trigger pulse that occurs near the origin of the R-wave. This measure may need to be modified after the results of clinical trials are available.

The instrument measures each R-R interval,  $\Delta T_i$ , and compares it with the average of the previous four intervals  $\overline{\Delta T}$ . If  $\Delta T_i/\overline{\Delta T}$  is less than an arbitrary constant, a <u>premature</u> beat is defined. Similarly,  $M_i$  is calculated for each QRS complex and is compared with  $\overline{M}$ , the average of the measures of the previous four <u>normal</u> QRS's. If  $M_i/\overline{M}$  is greater or less than an arbitrary constant, a VPC is defined. An APC then is defined as a premature contraction with a normal QRS complex.

The device uses digital circuitry for engineering simplicity and reliability. It consists of two separate subsystems, one that measures time intervals, and the other that analyzes waveforms. Although some elements are time-shared (the D/A converters), the device can be described best by discussing the two sections separately.

2. Timing Subsystem

The timing subsystem measures each R-R interval and compares it with a running average of the previous four intervals. A block diagram of the system is shown in Fig. XXXIII-1. The input pulse occurs at the beginning of each QRS waveform and, at present, is obtained from a cardiac monitor. The trigger pulse actuates the timing sequence shown in Fig. XXXIII-1. The counter which had been counting clock pulses is disabled by pulse 5 for a period of approximately 8 µsec during which the comparisons

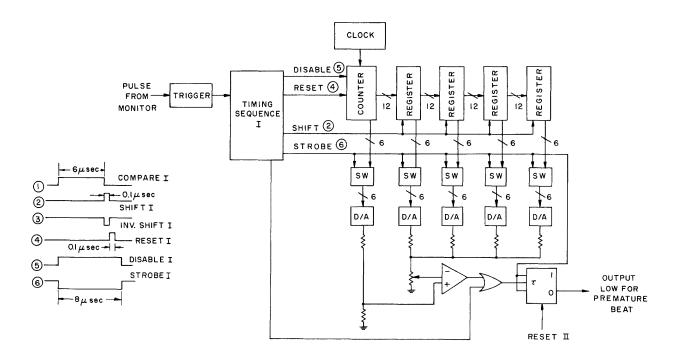


Fig. XXXIII-1. Timing subsystem.

are made. The number in the counter,  $N_I$ , is now proportional to the preceding R-R interval. By using a clock frequency of 40 per second and a 6-bit counter, the longest R-R interval that can be measured would be 1.6 sec, which corresponds to a heart rate of 37 1/2 beats per minute.  $N_I$  is compared with the average of the previous four R-R intervals (stored in the shift registers) by means of an analog comparator circuit. Pulse 3 (leading edge) complements a flip-flop to produce a negative level output if the R-R interval is shorter than the average by a fixed percentage. Thus, an output occurs for each premature beat. After the comparison, pulse 2 causes the contents of each register to shift into the following one, and the first register receives the contents of the counter. Contents of the fourth register are lost, thereby updating the running average. Finally, pulse 4 resets the counter, and at the end of the disabled pulse the counter restarts. The D/A converters are time-shared and pulse 6 serves to connect them to the appropriate counter and registers during the 8-µsec interval in which the comparison is made.

3. Waveform Subsystem

The waveform subsystem calculates the measure M for each QRS complex and compares it with the average of the previous four <u>normal</u> M's. The block diagram is shown in Fig. XXXIII-2. The EKG waveform, at the present time, is taken from the output of a conventional cardiac monitor. It is made compatible with this instrument

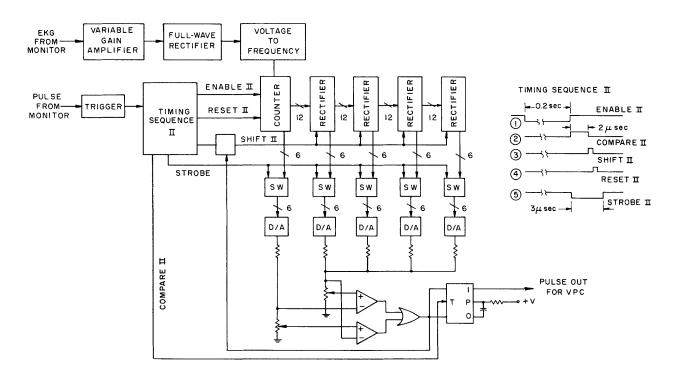


Fig. XXXIII-2. Waveform subsystem.

