

XIII. COMMUNICATIONS BIOPHYSICS

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A. A PROBABILISTIC APPROACH TO CERTAIN NEUROELECTRIC PHENOMENA

1. Basic Data

An acoustic stimulus presented at the ear of an anesthetized cat evokes an electrical response from the auditory nerve of that animal. Our primary stimuli to date have been clicks produced by feeding rectangular pulses of duration 0.1 msec into a PDR-10 ear-
phone. These short stimuli evoke spike-like responses, which are detected by a fine wire electrode placed within the bullar cavity. Suitable electrode placement makes these click responses substantially free of microphonic contamination (1, 2). A typical response is shown in Fig. XIII-1.

The earliest neural component, labeled N_1 , can be assumed to represent the synchronous and summated firing of first order auditory neurons. The peak-to-peak amplitude of N_1 (A_{pp}), taken as a measure of total activity, when plotted against the stimulus intensity (S), yields a monotonic function (Fig. XIII-2) referred to hereafter as the intensity function ($A_{pp} = f(S)$) (2). Each datum point represents the average of ten or more measurements.

If the click is presented in a background of continuous white noise (limited by the

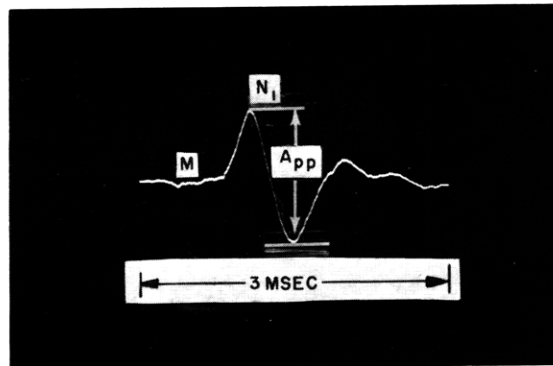


Fig. XIII-1

Typical peripheral response to click (-30 db re 1.29 volts) with very little microphonic content. M, microphonic; N_1 , first neural component; A_{pp} , peak-to-peak amplitude.

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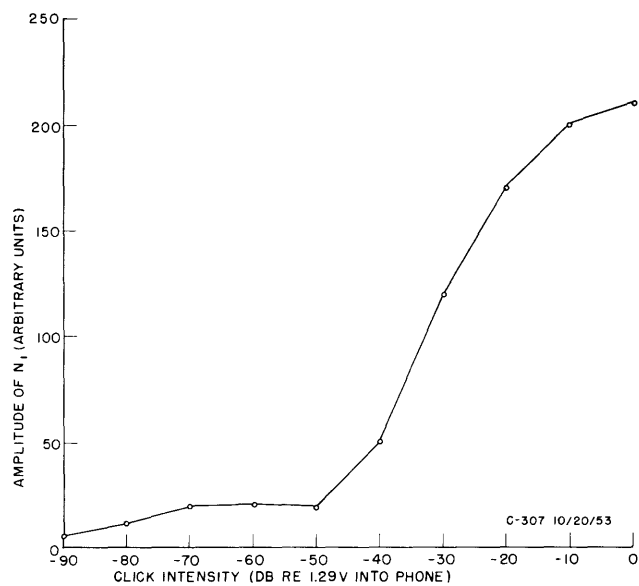


Fig. XIII-2

Intensity function obtained from Cat C-307. This is fairly typical of the functions obtained from animals whose thresholds seem to be normal.

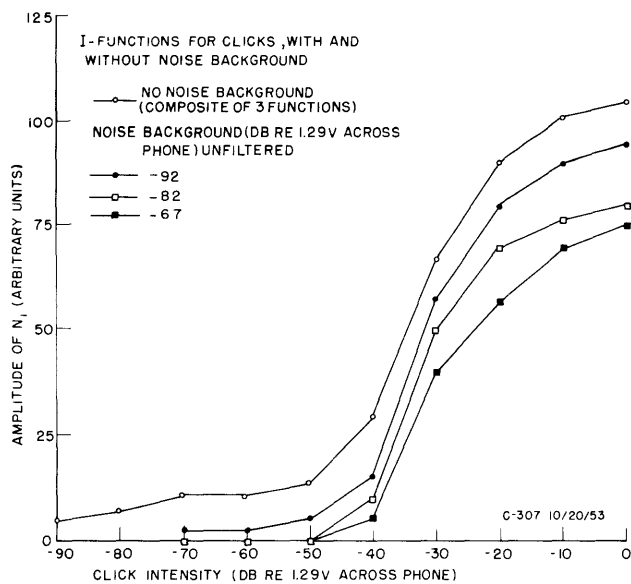


Fig. XIII-3

Masked and unmasked intensity functions.

