

XXI. COMMUNICATIONS BIOPHYSICS*

Prof. W. A. Rosenblith	Dr. J. W. Kuiper ^{‡‡}	G. E. Forsen
Prof. M. H. Goldstein, Jr.	Dr. T. T. Sandel	Mrs. Margaret Z. Freeman
Dr. J. S. Barlow [†]	W. A. Clark, Jr. ^{**}	C. D. Geisler
Dr. M. A. B. Brazier [†]	O. C. Gutierrez ^{***}	C. E. Molnar
Dr. Eda Berger [‡]	Aurice V. Albert	D. F. O'Brien
Dr. B. G. Farley ^{**}	J. Allan ^{†††}	W. T. Peake
Dr. G. L. Gerstein ^{††}	J. D. Cowan ^{‡‡‡}	R. W. Rodieck
Dr. N. Y-S. Kiang	A. H. Crist	T. F. Weiss

RESEARCH OBJECTIVES

This group continues to study the electrical activity of the nervous system with emphasis upon a quantitative and analytical treatment of specific responses to sensory stimuli and of so-called ongoing activity. We have made increasing use of special-purpose and general-purpose computers to the point where most of our experiments are now designed with a view toward data reduction by means of appropriate programs. This approach has been carried farthest in the "on-line" use of ARC-1 (average response computer, ref. 1), which, without delay, provides experimenters with numerically interpretable displays of average evoked responses.

Use of ARC-1 and of ERD (evoked response detector, ref. 2) has permitted us to carry further the analysis of potentials evoked by flashes (3, 4) and auditory stimuli (5, 6) and, in particular, has permitted us to detect responses – presumably of cortical origin – from the skull of awake subjects at stimulus intensities that are comparable to psychophysical thresholds (7).

A preliminary study of the combined effects of acoustic stimulation and electric stimulation of the auditory nerve has been reported (8). Certain adaptation phenomena in the somesthetic and auditory systems have been compared (9). The relation of intrinsic alpha activity to sensory after-discharges to photic stimulation has been further investigated (10). A technical report has been published (11) which summarizes a first study in the use of a general-purpose digital computer for giving a quantitative description of certain characteristic patterns in the electroencephalogram.

A review article (12) by Mary A. B. Brazier provides a historical perspective on the development of concepts relating to the electrical activity of the brain.

Our studies of statistical models for the description of evoked responses are being continued (13). An account of some of the earlier work has now appeared in print (14).

In psychophysical studies we have dealt with loudness judgments of clicks (15) and with reaction times to clicks delivered against a background of noise (16).

Completion of the construction of Eaton Peabody Laboratory of Auditory Physiology in the courtyard of Massachusetts Eye and Ear Infirmary has provided facilities for microelectrode studies and other physiological studies of the auditory system. Joint experimentation by members of Massachusetts Eye and Ear Infirmary and of the Research Laboratory of Electronics is under way.

W. A. Rosenblith

[See following page for references.]

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†From the Neurophysiological Laboratory of the Neurology Service of the Massachusetts General Hospital.

‡Postdoctoral Fellow of the National Institute of Mental Health.

**Staff Member, Lincoln Laboratory, M.I.T.

††Postdoctoral Fellow of the National Institute of Neurological Diseases and Blindness.

‡‡Sloan Postdoctoral Fellow of the School For Advanced Study, M.I.T.

***Doherty Foundation Fellow.

†††Ramo-Wooldrige Fellow in Systems Engineering.

‡‡‡Graduate Fellow of British Tabulating Machine Company, Ltd.

(XXI. COMMUNICATIONS BIOPHYSICS)

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A. DISPERSION MEASURES OF EVOKED ELECTROCORTICAL ACTIVITY

We recently programmed the TX-0 digital computer to provide a rough measure of the dispersion of the amplitude distributions seen at various fixed points in time following presentation of stimuli. A measure of dispersion is of interest to us because we feel that eventually with this information a logical reduction of the processes underlying evoked cortical activity, which is not possible on the basis of measures of central tendency alone, can be made.

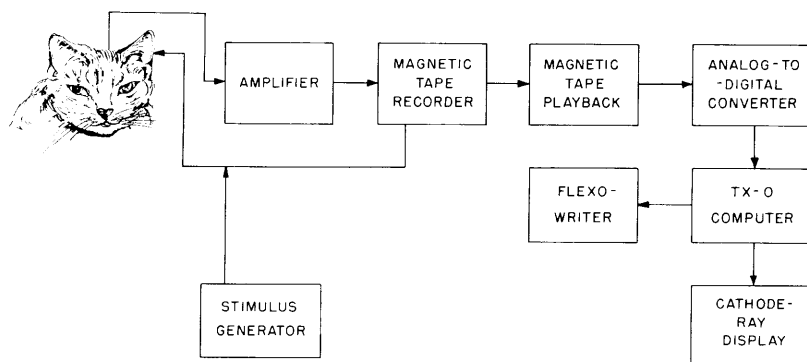


Fig. XXI-1. Block diagram of recording and computing procedure for TX-0 digital computer.