by means of a variable-gain buffer amplifier. A full-wave rectifier produces |v(t)|. A voltage-to-frequency circuit follows which produces an output pulse train whenever |v(t)| exceeds a certain small voltage  $\delta v$ . The number of output pulses  $N_{II}$ , is directly proportional to |v(t)|, and the total number of pulses is thus proportional to  $\int_t^{\Delta T} |v(t)| dt$ . These pulses are counted for a fixed period of time  $\Delta \tau$  (nominally 0.2 sec). The counter is a 6-bit device, and hence two safeguards must be provided. First, in order to permit comparison,  $N_{II}$  for normal QRS complexes should only half fill the counter. This is accomplished by adjusting the gain of the buffer amplifier. To aid in the adjustment, a light has been wired to the counter with the necessary logic such that for 24 <  $N_{II}$  <32 the indicator light flashes with each QRS. Second, PVC's often have large wide QRS complexes, and  $N_{II}$  may sometimes exceed the counter's capacity of 64. Hence the counter is wired so that it will not accept any more than 64 pulses, and cannot overflow.

Obviously, the waveform calculations can be done only at the end of the QRS waveform and the delay following the earlier timing calculation allows the same D/A converters to be used for both subsystems.

As in the subsystem described above, the trigger pulse actuates a timing sequence shown in Fig. XXXIII-2. Pulse 1 turns on the counter for the period  $\Delta \tau = 0.2$  sec. Next, with the counter disabled, N<sub>II</sub> is compared with the average of the contents of the four registers by means of the analog comparator circuit. Pulse 2 produces an output if N<sub>II</sub> is greater or less than arbitrary fractions of the average. If N<sub>II</sub> is within the established range of normal, a shift pulse (3) is produced which shifts the contents of the registers one place to the right and places N<sub>II</sub> into the first register. If N<sub>II</sub> is outside the normal range, no shift pulse is produced, and hence the registers contain only normal M's. A manual switch is provided to produce shift pulses during initial loading of the registers. Finally, the counter is reset by pulse 4, and is ready for the following QRS. The D/A converters are switched by pulse 5.

#### 4. Output Logic and Display

Having detected both premature contractions and all abnormal QRS waveforms, it is a relatively simple matter to count APC's and VPC's separately. All waveforms with abnormal M's are classed as VPC's and are counted as such. Premature beats with normal waveforms are counted as APC's. The device obviously cannot distinguish a nodal beat, wandering atrial pacemaker, or aberrent conduction. In the presence of atrial fibrillation, APC's have no meaning, and the APC counter should be switched off. At the present time, the output display consists only of two rachet counters. Printing counters which could provide periodic (e.g., hourly), counts of APC's and VPC's automatically, together with a cumulative recorder that would indicate not only the number of ectopic beats but also their time of occurrence, would be a better output display.

On the basis of clinical trials, thus far, it is apparent that the instrument functions well under ideal conditions. Several problems remain to be solved, however. The biggest problem, predictably, is the artifact problem which causes false positive counts. By improving electrodes and electrode configurations, as well as providing more filtering in the EKG preamplifiers, this problem should be soluble.

