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NEURAL INFORMATION PROCESSING IN THE PERIPHERAL AUDITORY SYSTEM OF THE GUINEA PIG

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FOREWORD

This work was performed in support of Project 7232, "Research on the Logical Structure and Function of the Nervous System," Task 723202, "Physical and Physiological Mechanisms Involved in the Reception of Acoustic Energy." The research was performed in the laboratories of the Neurophysiology Branch while the author was serving on active duty in the Medical Corps of the United States Air Force; author's present address is: Division of Neurology, University of Virginia, School of Medicine, Charlottesville, Virginia.

The author wishes to express his thanks to Doctors J.R. Mundie and H.E. von Gierke for their invaluable assistance and suggestions in the preparation of this study, and to the various members of the Neurophysiology Branch, Biodynamics and Bionics Division of the Aerospace Medical Research Laboratories who gave technical assistance.

This technical report has been reviewed and is approved.

> J.W. HEIM, PhD.
> Technical Director
> Biomedical Laboratory
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ABSTRACT

A number of first and second order neurons of the guinea pig auditory system were studied extensively in an attempt to determine the method by which information is conveyed. Single neuron electrophysiological techniques with anatomical controls were used in the study and in response to several different stimuli, various response patterns were observed. Statistical methods of analysis, using a digital computer, were employed. Each fiber in the auditory nerve appears to convey only fragmentary information; therefore, the information carried by a number of fibers is required to extract all the information about a single signal. The data suggest that a pulse density modulation system of encoding is used, in which the "carrier" appears to be the irregular spontaneous background activity, the pulse density of which is actively increased and decreased to convey information about both pitch and loudness. The system appears to be much more sensitive to sound changes than to absolute values. For example, pulse density correlated far better with rate-of-change of stimulus intensity than with absolute levels of intensity. In addition to frequency and amplitude, the interval between successive stimuli may be an important parameter of stimulation.

SECTION I

INTRODUCTION

Communication within the nervous system appears to be carried out
mainly by means of trains of pulses, traveling along axones. In a single
fiber these pulses are all virtually identical in duration and amplitude and
are probably due to rapid waves of chemical activity propagated along the
axonal membrane, altering its polarization as they pass. A series of ex-
periments was undertaken, using computer analysis, in an attempt to de-
termine the pulse modulation system used for the coding of actual neuro-
physiologic data obtained from the mammalian auditory system.

SECTION II

EXPERIMENTAL METHODS

Twenty-eight sound-responsive single neural units, with several
different response patterns, were studied extensively using the cathode ray
oscilloscope, photographic records, and the real time digital analysis system
for biological data (described in ref 8 and illustrated in figure 1). Other
units were observed more briefly. The animals used were young adult guinea
pigs which had been tested for intact hearing. This was done by means of
the pinna reflex in response to sounds, which is consistently absent in
animals with middle ear infections and acoustically damaged hearing. The
animals were operated on under lidocaine local analgesia and succinyl
choline immobilization. Tracheostomy was performed and artificial respiration
was provided by means of an endotracheal tube attached to a Harvard Respirator
Pump. Body temperature was maintained at 37.5 C by means of a direct-
current heating blanket, automatically regulated with a rectal-temperature-
controlled switch. A modified Johnson stereotaxic surgical instrument was
used to insert the electrodes into the auditory nerve by means of coordinates
determined on fresh and formalin-fixed heads (ref 1). Anatomical controls were
run to determine the location of our electrode tip.

The stereotaxic instrument was modified to accept, in place of the
electrode carrier, a specially designed hydraulic microdrive for the electrodes.
This microdrive was operated from a remote position and allowed the electrode
to be advanced or retracted in controllable increments as small as 0.5μ without
appreciable lag time or backlash. One of the earbars was modified to contain
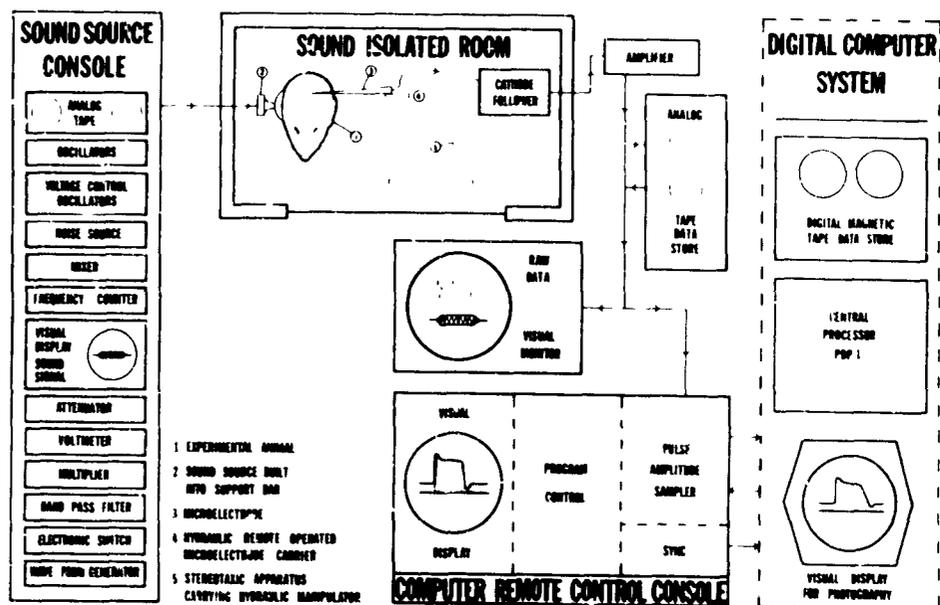our sound source, a condenser microphone driven as a loudspeaker, coupled

Figure 1. **Equipment for Analysis of the Function of a Single Nerve Cell in Peripheral Auditory Nervous System.** Electrical driving signal for calibrated sound source is generated by equipment on the left. Experimenter observes the electrical activity as it comes from the cell in response to the sound and is also given visual display of data analyses performed by the compute. system. Stereotaxic coordinates are used to place the electrode into the auditory cranial nerve; final positioning is done by experimenter from outside sound isolated room with remotely operated, hydraulic microelectrode carrier.