Figure XXI-1 is a block diagram of the system that we have employed. In keeping with methods previously used (1,2) the cortical signals are recorded and played back on FM magnetic tape. An analog-to-digital converter is used to provide an adequate input to the TX-0 computer. The computer has been programmed to calculate the median, the first and third quartiles, and the interquartile range for 8 time intervals or "instants." Programs have been written to display the amplitude histograms on a cathode-ray tube and to print the associated numerical values on a typewriter. Figure XXI-2 shows a typical display that was photographed from the cathode-ray tube. The numbers in the upper left-hand corner represent, from top to bottom: identification number; first quartile, Q_1 ; median, Q_2 ; third quartile, Q_3 ; absolute difference of Q_1 and Q_3 ; a crude measure of skewness ($2Q_2 - Q_1 - Q_3$); number of responses sampled.

When the information produced by these operations is plotted as a function of time, a representation such as that shown in Fig. XXI-3 is produced. Here, the points along the heavy line represent the medians of the amplitude distribution for the various instants of time following the presentation of the stimulus ($T=0$). The vertical bars represent the magnitude of the interquartile ranges around the

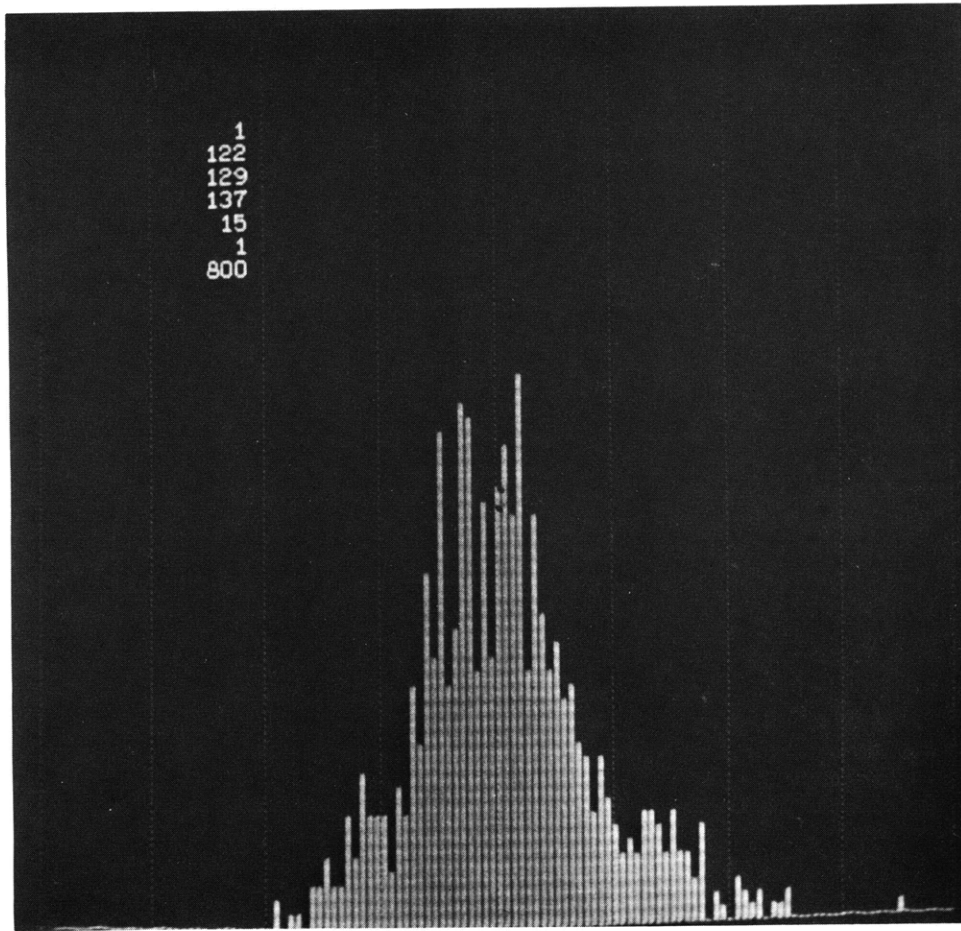


Fig. XXI-2. Amplitude histogram on TX-0 cathode-ray tube display.