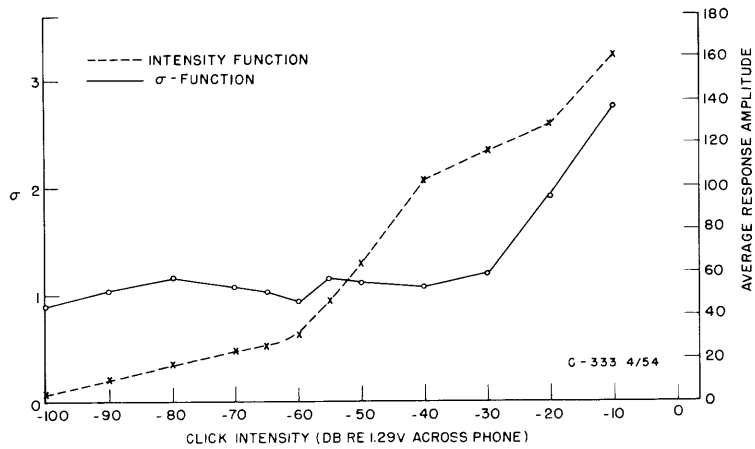


Fig. XIII-4

Standard deviation of response amplitudes to a given stimulus intensity plotted as a function of stimulus intensity. Each point is based on about 100 responses. Plotted with it (dashed line) is the intensity function obtained from the same data.

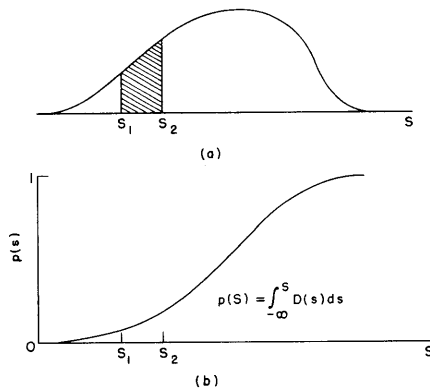


Fig. XIII-5

(a) A possible threshold probability distribution function, $D(S)$. The shaded area equals the probability of finding the threshold in the interval S_1 to S_2 . The total area under the curve is 1.
 (b) $p(S)$, the probability of a unit responding to stimulus S .

(XIII. COMMUNICATIONS BIOPHYSICS)

characteristics of the system that delivers the acoustic stimulus), the peak-to-peak amplitude of N_1 is reduced. Plotting this amplitude vs. click intensity for a fixed noise level yields (3) a modified, or masked, intensity function, $A_M = f(S, N)$. Several such masked functions for several noise levels, together with the corresponding unmasked functions, are presented in Fig. XIII-3. Each point represents the average of the peak-to-peak amplitude of ten or more responses to identical stimuli.

We have studied the variability of these response amplitudes and have shown (4) that many more than ten responses to a single stimulus intensity were needed to obtain a statistically meaningful measure of variability. From a sequence of 100 responses to a given stimulus setting, the standard deviation of the peak-to-peak amplitudes was determined for a number of stimulus values. The resultant function, $\sigma = f(S)$, is plotted in Fig. XIII-4.

2. The Model

The neural unit is the elemental concept of our model. Its relation to the basic physiological entities, the neuron, the sense-cell, and the junction between them, has been discussed in previous reports (2, 3).