2

directly into the external auditory canal with a speculum. The device was acoustically calibrated in situ in terms of sound pressure level (re .0002 microbar) at the eardrum. This arrangement also enhanced acoustic isolation. The animal was placed in an acoustically quiet room. The operator controlled the electrode penetration from the adjacent room, which also contained all the sound-generating and recording equipment except the microphone-speaker and the recording preamplifier.

Electrodes used were either electrolytically sharpened steel needles or capillary micropipettes of drawn glass with liquid electrolyte cores. Steel needles used were ordinary sewing needles, electrolytically sharpened to the desired taper and tip size, and insulated with varnish or lacquer. The usual diameter of the uninsulated recording surface in either type of electrode ranged from 0.5 to 3 μ. Pipettes were filled with 3M KC1, or more usually with saturated ferric ammonium sulfate solution. The iron core electrodes (glass and steel) were used to mark the location of the electrode by ionto-phoresis of ferric ions from the tip into the tissue, which was later perfused with a reagent to give the Prussian Blue reaction. A Nissl counterstain of the tissue with Neutral Red gave good contrast. In some of the earlier ex-periments, gross anatomical location was used, but the histologic method was adopted because of its greater precision.

The hydraulic microdrive unit consisted of a micrometer screw, connected to a bellows head stage by a small diameter stainless steel tubing. The tubing was sufficiently long to allow operation from the adjacent room. Resistance due to hydraulic friction was minimized by using alcohol, rather than oil, to charge the system. Vacuum-boiling of the entire system while filling eliminated most of the air. In this way it was possible to obtain a high degree of precision (to the limits of resolution of a light microscope) and stability (recording extracellularly from a single neural unit for up to 8 hours).

Since the target was the acoustic nerve within the internal auditory canal, the approach was made through the most lateral portion of the cerebellum from a dorsocaudal direction, thereby passing under the tentorium cerebelli with the electrode tip, at an angle of 40° elevation from the basal plane. This approach also had the advantage of putting the electrode track nearly parallel to our plane of section of the histological material, (which was cut at right angles to the long axis of the brainstem) making the marking stain easier to locate.

Due to the oblique medial surface of the petrous bone in the guinea pig, the approach described above allowed entry to the internal auditory meatus with the tip of the electrode, recording from the nerve within the canal. If the electrode should pass medial to the internal meatus, it would usually pass through the acoustic nerve as it emerged from the meatus, or in other instances

3

it would enter the dorsal or ventral cochlear nucleus of that side. To distinguish these locations at the time of the experiment, the criteria of Rupert, Moushegian, and Galambos (ref 9) may be used.

While the glass micropipettes have the advantage of better insulation, smaller diameter of the penetrating portion and smaller potential tip size, there are some disadvantages which should be enumerated. The ferric ammonium sulfate electrolyte records the unit potentials very well and is apparently not sufficiently toxic to injure the fibers noticeably during the periods of the recording. Glass tips in this size range were found to tolerate current densities of 100 or 200 amperes per square centimeter. Although this is a high current density, it is actually only a few microamperes of current in a 1-μ diameter electrode. This will deposit only a very small quantity of iron in a reasonable length of time, and may be difficult to find in the histological sections. Also, electrical impedance of the tip may vary considerably during the iontophoresis, perhaps due to poisoning of the tip or to plugging with coagulated protein during the current flow. This is a problem that could not be overcome entirely, as the cause was uncertain.

The steel needle electrodes are easily made by electrolytically sharpening ordinary sewing needles or a variety of other iron alloy wires. By inspection under the microscope, and regulating the voltage and depth of immersion, the tip can be molded into a variety of shapes. Wires can be sharpened to a point (as visible under the light microscope) but the diameter of the recording tip is limited by the ability to insulate these small diameters, due to surface tension of insulators when applied as a liquid. Insulation can be checked by microscopic observation of the electrolytic decomposition of distilled water, being sure to attach the negative pole of the battery to form hydrogen bubbles at the tip. Reversal of the poles will destroy the tip. For marking, the solid iron electrodes deposit a great deal more iron per microampere of current than do glass pipettes. As current is passed the tip disintegrates, and the resistance decreases due to increasing diameter, rather than the reverse which is sometimes seen in glass electrodes.

The degree of normal variation found between different guinea pigs is not large when using the references for stereotaxic surgery (ref 9). However, some variation is present both in the size and configuration of the bones of the skull and can lead to occasional difficulties at operation. In a few cases, there is a portion of the petrous bone which actually overhangs the internal meatus. Under these circumstances, insertion of the electrode into the meatus at the angle of approach given earlier is impossible. An attempt was made to diagnose this condition in advance by means of various measurements and skull x-rays. However, these were of little assistance. The animals are difficult to position accurately enough to make a reasonable interpretation of the x-ray films. In addition, the overhanging bone, when present, is not very dense when contrasted with the underlying portion of the petrous bone, adding to the difficulty of interpretation. Fortunately, the condition does not occur often enough to be a serious drawback. A recent modification of the stereotaxic instrument has been made, which should enable

4

the experimenter to avoid the overhang by using a slightly different angle of approach in future studies.

The single neural unit potentials detected by the electrode were appropriately amplified, and filtered, when necessary, to remove unwanted slow waves and nr . Low frequency cutoff varied between 1 cps and 1 Kcps. High freq_ cy cutoff was usually set at 4 Kcps. The data could be displayed on an oscilloscope, photographed, recorded on magnetic tape (FM) for further study, and fed "on-line" into the digital computer, where the first analysis was performed, and the data stored in digital form on magnetic tape.

Conversion to digital form is achieved by passage through a pulse height analyzer, producing a standard rectangular pulse for every spike within a voltage "window," of which the upper and lower limits are controllable. The computer repeatedly samples the input at equal short-time intervals (0.3-2.0 msec) to determine the presence or absence of a pulse during that interval, this information being stored. The number and duration of sequential intervals sampled determine the analysis period. A sound stimulus is made to begin at the same point in time during each analysis period, and the neural responses to an ensemble of identical stimuli are then collected.

Three principal methods of data analysis were used. The first was the Pulse Occurrence Histogram, which gives a display of the total number of pulses occurring at each time interval during the ensemble of analysis periods. The se cond, a moving average technique, gives a plot of the average pulse rate at any given point in time during the analysis period. The time over which rate is computed and the points in time at which it is plotted are both independent variables in this program. The third method was a program written to study the possibility of an interval coding system, and allows intervals to be studied with reference to a common pulse, or with reference to the last previous pulse. It also contains a device allowing examination of peaks of activity where they occur. This is done by selecting time segments of the analysis period, during which pulses are counted and their intervals computed, while other segments may be ignored.