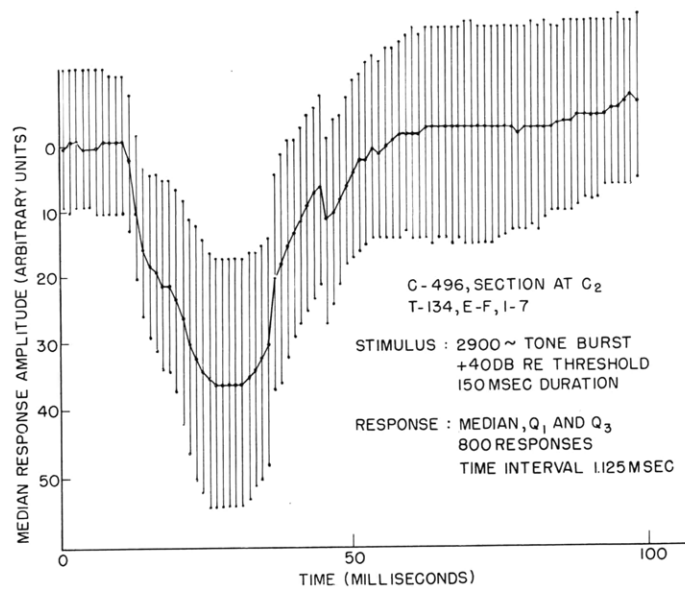


Fig. XXI-3. Medians and interquartile ranges as functions of time.

(XXI. COMMUNICATIONS BIOPHYSICS)

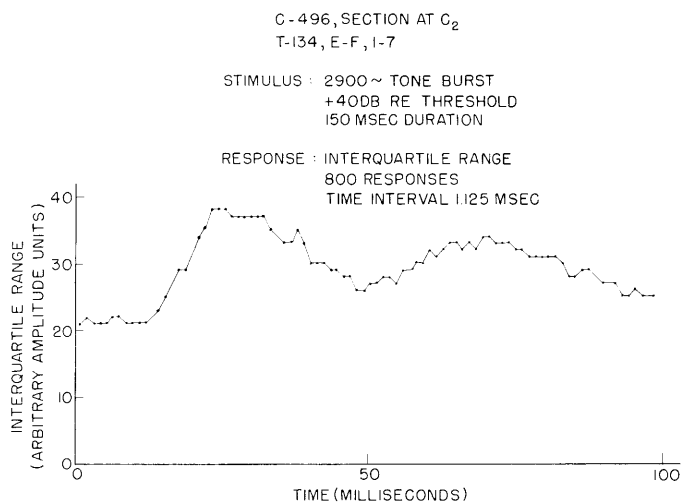


Fig. XXI-4. Absolute magnitude of interquartile range as a function of time.

corresponding medians. Figure XXI-4 shows the interquartile ranges plotted as magnitudes.

Figures XXI-3 and XXI-4 suggest that although the median of the late activity of evoked responses returns to values quite close to zero, the variability remains relatively high. This leads to the tentative conclusion that in some way a representation of a signal persists beyond the initial deflection that is ordinarily identified as the "early" or "late" components of evoked-response activity.

This conclusion gives us reason to believe that further study of measures of dispersion is pertinent to our investigations. We anticipate writing more elaborate programs for computing other possibly meaningful statistics of the process.

T. T. Sandel, T. F. Weiss, C. E. Molnar, G. L. Gerstein

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B. RESPONSE OF AN IDEALIZED NEURAL POPULATION TO A TRAIN OF REPETITIVE STIMULI

Electrophysiological responses to repetitive stimuli are of interest in studies of sensory systems in which such stimuli correspond in some ways to "natural" stimuli,

and as a means of studying the dynamical properties of the neural elements contributing to the responses. Here we shall consider a very simple statistical model of a population of "neural units." It is a zero-interaction model in which the dynamical properties of the units are described by a single random variable. The response is taken as the summated activity of the units of the population. The postulates defining the mathematical model are:

I. A population is composed of N statistically homogeneous units that have no mutual interaction.

II. At the presentation of a stimulus, each unit of the population either "fires" or "does not fire." Units do not fire spontaneously.

III. Recovery time, ξ , is the time interval required before a unit which has fired will be refired by a stimulus of given intensity. Recovery time for any unit is not a constant but is a random variable described by a probability density function. Since the units are statistically homogeneous, recovery time of each unit is described by the same probability density function. The random variable, ξ , is a function of stimulus intensity.

IV. The response, n_k , of the population to the k^{th} stimulus in a train is equal to the number of units that fire when this stimulus is presented. The relative response to the k^{th} stimulus is n_k/N .

In the postulated model there is no explicit consideration of a neural threshold. The fluctuating threshold of a unit and the recovery of responsiveness following the time when a unit fires are both represented in the random variable ξ .