The neural unit has the following properties:

- a. It obeys the all-or-none law; that is, it is characterized by only two states, maximal response or no response.
- b. Its threshold, or "triggering level" of stimulation, fluctuates in time. No attempt is made to specify the detailed time course of this fluctuation. Rather, the description is limited to a specification of the fraction of the time the unit spends in any threshold interval, i. e., by a threshold probability distribution, Fig. XIII-5. It is, in addition, assumed that the characteristic time of fluctuations is very small compared to the interval (about two seconds) between stimulus presentations.
- c. The firing of a unit alters its threshold distribution, which then becomes a function of the time $\Delta\tau$ since firing. For times $\Delta\tau$ that are sufficiently long (greater than 0.1 sec) the unit returns to the resting distribution. For $\Delta\tau$'s that are less than 2 msec the unit will respond to no stimulus, whatever its intensity. This time interval is called the absolute refractory period of the elemental unit.

Our model requires a second concept: a population of neural units; that is, an aggregate of neural units whose properties a, b, and c involve identical parameters.

The present model assumes that at least two populations of neural units are contributing to the peak-to-peak amplitude of the responses. This classification is based mainly on differences in mean threshold values, with each unit labeled as either sensitive or insensitive. It may eventually be found necessary to subdivide one or both of these populations into subpopulations.

No interaction between neural units has been introduced explicitly into the model.

Moreover, the threshold fluctuations occurring in any two units are assumed to be statistically independent.

3. The Model and the Data; Predictions

A single neural unit, presented with a stimulus S , will respond if its threshold is less than or equal to S and not otherwise. If the threshold probability distribution (Fig. XIII-5(a)) is represented by $D(S)$, then the probability of finding the unit with threshold less than S , and therefore the probability that the unit will respond to a stimulus S , is given by (Fig. XIII-5(b))

$$p(S) = \int_{-\infty}^S D(s) ds \quad (1)$$

A single population of neural units, all of which have the same threshold probability distribution $D(S)$, gives rise to an intensity function

$$A(S) = rN p(S) = rN \int_{-\infty}^S D(s) ds \quad (2)$$

where r is the magnitude of the response of a single unit and N is the number of units in the population. If a single population were involved, the function $D(S)$ could be inferred at once by differentiating the observed intensity function and making use of the normalization

$$\int_{-\infty}^{+\infty} D(s) ds = 1 \quad (3)$$

If we are dealing with two independent populations, we obtain

$$A(S) = A_1(S) + A_2(S) = r_1 N_1 \int_{-\infty}^S D_1(s) ds + r_2 N_2 \int_{-\infty}^S D_2(s) ds$$

where the subscripts 1 and 2 refer to the two populations. The situation is particularly simple if $D_1(S)$ and $D_2(S)$ are disjoint (Fig. XIII-6). Then again differentiation plus the normalization conditions

$$\int_{-\infty}^{+\infty} D_1(s) ds = 1 \quad , \quad \int_{-\infty}^{+\infty} D_2(s) ds = 1$$

permit immediate inference of $D_1(S)$ and of $D_2(S)$. If the distributions overlap,

(XIII. COMMUNICATIONS BIOPHYSICS)

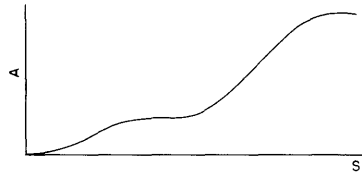


Fig. XIII-6

The type of intensity function obtained from two disjoint, or nearly disjoint, populations.

separation in the region of overlap on the basis of the observed intensity function is no longer possible.

The unmasked intensity functions of Figs. XIII-2 and XIII-3 are of the type shown in Fig. XIII-6 and are, therefore, interpretable within a framework of fluctuating threshold and two populations. Indeed, it was data of this sort that originally suggested the two populations hypothesis.

We now apply the model to the problem of masking. A population characterized by fluctuating thresholds and a period of nonresponsiveness after firing could be rendered nearly incapable of responding to a stimulus, such as a click, by a continuous stimulus such as noise, even at a very low level. This conclusion is reached in the following manner (3): neural units continually drop in threshold below the average level of the masking noise, and fire. The "location" of the noise in the distribution determines the rate at which such firing occurs. The weaker the noise, the less often a unit fires. If threshold fluctuation is sufficiently rapid, nearly all units will have fired in response to even a weak noise in the 2 msec preceding the click. Hence practically all units will be absolutely refractory at the time the click is presented, and none will respond to it.