SE TION III

OBSERVATIONS ON RAW DATA

Observations on the raw data were in general agreement with those of others who have studied this system (refs 2-5, 7, 9, 10). All sound-responsive units were more-or-less frequency specific, and responded to an increasing range of frequencies as the stimulus was made louder. Fibers adjacent to one another were found to have similar frequency sensitivities, as a rule. All

had some spontaneous firing in the absence of intentional stimulation.
(Although precautions were taken to insure acoustic isolation, as described,
the animal may have heard its own vascular or respiratory sounds.)
Spontaneous activity was noted to be quite irregular (figure 2). In a number
of fibers, the spontaneous firing rate was seen to change appreciably during
the period of observation.

Figure 2.   Spontaneous Neural Activity of Two Fibers.   Duration of
            each trace is 220 msec.   Note irregularity of pulse occurence
            and the character of "neural noise" between larger pulses.

Stimulation was produced by giving a tone. In most cases, this caused
an increased rate of firing, which gradually diminished. When the tone was
turned off, firing abruptly decreased, then gradually returned to the previous
level of spontaneous activity. The time required for return to background
level of firing, after stimulus, was dependent upon the level of spontaneous
activity. Those fibers with high rates of spontaneous firing recovered fairly
quickly (50 to 100 msec), while those with very low rates of background
activity recovered much more slowly. In one case, firing was suppressed,
after each stimulus, for at least 1 minute

ʾuring stimulus, activity was also irregular. When a series of identical
tones was presented, the neural response pattern was quite different for each
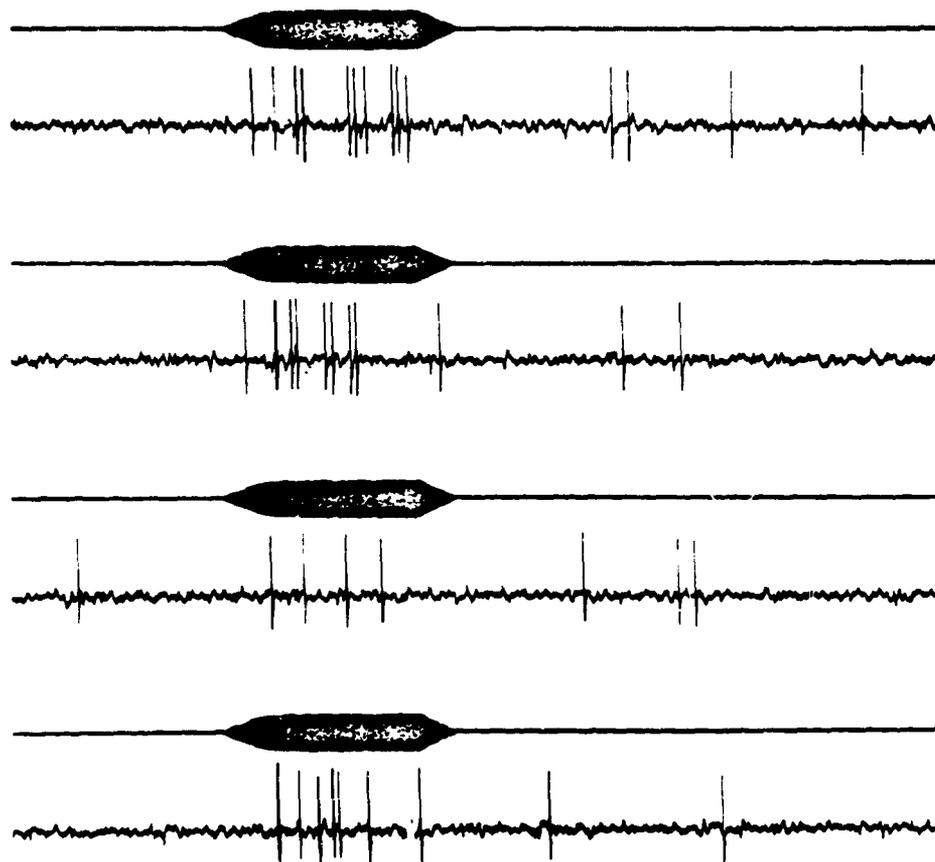tone, although there was an overall similarity (figure 3).

6

Figure 3. <u>Variable Response to Identical Stimuli</u>.
Stimulus duration 110 msec.

An interesting observation was made concerning the occurrence of slow
waves in these preparations. When stimuli with very short rise times were
presented, there appeared on the record a striking evoked slow wave response.
This presumably was caused by pickup of potentials from adjacent fibers, which
normally are visible in the records as numerous very low voltage spikes, termed
"neural noise." This neural noise diminishes with hypoxia
and hypothermia, and increases during stimulus. With signals having high
rates of onset, these small spikes appear to be synchronized and summed by
the electrode, giving the appearance of a high voltage slow wave, and re-
sembling a typical evoked response. The effect is greatest in response to

7

clicks and tones with square wave envelopes, and can be eliminated by lengthening rise time. It is much greater when electrodes with relatively large tips (2-3 μ) are used, than when using small-tipped electrodes (1 μ or less). With electrodes accidentally broken during the experiment, the effect may be overwhelming. The appearance of slow waves in each experiment was predictable on the basis of observed signal-to-noise (neural) ratio of the electrode. The slow waves, when present, were removed with an electronic filter prior to computer analysis of the data.

SECTION IV

COMPUTER ANALYSIS

From the inconsistency of single fiber responses to identical stimuli, it was concluded that the animal must extract information by integrating the outputs from a number of fibers firing at once. It was felt that temporal averaging of responses to sequential identical stimuli might approximate the net neural output. This makes necessary the assumption that each unit is acting as a member of a population, all carrying similar information about the stimulus, but does not exclude the possibility of other homogenous populations carrying different information about the same stimulus.