We shall derive the relationship between the statistical average of the responses of a neural population to a train of repetitive stimuli and the probability density of recovery time. The averages would be obtained experimentally by presenting the train of stimuli to the preparation many times and averaging the responses to the first stimulus in the train to obtain $E(n_0)$, the responses to the second stimulus to obtain $E(n_1)$, and so forth. The relationship of these average responses to the probability density of ξ takes the form of difference equations, the solutions of which are the sum of two parts: a transient part, and a steady-state part. We shall consider both parts.

Assume that the population is excited by a train of stimuli occurring at times $0, T, 2T, \dots, kT, \dots$. Call the responses of the population to these stimuli $n_0, n_1, n_2, \dots, n_k, \dots$.

The expectation of n_{k+1} can be expressed by

$$E(n_{k+1}) = \sum_{n_{k+1}=1}^N P(n_{k+1}) \cdot n_{k+1} \quad (1)$$

in which $P(n_{k+1})$ is the probability distribution of n_{k+1} . It follows that

$$\begin{aligned}
E(n_{k+1}) &= \sum_{n_{k+1}=1}^N \sum_{n_k=1}^N P(n_{k+1} | n_k) P(n_k) n_{k+1} \\
&= \sum_{n_k=1}^N E(n_{k+1} | n_k) P(n_k)
\end{aligned} \tag{2}$$

We shall consider the case in which the probability density function of the recovery time ξ is zero for ξ greater than $2T$. Then

$$\begin{aligned}
\int_0^{2T} p(\xi) d\xi &= 1 \\
p(\xi) &= 0 \quad \xi \geq 2T
\end{aligned} \tag{3}$$

where T is the time between the stimuli of the train. Call

$$\int_0^T p(\xi) d\xi = P_1 \tag{4}$$

which gives the probability that a unit recovers in a time less than T . Consider the response at the time $(k+1)T$. If we know that n_k units fire at time kT , then from Eqs. 3 we know that the remaining $N - n_k$ units will fire at time $(k+1)T$. On the average, $P_1 \cdot n_k$ units will also re-fire at time $(k+1)T$. Thus

$$\begin{aligned}
E(n_{k+1} | n_k) &= N - n_k + P_1 n_k \\
&= N - n_k(1 - P_1)
\end{aligned} \tag{5}$$

Therefore

$$E(n_{k+1}) = \sum_{n_k=1}^N P(n_k) [N - n_k(1 - P_1)] \tag{6}$$

and it follows that

$$E(n_{k+1}) + (1 - P_1) E(n_k) = N \tag{7}$$

The solution (1) of this difference equation with the condition that $E(n_0) = N$ (i. e., all units fire in response to the first stimulus) is

$$E(n_k) = \frac{N}{2 - P_1} \left[(-1)^k (1 - P_1)^{k+1} + 1 \right] \tag{8}$$

The mean relative response,

(XXI. COMMUNICATIONS BIOPHYSICS)

$$E\left(\frac{n_k}{N}\right) = \frac{1}{2 - P_1} \left[(-1)^k (1 - P_1)^{k+1} + 1 \right] \quad (9)$$

is independent of N .

If instead of the condition of Eqs. 3 the probability density function

$$\int_0^{3T} p(\xi) d\xi = 1 \quad (10)$$

$$p(\xi) = 0 \quad \xi \geq 3T \quad (11)$$

with the notation

$$\int_0^T p(\xi) d\xi = P_1$$

$$\int_0^{2T} p(\xi) d\xi = P_2$$

By a similar procedure, we obtain the difference equation

$$E(n_{k+2}) + (1 - P_1) E(n_{k+1}) + (1 - P_2) E(n_k) = N \quad (12)$$

The roots of the homogeneous solution may be real, equal, or complex, as determined by whether

$$\left(\frac{1 - P_1}{2}\right)^2 \left\{ \begin{array}{l} > \\ = \\ < \end{array} \right\} (1 - P_2) \quad (13)$$

In Fig. XXI-5 an example of the solution of Eq. 12 with the initial condition $E(n_0) = N$ is presented for each of the three conditions of Eq. 13. The parameters have been chosen so that the three examples have identical steady-state behavior.

Following the same procedure, we can derive the difference equation for the mean response in the general case in which

$$p(\xi) = 0 \quad \xi \geq RT$$

$$\int_0^{RT} p(\xi) d\xi = 1 \quad (14)$$

The resulting expression is

$$E(n_{k+R-1}) + \sum_{m=0}^{R-2} E(n_{k+m}) (1 - P_{R-1-m}) = N \quad (15)$$

where

$$\int_0^{sT} p(\xi) d\xi = P_s \quad s = 1, 2, \dots, R-1$$

The steady-state solution of this general case has the form

$$E(n_k)_{ss} = \frac{N}{R - \sum_{m=1}^{R-1} P_m} \quad (16)$$

The relative steady-state response is plotted against frequency for three different $p(\xi)$ in Fig. XXI-6. Note that a continuous $p(\xi)$ (Fig. XXI-6a) leads to a continuous decrease in response as a function of frequency; a sharply truncated $p(\xi)$ (Fig. XXI-6b) corresponds to a "scalped" function; and the limiting case, in which recovery time has some given value T_0 (with a probability of 1) corresponds to the staircase function (Fig. XXI-6c). The third case would result if the response of a neural population to repetitive stimuli were viewed in the light of the simplest interpretation of the Wever volley principle (2).