If a second population is present as well, whose threshold range lies far above the noise level, it will not be affected. As the noise level is further raised, the number of units belonging to this population that respond to the click will also decrease. The data of Fig. XIII-3 support these predictions. They show that a weak noise eliminates the sensitive population completely, leaving the growth of the insensitive portion of the intensity function substantially intact. A still weaker noise permits the appearance of a partial response from the sensitive population. As suggested above, the noise level at which the masked response is, for example, one half as large as the unmasked response, depends on the rate of threshold fluctuation. On the basis of a simple model of fluctuations, involving random transitions between threshold states, this calculation has been carried out and the rate determined (3). The characteristic time of occupancy of a threshold state is found from these data to lie between 0.25 msec and 0.5 msec.

The significant features of the masking curves are thus seen to follow from the assumptions of the model.

(XIII. COMMUNICATIONS BIOPHYSICS)

Finally, let us inquire as to the variability in response amplitudes expected on the basis of this model. At a given level of stimulation, S , the probability of a unit firing is $p(S)$. The probability that exactly n units out of a population of N will fire is

$$P(n) = \binom{N}{n} p^n (1-p)^{N-n} \quad (4)$$

Plotted as a function of n , $P(n)$ is peaked at $n = Np$; for sufficiently large N , $P(n)$ may be fitted by a gaussian distribution. Such a fitting procedure yields the result that

$$\sigma = [Np(1-p)]^{1/2} \quad (5)$$

If we introduce now an explicit dependence on S ,

$$\sigma(S) = [Np(S)(1-p(S))]^{1/2}$$

For $A = rn$, $P^*(A) = P(n)$, where $P^*(A)$ is the probability of a response amplitude A . Since the distributions $P(n)$ and $P^*(A)$ are related by a scale factor r , it follows that the standard deviation of response amplitudes to a stimulus S is given by

$$\sigma^*(S) = r\sigma(S) = r [Np(S)(1-p(S))]^{1/2}$$

The average, and most probable, response is given by

$$A_{av}(S) = rNp(S) \quad (6)$$

This expression is, of course, the intensity function (Eq. 2). Figures XIII-7(a) and XIII-7(b) show an intensity function for one population and the corresponding function $\sigma^*(S)$. Note that for both very strong and very weak stimuli, $\sigma^*(S) = 0$, since for a maximal stimulus ($p(S) = 1$) all units respond all of the time, while for a minimal stimulus ($p(S) = 0$) no unit will ever respond. $\sigma(S)$ is maximal for S such that $p(S) = 1/2$. The relative variability, given by

$$\frac{\sigma^*(S)}{A_{av}(S)} = \frac{1}{N^{1/2}} \left[\frac{1-p(S)}{p(S)} \right]^{1/2} \quad (7)$$

is determined primarily by the population size.

If, in addition, a stimulus-independent source of variability is present (for instance, amplifier noise) the total standard deviation of the response is

$$\sigma_T(S) = \left[(\sigma^*(S))^2 + \sigma_A^2 \right]^{1/2} \quad (8)$$

Here σ_A represents all additional sources of variation and is assumed to be independent of S . Figure XIII-7(c) shows the function σ_T for a given value of σ_A .

If two more or less disjoint populations are involved, one would expect $\sigma_T(S)$ to have

(XIII. COMMUNICATIONS BIOPHYSICS)

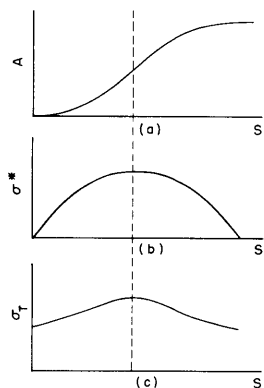


Fig. XIII-7

(a) A one-population intensity function for a gaussian threshold probability distribution. (b) The corresponding function $\sigma^*(S)$ predicted from the model. (c) The function $\sigma_T(S)$ obtained from the model for a given value of σ_A .