Using the analysis methods mentioned under Experimental Methods, it was seen that for most fibers, there was an initial peak of activity at the onset of the stimulus, that is, an increase in pulse density. I had originally discussed it as being related to "rise time" of the signal, that is, the time from onset to maximum amplitude. However, this turned out to be relatively unimportant as compared to rise rate. The initial peak could be reduced to imperceptibility by reducing the rate of onset, either by lengthening the rise time, or by reducing the amplitude while keeping the rise time constant. The striking initial peak was most often seen at onset rates of 2-3 dB per msec, or greater (figure 4). It appears to be due in part to synchronization of the spikes with respect to the onset of the stimulus, in addition to an actual increase in their number.

After the initial peak, the rate of firing diminished by what appeared to be an exponential curve, towards a firing level characteristic of that stimulus. (figure 5). The diminution was minimal at "best frequency" of the fiber, and progressively greater as the stimulus tone deviated from best frequency. Best frequency here means that frequency of tonal stimulus which produces a neural response at the lowest sound pressure level.
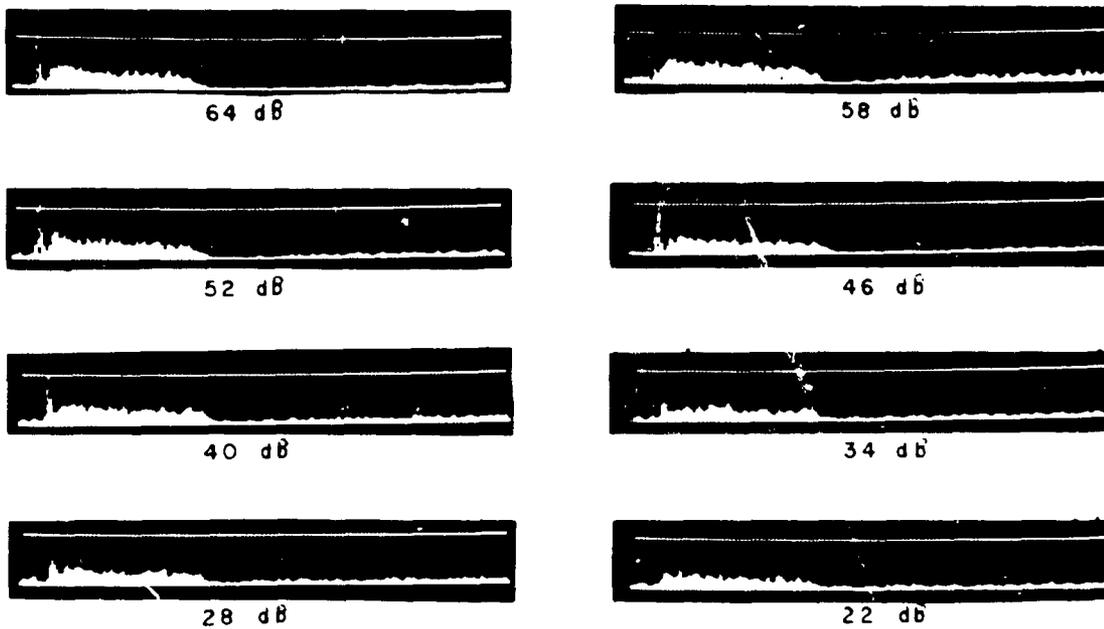
8

Figure 4. <u>Pulse Occurrence Histogram of 100 Consecutive Samplings at each Amplitude</u>. Coordinates represent: (x) time after onset--(total 250 msec); (y) number of pulses occurring at each point in time. (reference line is 25 pulses.) Rise rate was reduced by reducing stimulus amplitude, while rise time remained constant. Note also the variation in spontaneous firing (latter half of each trace), and the poststimulus suppression of activity (best seen in upper right trace).

9

Figure 5. Moving-average Rate Analysis of 100 Consecutive
Samplings. Coordinates represent: (x) time after
onset (Stimulus duration here is one second; total
sweep is 1.3 seconds.); (y) average rate in pulses
per second. (Reference line here represents 25
pulses per second.) Note diminution of firing rate
during stimulus.

A stimulus envelope was made which turned on, then increased 10
dB, then turned off. The initial plateau was 20 or 30 dB above threshold,
determined at best frequency. The response pattern to this stimulus illustrates
several of the firing characteristics of auditory neurones observed (figure 6).
Although the initial rise of the signal was a linear voltage gain for 16 msec,
the initial peak of neural activity in the response occurred during the first 5
msec. However, the second rise period caused a neural response rate in-
creasing approximately proportional to the amplitude of the stimulus. These
findings are not surprising in a system known to be sensitive to amplitude
changes on a decibel scale. Transposing, it is easily seen that the initial
rise above threshold represents a much higher rate (in dB/msec), than the
second rise period.

The total neural response was a few milliseconds less in duration than
the stimulus, indicating that part of the stimulus was below threshold. This
duration difference became greater as the stimulus frequency deviated from
best frequency, confirming my observations from other experiments that am-
plitude threshold is frequency dependent. Also illustrated with this signal is
the diminution of firing rate during stimulus, and its dependence upon tonal
distance from best frequency.

When the stimulus was turned off the usual response was diminution
to well below background levels of firing, toward which it recovered by what
appeared to be another exponential curve. The rate of recovery was dependent
upon the background rate of firing, as observed in the raw data. As would be
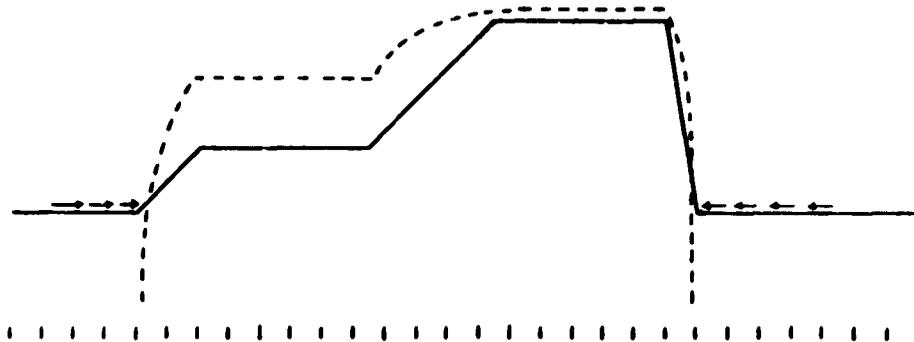
10

Figure 6 (a). <u>Voltage (Solid) and Decibel (Dashed) Plots of Envelope of Stimulus used in Figure 6b</u>. Time marks along base are 8 msec. intervals. Arrows indicate hypothetical threshold. See text.