Further theoretical work will include investigation of statistics other than the expectation.

The present work is in some respects an extension of the model discussed by

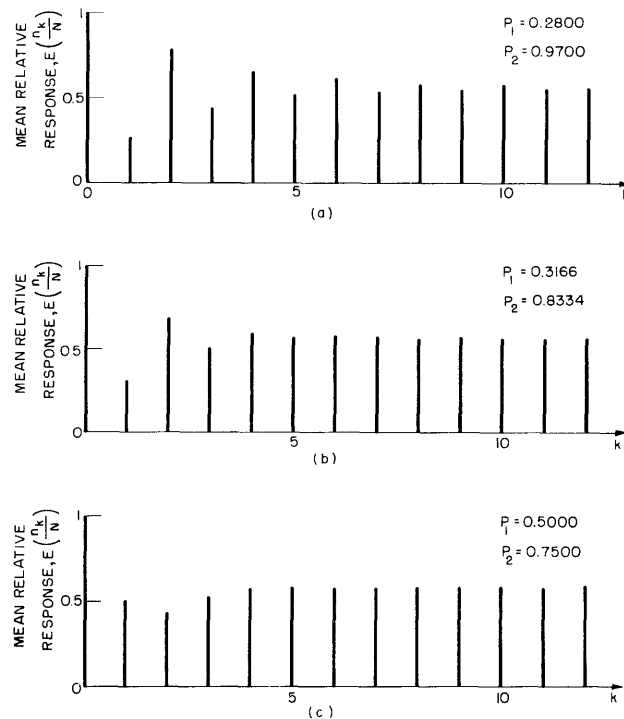


Fig. XXI-5. Mean relative response to a train of stimuli for three conditions.

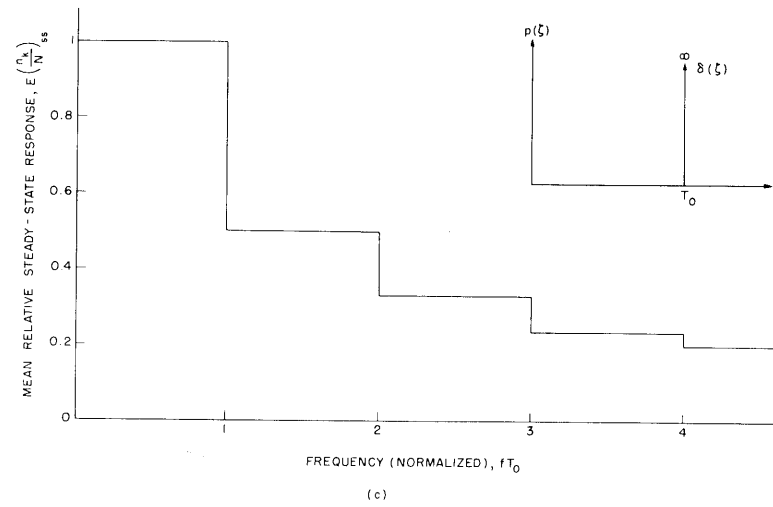
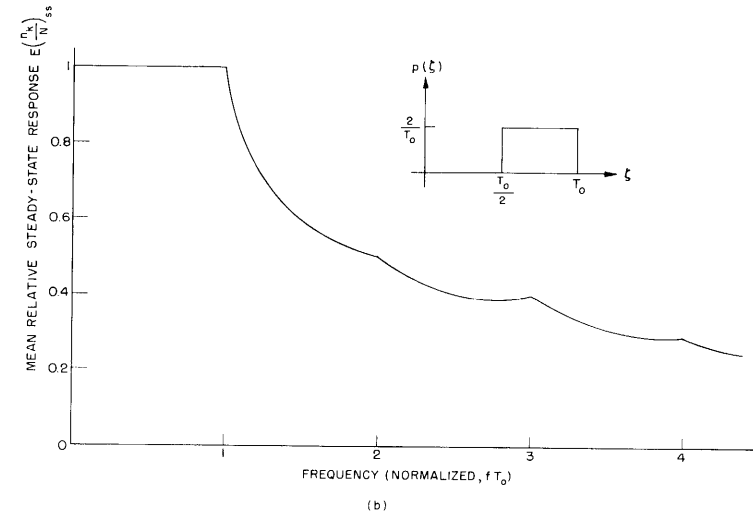
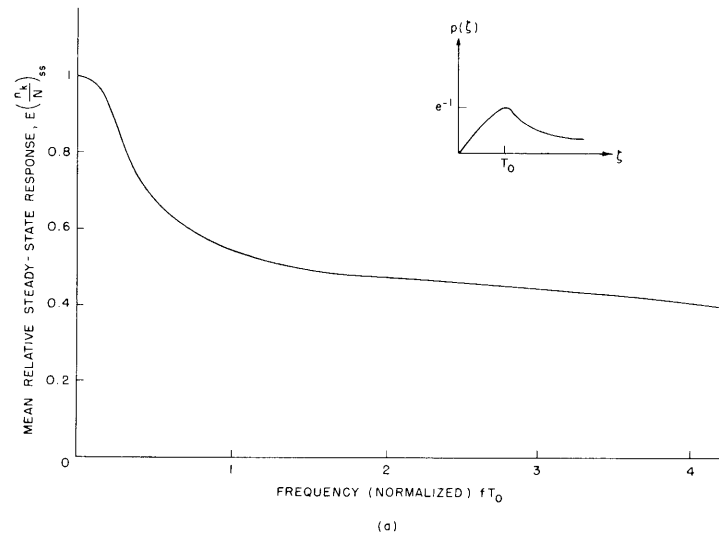