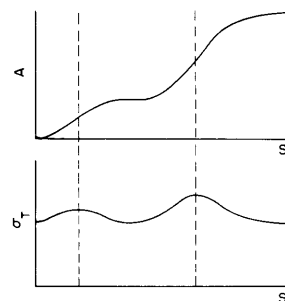


Fig. XIII-8

(a) A two-population intensity function. (b) A corresponding function $\sigma_T(S)$ of the kind predicted by the model.

two peaks. The peaks occur at $p_1(S) = 1/2$ and at $p_2(S) = 1/2$; here the subscripts 1 and 2 refer to the two populations. Figure XIII-8 shows both σ_T and the corresponding intensity function for the two-population case.

If we compare σ_T from Fig. XIII-8 with the variability data of Fig. XIII-4 there is good qualitative agreement with the prediction of the model in the range of the sensitive population. The experimental curve $\sigma(S)$ exhibits a peak at a point where on the basis of the intensity function we conclude that approximately 50 per cent of the units of the sensitive population have contributed. $\sigma(S)$ for the insensitive population does not show the expected behavior. This may be due to our inability to deliver a truly maximal stimulus. Such a stimulus might, of course, overload the mechanical system of the cat's ear.

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References

1. W. A. Rosenblith, M. R. Rosenzweig, Electrical responses to acoustic clicks: influence of electrode location in cats, *J. Acoust. Soc. Am.* 23, (September 1951).
2. Quarterly Progress Report, Research Laboratory of Electronics, M. I. T., Oct. 15, 1953, pp. 45-50.
3. Quarterly Progress Report, Research Laboratory of Electronics, M. I. T., Jan. 15, 1954, pp. 67-70.
4. Quarterly Progress Report, Research Laboratory of Electronics, M. I. T., July 15, 1954, p. 80.

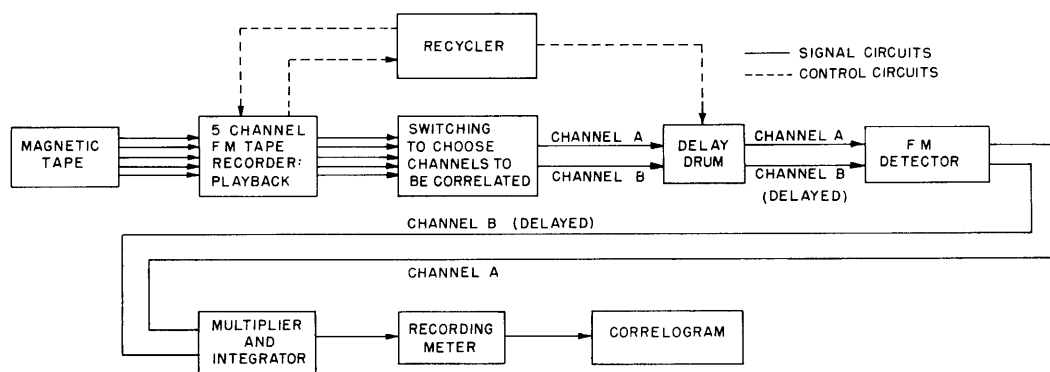


Fig. XIII-9

Block diagram of analog correlator.

B. ANALOG CORRELATOR FOR ELECTROENCEPHALOGRAPHY

With the completion of the recycler and magnetic delay drum (with associated electronics) the analog correlator (Fig. XIII-9) has successfully produced a correlogram from a tape-recorded EEG. The delay drum has already been described (1, 2). The recycler plays through the desired sample of tape, rewinds it to the beginning of the sample and then automatically repeats the play and rewind operations until the correlogram is completed. During each rewinding operation, the recycler advances the movable arm of the drum through one time delay unit ($\Delta\tau$). A piece of silvered tape stuck to the back of the magnetic tape at both ends of the sample to be correlated reflects light into a photocell providing signals for the cycling operations.

A technical report describing the detailed functioning of the complete correlator will be published.

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References

1. Quarterly Progress Report, Research Laboratory of Electronics, M. I. T., Jan. 15, 1954, pp. 71-72.
2. K. Goff, The development of a variable time delay, Proc. I. R. E. 41, 1578-1584 (1953).