6,500 cps

10,500 cps

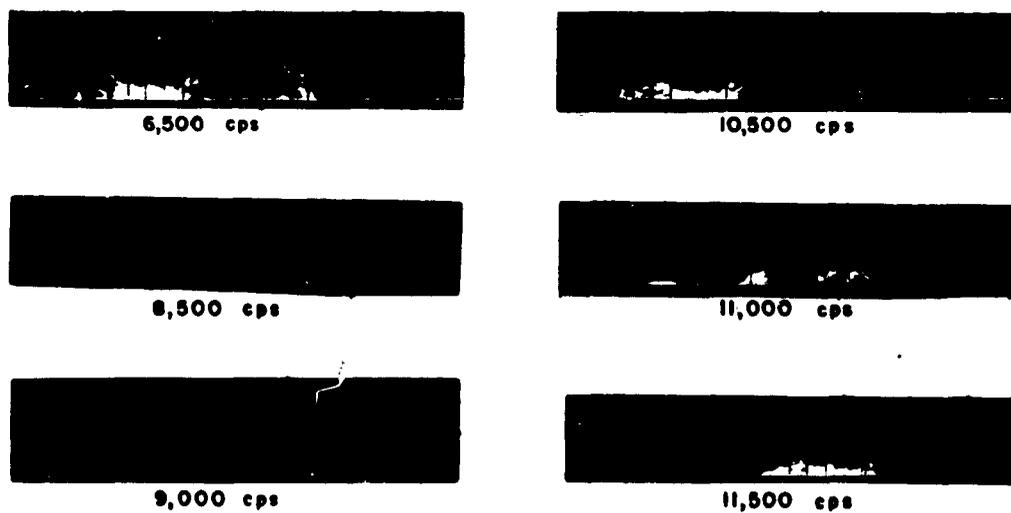
8,500 cps

11,000 cps

9,000 cps

11,500 cps

Figure 6 (b). <u>Response Patterns of a Single Neuron to Stimulus Envelope Represented in Figure 6a</u>. Moving-average rate analysis was used. Stimulus amplitude was the same for each response. Frequencies are indicated. See text.

expected from this poststimulus response, rapid repetition of the tone produced a marked effect on the average response (figure 7). This, presumably, is caused by starting the new stimulus during the poststimulus suppression from the last previous tone. It resulted in fewer neural pulses, but a high degree of synchronization with respect to the onset of the tone. The averaged response was a series of peaks and valleys. The effect could be reduced by making the interstimulus period longer or irregular.
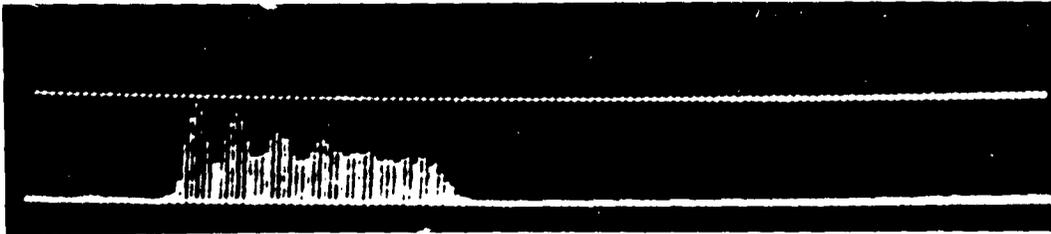

Figure 7. Response Pattern to Rapidly Repeated Stimulus.
Moving-average rate analysis was used. Repetition
rate was 10 per second.

All neurones were also studied in the absence of stimulation. As mentioned, this activity was quite irregular. The intervals of this spontaneous activity were plotted in histograms, the resultant frequency curves of which were skewed far to the left (figure 8).

I msec   intervals

Figure 8. Frequency Distribution Curve of a Pulse Interval
Histogram taken during Spontaneous Activity.
Coordinates: (x) Duration of interpulse interval;
1 to 64 msec. (y) Relative number of intervals of
each duration. This was computed by sampling
approximately 100 seconds of spontaneous activity
of a single fiber. The most frequently encountered
interval was 5 msec, but a few were over 60 msec
long.

12

SECTION V

CLASSIFICATION OF CELL RESPONSES

Several types of cell responses were encountered. Most responded by increased firing during stimulus.

1. Some responded throughout the stimulus, including:

a) Some, excited by very low sound pressure levels (about 10 dB), were very sensitive to small changes in frequency, but small changes in amplitude did not influence them greatly (figure 10, page 15).

b) Others were excited only by somewhat higher levels (above 40 dB). These were less sensitive to changes in frequency, but very responsive to amplitude changes (figure 9). Both were sensitive to changes of both frequency and amplitude, however.

2. Some responded chiefly at onset of the stimulus. These, as a rule, had very low rates of background activity.

3. A few fibers were observed which responded by decreased firing during stimulus. Because they were infrequently encountered, they were difficult to classify.