Fig. XXI-6. Mean relative steady-state response versus normalized frequency for three $p(\xi)$.

Frishkopf and Rosenblith (3). A treatment of steady-state responses similar to ours was derived independently by David (4).

R. W. Rodieck, M. H. Goldstein, Jr.

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C. AN INVESTIGATION OF THE FINITE-TIME SAMPLE AUTOCORRELATION FUNCTION OF THE EEG

(This report is an abstract from a forthcoming thesis for the degree of Master of Science, Department of Electrical Engineering, M.I. T.)

The autocorrelogram (machine-computed estimate of an autocorrelation function) of the electroencephalogram (EEG) of many human subjects has been known to show a considerable amount of cyclic activity at large values of delay (see Fig. XXI-7). There has been some conjecture concerning the physiological significance of this apparent marked in-phasesness in the EEG when it exhibits the 10-cps alpha rhythm. The present investigation attempts to demonstrate that this type of cyclic behavior may be explained by the finite length of the time sample used for computing the autocorrelation function.

In general, the autocorrelation function of a stationary, random time series is defined as

$$\phi_x(\tau) = \lim_{T \rightarrow \infty} \frac{1}{2T} \int_{-T}^T x(t) x(t-\tau) dt \quad (1)$$

By machine computation methods (1) an estimate of this function can be obtained by computing the function

$$\phi_x(T, \tau) = \frac{1}{T} \int_0^T x(t) x(t-\tau) dt \quad (2)$$

This finite-time sample autocorrelation function is, itself, a random variable with parameters T and τ . Thus far, the problem of finding the probability density function of this random variable has not been solved (2). Davenport (3) and others have, however, given the following expressions for the mean and second moment

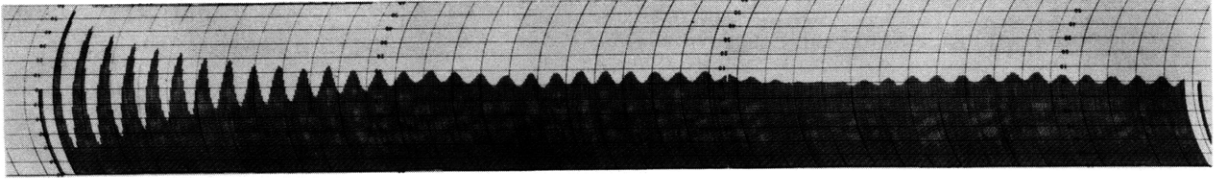


Fig. XXI-7. Correlogram of EEG of a "resting" subject (left parieto-occipital used). Sample length, 3 minutes; maximum delay, 4.6 sec; delay increment, 6.25 msec.

of the finite-time sample autocorrelation function:

$$E[\phi_x(T, \tau)] = \phi_x(\tau) \quad (3)$$

$$E[\phi_x^2(T, \tau)] = \frac{2}{T} \int_0^T \left(1 - \frac{\tau_0}{T}\right) E[x(t) x(t-\tau) x(t-\tau_0) x(t-\tau-\tau_0)] d\tau_0 \quad (4)$$

Equation 4 shows that the fourth-order moment of the random variable x_t must be known in order to estimate a measure of the errors of a finite observation time on the autocorrelation function of x_t . It can be shown, however, that $\phi_x(T, \tau)$ converges in the mean to $\phi_x(\tau)$ as T approaches infinity (4).