R. G. Mark

# B. PHENOMENOLOGICAL MODEL FOR A FORM OF ADAPTATION IN PRIMARY AUDITORY-NERVE FIBERS

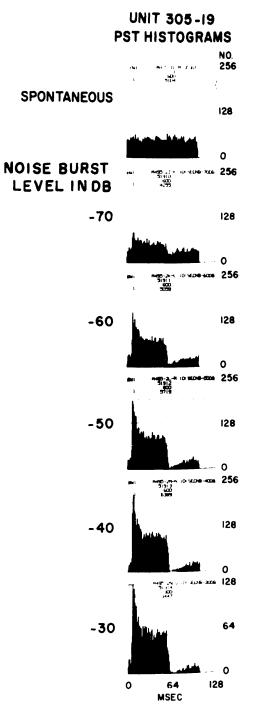
As is true with most excitable cells, the firing patterns of auditory nerve fibers show a form of "accommodation" or "adaptation" to a sudden change in stimulus level. For example, Fig. XXXIII-3 is a collection of PST histograms for a typical fiber in response to periodically presented noise bursts of various intensities. Characteristically, the high rate of firing at the onset of the sound burst rapidly decays to a more moderate level. At the termination of the burst, moreover, the rate falls initially below the spontaneous level and then gradually recovers. Similar effects are also apparent in Fig. XXXIII-4 which shows histograms for another unit as a function of the duration of a tone burst for fixed intensity and repetition rate.

The histogram shapes of Figs. XXXIII-3 and XXXIII-4 are reminiscent of the pulse response of a highpass linear electric circuit of the form shown in Fig. XXXIII-5. But in spite of obvious similarities, there are also substantial differences. Most notably, the histograms of Figs. XXXIII-3 and XXXIII-4 have markedly unequal rising and falling discontinuities, never go negative, and exhibit strong influences of pulse durations and amplitudes on discontinuity heights and time constants of decay. Recently, it occurred to us that the pulse responses of the simple nonlinear system of Fig. XXXIII-6 would have at least qualitatively many of the same properties as the physiological histograms. To investigate this relationship more quantitatively, the response of the system of Fig. XXXIII-6 was derived analytically and (for simplicity in manipulating parameters) the response to a periodic pulse was simulated on the PDP-4 computer.

The calculated step response is indicated in Fig. XXXIII-7. Two particular properties of special interest follow from the results of Fig. XXXIII-7, or indeed can be easily derived directly from the system of Fig. XXXIII-6.

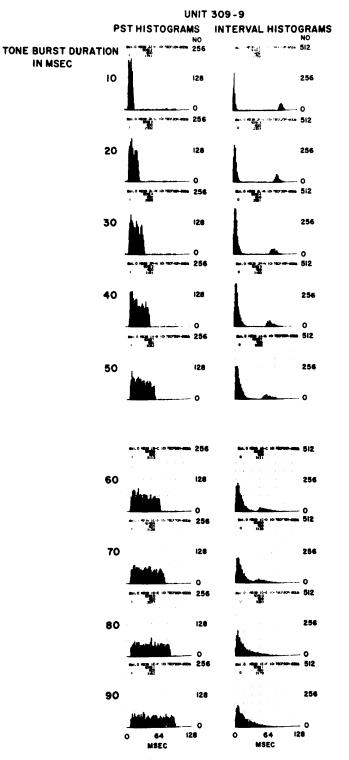
(i) the steady-state response to a constant input is proportional to the square root of the input amplitude.

(ii) At a discontinuity in the input waveform there is a discontinuity in the output waveform, and the values of input and output immediately before and immediately after are related (under the assumption that the discontinuity is at t = 0) by the equation



CF: 4.49 kc. Stimuli: noise bursts, 50-msec duration, 2.5-msec rise-fall time, 10 bursts/sec. Reference level for noise bursts: 70.7 V rms into condenser earphone. Each histogram represents 1 minute of data except at -30 db when only 30 seconds of data were obtained. Zero time of each histogram is 2.5 msec before the onset of the electric input to the earphone.

Fig. XXXIII-3. PST histograms of a primary auditory-nerve fiber to bursts of noise as a function of stimulus level. (Reproduced from N. Y. S. Kiang, et al., <u>Discharge</u> <u>Patterns of Single Fibers in the Cat's Auditory</u> <u>Nerve</u>, The M.I.T. Press, Cambridge, Mass., 1965, Fig. 6.3, p. 72.)



Zero time of each PST histogram is 2.5 msec before the onset of the electric input to the earphone. Stimuli: tone bursts, 2.5-msec rise-fall time, approximately 10 bursts/sec, -80 db.