80 dB   80 dB

90 dB   90 dB

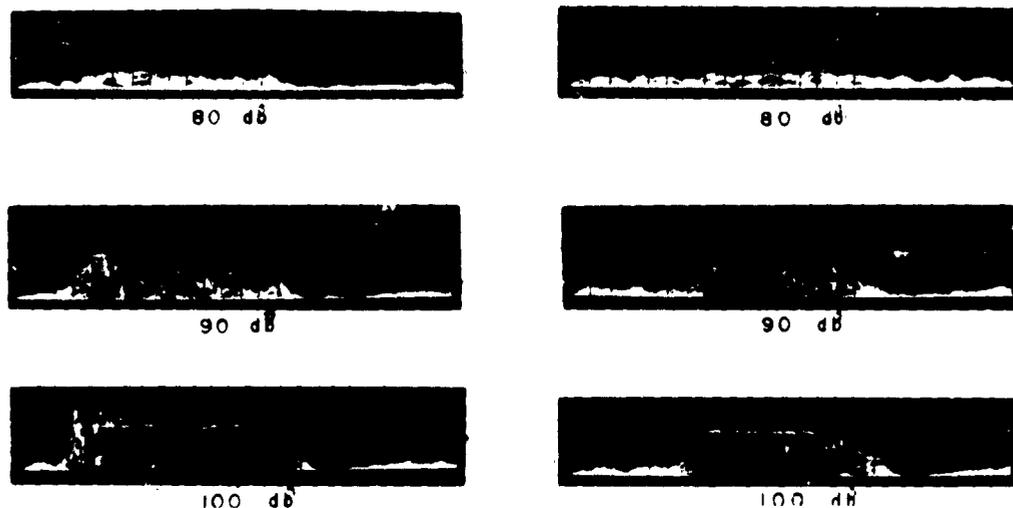100 dB   100 dB
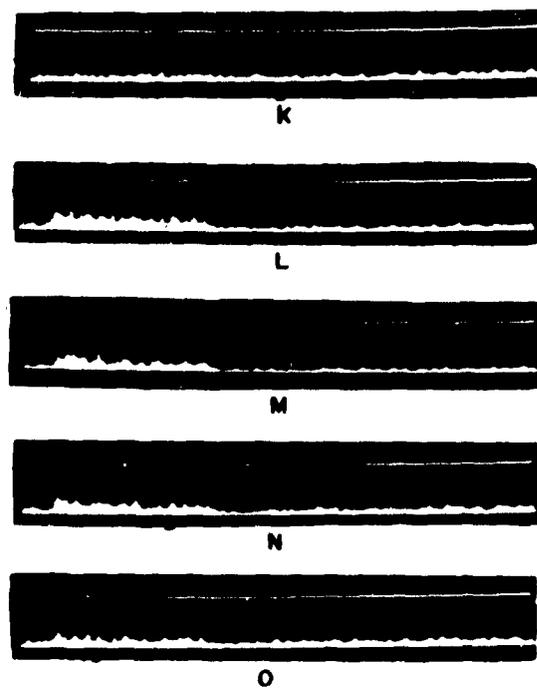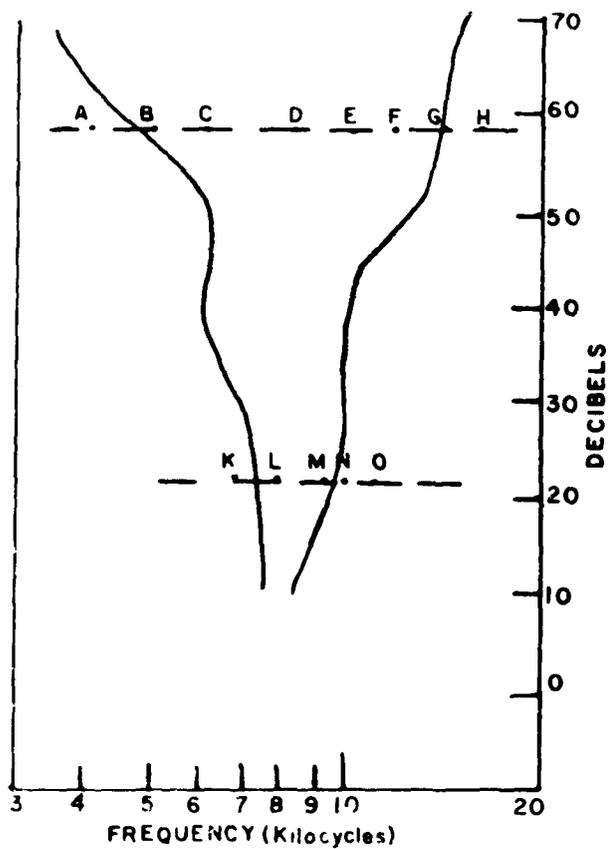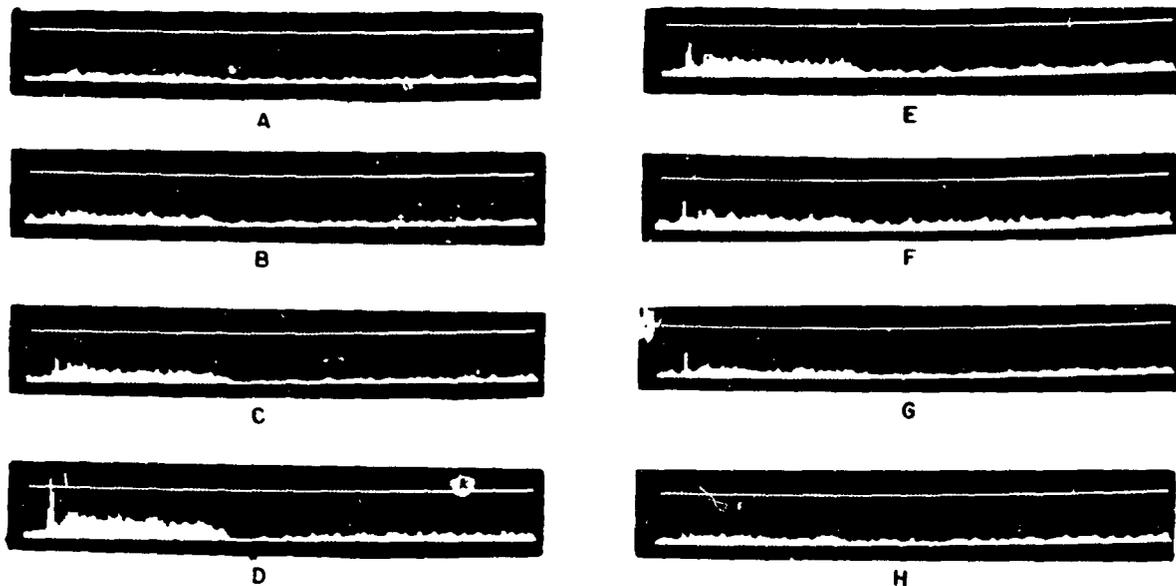
Figure 9.   Neuron Responding by a Striking Increase in
             Average Pulse Rate as Stimulus Amplitude is
             Increased. This fiber had no detectable
             response at 60 dB SPL. Moving-average rate
             analysis is used. Compare with figure 10.
             Left column has higher onset rate than right.