For the particular, and very interesting, case of a Gaussian random variable with zero mean, the fourth-order expectation factors and the variance can be shown to be

$$\sigma_\phi^2(T, \tau) = \frac{2}{T^2} \int_0^T (T - \tau_0) \left\{ \phi_x^2(\tau_0) + \phi_x(\tau + \tau_0) \phi_x(\tau_0 - \tau) \right\} d\tau_0 \quad (5)$$

Now consider the case in which $\phi_x(\tau)$ is a narrow-band, quadratic function such as

$$\phi_x(\tau) = e^{-a|\tau|} \cos \omega_0 \tau \quad (6)$$

where $2a$ is the bandwidth, and ω_0 the central frequency. For a value of T that is large compared with the maximum value of τ , and for a value of τ that is large compared with $\frac{1}{a}$, the variance can be shown to approximate

$$\sigma_\phi^2(T, \tau) \approx \frac{1}{2aT} \quad (7)$$

Similar results were derived independently by Bendat (5).

Equation 7 indicates that for values of delay that are large compared with the time

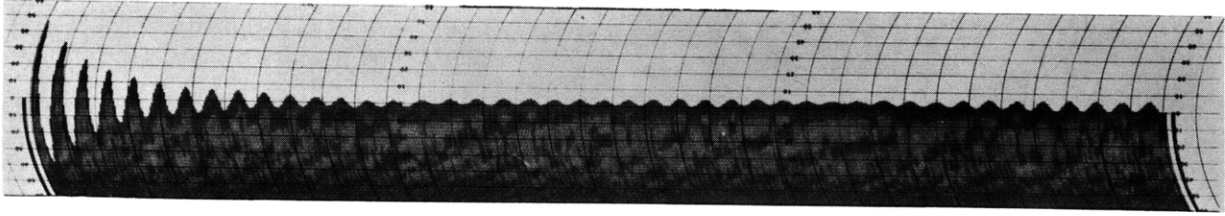


Fig. XXI-8. Correlogram of narrow-band, Gaussian noise (central frequency, 237 cps; bandwidth, 13.2 cps). Sample length, 7.5 sec; maximum delay, 185 msec; delay increment, 0.25 msec.

constant of the autocorrelation functions, the ratio of "signal" (autocorrelation function) to "noise" (variance of the finite-time sample autocorrelation function) is very low. Consider the form of the finite-time sample autocorrelation function for large values of delay. Figure XXI-8 shows this function computed for narrow-band, Gaussian noise. Note the recurrence of the cyclic activity at large values of delay for which the theoretical autocorrelation function is essentially zero. Figure XXI-8 suggests that successive samples of the finite-time sample autocorrelation function for large delay are correlated, whereas the samples of the theoretical autocorrelation function are uncorrelated for large delay. Consider the correlation of two samples of the finite-time sample autocorrelation function separated by an interval of delay τ'

$$\mu = E[\phi_x(\tau, T) \phi_x(\tau + \tau', T)] \quad (8)$$

The random process x_t is again assumed to be a narrow-band, Gaussian noise with zero mean, and τ is assumed to be large enough so that x_t and $x_{t-\tau}$ can be assumed to be statistically independent. After some manipulations, Eq. 8 can be shown to approximate

$$\mu \approx \frac{1}{2\alpha T} e^{-\alpha\tau'} \cos \omega_0 \tau' \quad \text{for } \tau' \geq 0 \quad (9)$$

which means that the errors attributable to the finite time of observation of $\phi_x(\tau)$ give rise to cyclic activity in the finite-time sample autocorrelation function, as has been shown experimentally. Further experimental work has been done to confirm the fact that the cyclic activity at large delays decreases as the sample length is increased. If statistically independent samples of noise are used for the computation of each point in the correlogram, then the cyclic activity at large values of delay is replaced by random activity, as shown in Fig. XXI-9.

It has been shown, therefore, that the long-delay cyclic activity of the finite-time sample autocorrelation function of narrow-band, Gaussian noise results from the errors

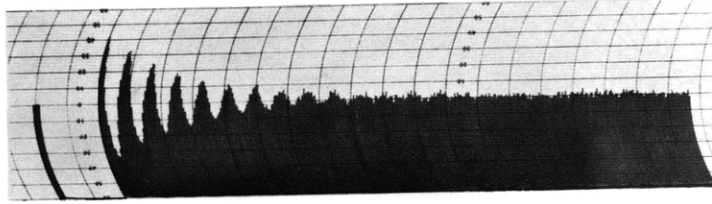


Fig. XXI-9. Correlogram of narrow-band, Gaussian noise (central frequency, 237 cps; bandwidth, 13.2 cps) computed from statistically independent samples for each point of delay. Sample length, 7.5 sec; maximum delay, 90 msec; delay increment, 0.25 msec.