Fig. XXXIII-4. PST histograms of a primary auditory-nerve fiber to tone bursts as a function of burst durations. (Reproduced from N.Y.S.Kiang, et al., <u>Discharge Patterns of Single Fibers in the Cat's Auditory Nerve</u>, The M.I.T. Press, Cambridge, Mass., 1965, Fig. 6.5, pp. 76-77.)

$$\frac{y(0+)}{y(0-)} = \frac{x(0+)}{x(0-)}.$$
(1)

When x(t) is a pulse as shown in Fig. XXXIII-8, Eq. 1 implies that

$$\frac{y(0+)}{y(0-)} = \frac{A_1}{A_0} = \frac{y(T-)}{y(T+)}.$$
(2)

The histograms of Figs. XXXIII-3 and XXXIII-4, as well as many other similar histograms from auditory nerve data, are approximately in agreement with Eq. 2, although the test is not a particularly sensitive one because often y(T+) cannot be estimated accurately from a limited amount of data, and y(0+) is often critically dependent on the bin width used in constructing the histogram.

A more satisfactory test is provided by the tracings of computer-simulated periodic

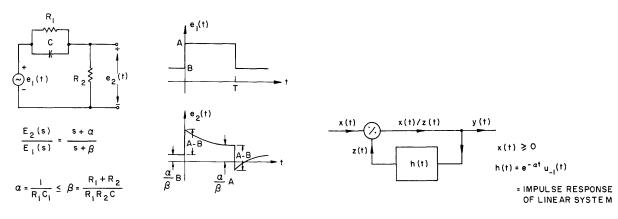
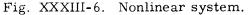


Fig. XXXIII-5. A simple highpass filter.



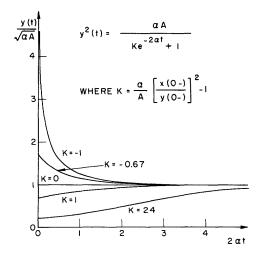


Fig. XXXIII-7. Response to x(t) = A, t > 0.

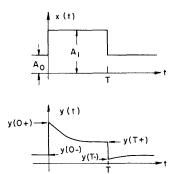


Fig. XXXIII-8. Input and output. Illustrating Eq. 2.

pulse responses shown in Figs. XXXIII-9 and XXXIII-10. Parameter values were selected to make the results correspond in a very rough way to the histograms of Figs. XXXIII-3 and XXXIII-4, but no attempt was made to optimize the parameter

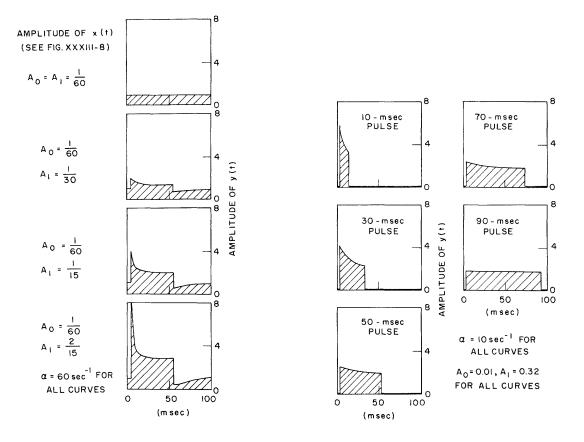


Fig. XXXIII-9. Waveforms for comparison with Fig. XXXIII-3. Fig. XXXIII-10. Waveforms for comparison with Fig. XXXIII-3.

choices. Nevertheless, there is obviously substantial similarity, even with respect to many details. We have also tried to simulate a number of PST histograms, including those obtained under masking and more complex stimulus conditions, and in each case it has been easy to choose values of a and the input levels  $A_1$  and  $A_0$  such that a quite successful match is obtained.

Since we have virtually no understanding of the physiological mechanisms responsible for this type of adaptation in auditory nerve fibers, it would clearly be unreasonable to imply that the system of Fig. XXXIII-6 in any sense accounts for or explains the phenomenon. But perhaps the simplicity of the system does suggest that the true explanation of this adaptation phenomenon need not be very complicated.

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