13

Figure 10. <u>Frequency Versus Amplitude Plot of a Single Neuron
Response Pattern</u>. Representative pulse occurrence
histograms are shown from the points indicated on
the graph A-O. The curved lines on the graph indicate
approximate thresholds at the various frequencies and
amplitudes. Cutoff is approximately 60 dB per octave.
Except for the burst of activity occurring at high onset
rates, there is little difference, in number of pulses,
between response (L) and response (D). There is nearly
a 40 dB difference in stimulus amplitude, however.
Again note variability in spontaneous (interstimulus)
activity. Stimuli are 110 msec duration; analysis periods
are 250 msec.

14

A

B

C

D

E

F

G

H

K

L

M

N

O

A   B   C   D   E   F G   H   60

K   L   M N   O

70

60

50

40

30

20

10

0

DECIBELS

3   4   5   6   7   8   9 10   20

FREQUENCY (Kilocycles)

15

Those fibers which, in the raw data, would be classified as "onset" detectors, are, on analysis, more likely rate-of-change detectors. When the stimulus onset rate was made sufficiently slow, these fibers could be made to fire slowly for rather protracted periods (figure 11, a & b). Such fibers usually had low rates of spontaneous firing.
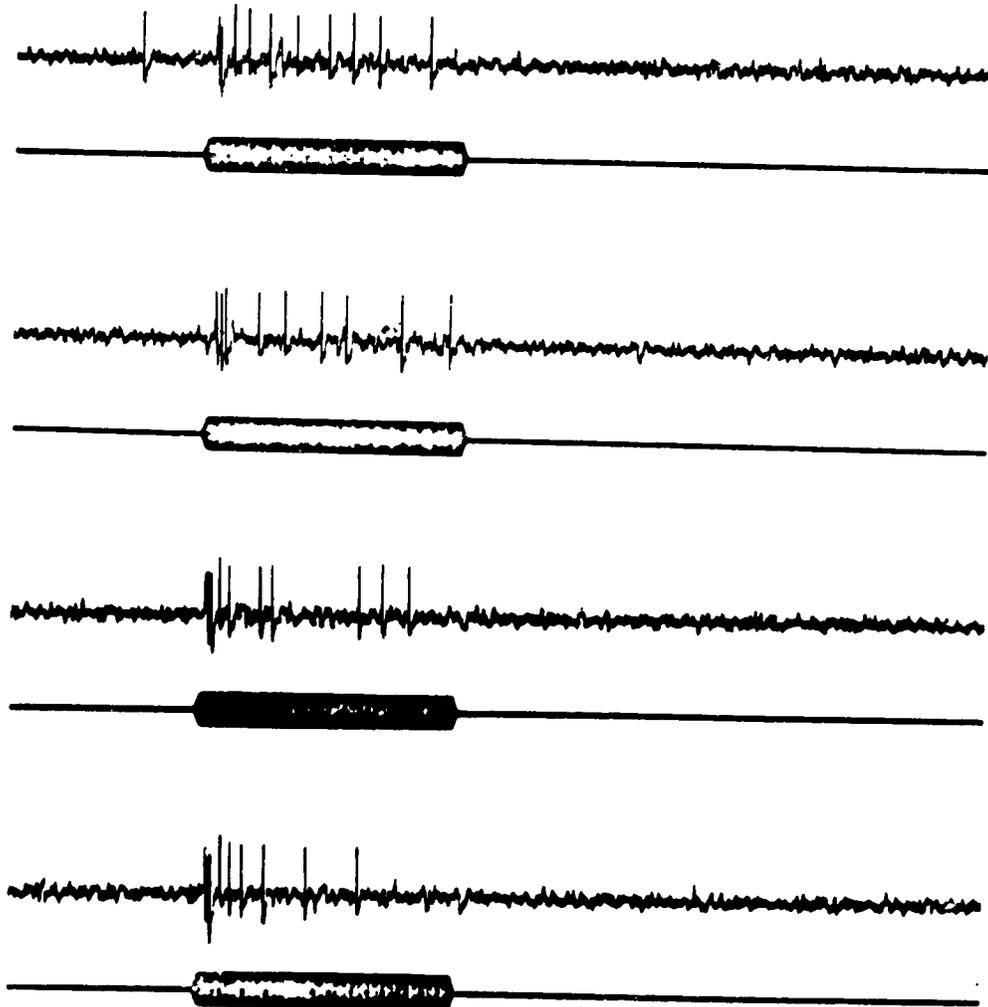
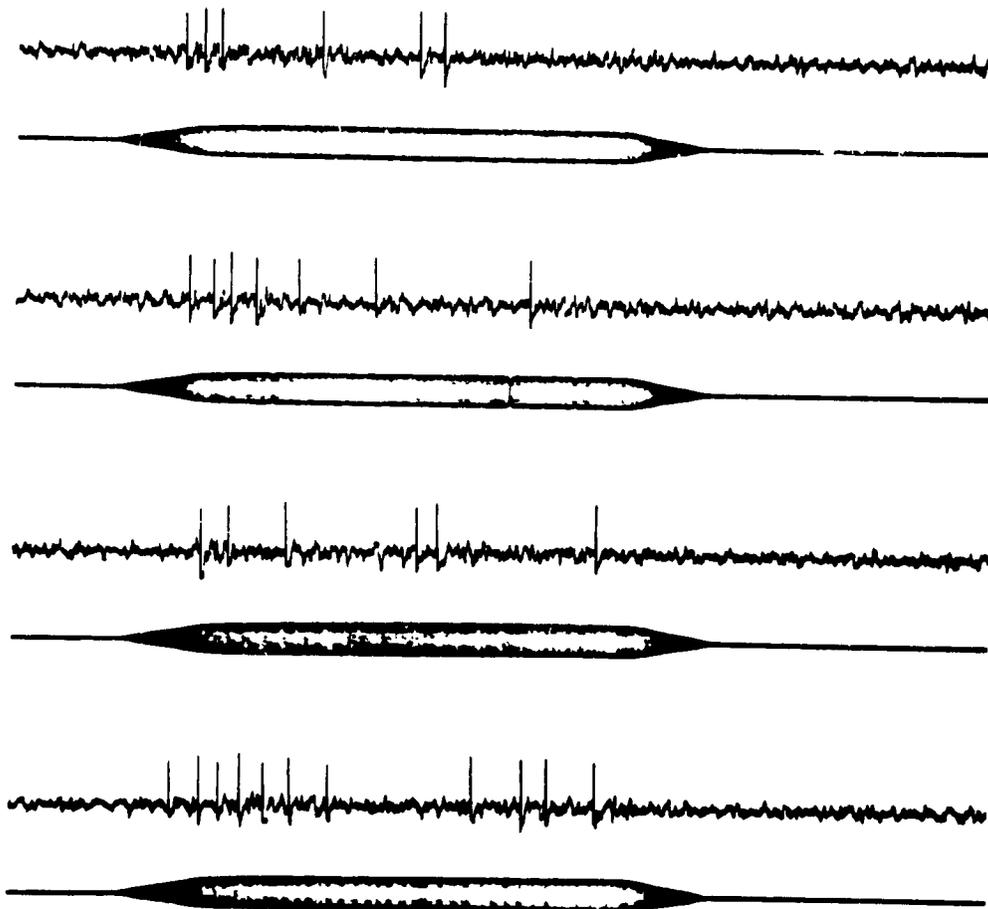Figure 11 (a). Fiber Responding Mainly to Onset.
Stimulus has high rate of onset.