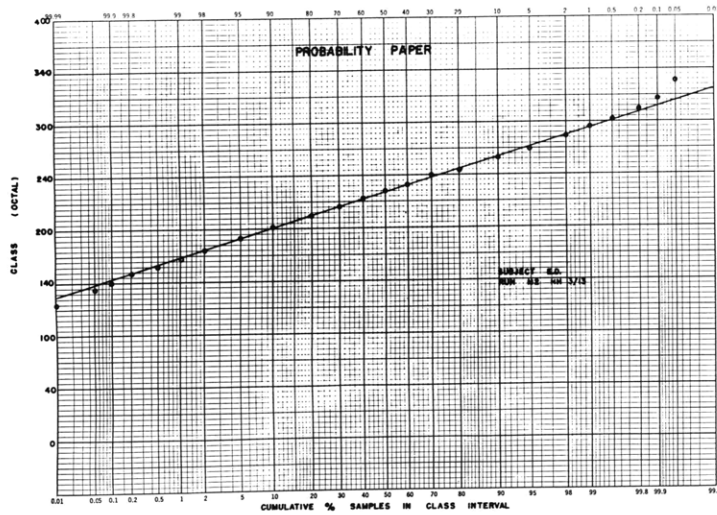


Fig. XXI-10. Cumulative histogram of EEG of a "resting" subject plotted on probability paper (50,000 samples).

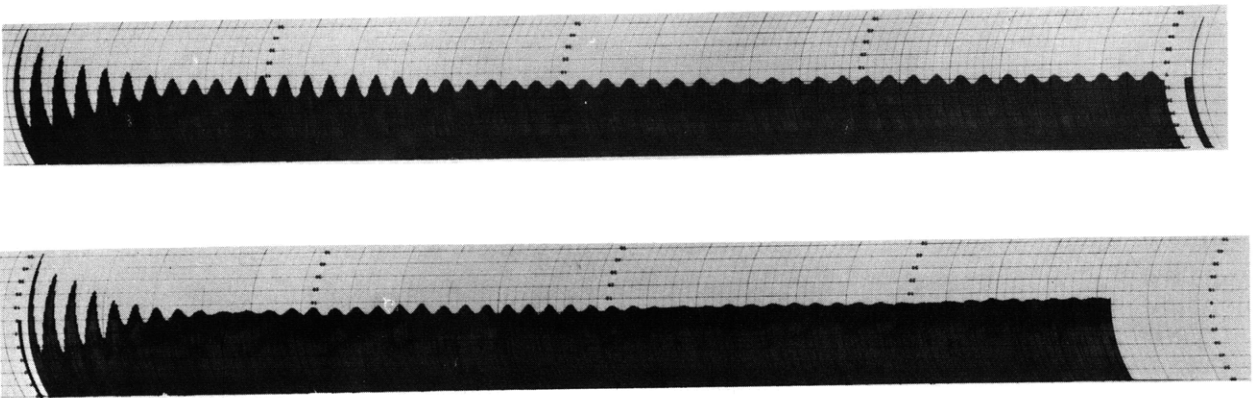


Fig. XXI-11. Correlograms of EEG of a "resting" subject for two values of sample length of EEG (left parieto-occipital used). Sample length (top), 100 sec, (bottom), 400 sec; maximum delay, 4.6 sec; delay increment, 6.25 msec.

caused by the finite-time sample.

The implications of these results on the problem of estimating the autocorrelation function of the EEG are not entirely clear. Certainly, the EEG's of many subjects in the "relaxed state" exhibit alpha activity which results in correlograms that resemble those of the narrow-band noise signal (witness Figs. XXI-7 and XXI-8). Preliminary tests on the histogram of amplitudes of the EEG of a few subjects indicate that a Gaussian distribution can be fitted reasonably well to the central part of the curve. Figure XXI-10 shows one such histogram plotted on probability paper, which plots Gaussian distributions as straight lines. However, the narrow-band noise model is a stationary model, and it has been shown that some statistics (6) of the EEG of a subject deprived of auditory and visual stimulation decrease with time (7). Thus all of the statistics of the EEG computed here must be considered as time-average statistics, and the narrow-band noise model must be interpreted as being a model of these time-average statistics.

For a sample from a single subject whose EEG shows little time dependence in its statistics, our model has been verified. Figure XXI-11 shows the autocorrelograms of this subject for sample lengths of 100 and 400 seconds. Note the decrease of the amplitude of the long-delay cyclic activity, which indicates strongly that this cyclic activity is a result of the finite length of the sample of EEG processed. An estimate of the root-mean-square values of the long-delay cyclic activity for the two correlograms yields a ratio of 2.2, as opposed to a predicted value of 2.

T. F. Weiss

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