16

Figure 11 (b). <u>Same Fiber as in 11a, with Stimulus having
Low Rate of Onset</u>. Note that this neuron
has a very low rate of spontaneous firing.

17

SECTION VI

COMMENT AND CONCLUSIONS

As this was a study of the auditory system as an information processor, attention was directed to the coding characteristics of the system. As mentioned in Experimental Methods, gross anatomical controls were used in some of the earlier experiments, and it is not definitely known whether these records were taken from first or second order neurones. By these methods, the coding characteristics of first and second order neurones are not readily distinguishable.

During a stimulus, the average rate of firing usually declines as the stimulus is prolonged. This could be fatigue, but more likely it is an active inhibition process, in view of the fact that in some fibers it diminishes to a level below that of spontaneous background activity. When the stimulus is turned off there is a sharp decrease in activity, which recovers towards resting rate. The temporal characteristics of diminution and recovery are fairly consistent with the observation of Fex (ref 2) in the cat cochlear inhibitory system, but no specific correlation with those results was attempted in this study.

These findings suggest that threshold drifts or is driven during stimulus, returning the rate of firing toward the resting rate. The deviation is usually minimum at best frequency, and tends to increase as stimulus frequency gets farther from best frequency. As this is followed through the frequency spectrum, it can be seen to account for some fibers which would be called "during" responders at some frequencies and "onset" responders at others. Although most fibers did not have this degree of alteration of their firing pattern, the tendency was characteristic.

Energy is transmitted along the basilar membrane in waves at the actual frequency of the stimulus, which gives one complete cycle of displacement for every cycle of the stimulus tone. At frequencies of several kilocycles, a neuron is incapable of response, but at lower frequencies, with periods of several milliseconds, many of the neurons observed could have fired with each successive wave of displacement.

The frequency specificity may be due mainly to the physical location of the units along the basilar membrane, but frequency information may be enhanced in a number of ways. One is by firing in synchrony with, or phase-locked to the signal, as has been observed with low tones. However, von Békésy's observations (ref 11) strongly suggest that the excitatory characteristics of nerve endings are the same for all tones. This simple phase-locking seems unlikely to be a major factor in view of the observation that the number of

pulses decreases during stimulus, at a rate dependent upon tonal distance from best frequency and background rate of spontaneous activity. However, this diminution mechanism can produce a great sharpening effect on frequency and amplitude information. It is quite possible that the phenomenon of phase-locking is only coincidental, and dependent on threshold recovery curve and availability for firing of the neuron.

It would be predicted on the basis of these observations that such a system, in which all units are sensitive to both frequency and amplitude changes, would lead to confusion, at times, between pitch and loudness changes, a phenomenon known to occur in man (ref 6).

Several conclusions were drawn from these observations.

1. Spontaneous activity in this system is highly irregular, but each fiber has a mean response rate or interval, about which pulses are distributed in a characteristic fashion. This mean rate of spontaneous firing appears to be subject to change under some circumstances.

2. The response characteristics of each cell appear to be determined, in large part, by the level of background activity, or, at least, are predictable on this basis.

3. There appears to be an active inhibitory system, which produces a contrast-effect by turning down response rate of neurons during stimulus, the degree of which is related to background rate of firing and tonal distance from best frequency of the neuron.

4. Stimulation to increased firing influences the poststimulatory firing rate for a significant period of time (in one instance seen, for at least 1 minute), thereby making repetition rate of serial signals an important parameter of the stimulus. In most cases observed, this poststimulatory influence was only a fraction of a second in duration.

5. The system is more sensitive to changes than to steady states, accounting for the rapid response fluctuations seen when the stimulus was turned on, off, or changed, as compared with the gradual drift towards a stable firing rate when the stimulus remained on or off. Rate of firing of cells appears to be closely related to rate of change of intensity and frequency.

6. From the extreme inconsistency of response patterns to identical stimuli, and for anatomical reasons, it seems unlikely that all the information about a stimulus is carried in a single response pattern. It seems more likely that each fiber in this multichannel system carries fragmentary information about the stimulus, which is summarized at a later stage of analysis.

7. It is proposed that the method of transmission of information is a modulation of the density of pulse occurrences in a population of neurons; the number of pulse occurrences in the population at any given time is actively increased and decreased to convey information. The information conveyed is primarily rate of change of frequency and amplitude, which is extracted at a later stage of analysis by means of spatial integration of a number of simultaneous responses.

19

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13 ABSTRACT

A number of first and second order neurons of the guinea pig auditory system were studied extensively in an attempt to determine the method by which information is conveyed. Single neuron electrophysiological techniques with anatomical controls were used in the study and in response to several different stimuli, various response patterns were observed. Statistical methods of analysis, using a digital computer, were employed. Each fiber in the auditory nerve appears to convey only fragmentary information; therefore, the information carried by a number of fibers is required to extract all the information about a single signal. The data suggest that a pulse density modulation system of encoding is used, in which the "carrier" appears to be the irregular spontaneous background activity, the pulse density of which is actively increased and decreased to convey information about both pitch and loudness. The system appears to be much more sensitive to sound changes than to absolute values. For example, pulse density correlated far better with rate-of-change of stimulus intensity than with absolute levels of intensity. In addition to frequency and amplitude, the interval between successive stimuli may be an important parameter of stimulation.

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