

XVI. COMMUNICATIONS BIOPHYSICS*

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A. RANDOM PROCESS MODEL FOR THE FIRING PATTERN OF SINGLE AUDITORY NEURONS

The principal consequence of the "all-or-none" law for neural activity is that the information conveyed by a neural fiber can be completely described by giving the times at which the events (action potentials) occur. The available mathematical models for processes characterized by events at distinct times are either limited to stationary situations (e. g., recurrent event models such as Poisson) or are exceedingly clumsy (e. g., crossings through a time-variant threshold of some continuous process such as band-limited Gaussian). We have been exploring a phenomenological random process model for nonstationary neural activity which appears both to match experimental data (e. g., auditory primary units) and to be analytically manageable.

1. Definition of the Process

The stochastic process considered here can be defined in a way similar to the usual engineering definition of the Poisson process. Let δ be a small increment

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of time. We define

$$\text{Pr} [1 \text{ event in } (t, t+\delta) \mid \text{past events at } t_1, t_2, t_3, \dots] = g[r(t), t_1, t_2, t_3, \dots] \delta, \quad (1)$$

where

$$t > t_1 > t_2 > t_3 \dots; \quad (2)$$

$g[\cdot]$ is a positive functional on $r(t)$ and the times of the past events $t_1, t_2, t_3 \dots$; $r(t)$ is called the intensity function and may be thought of as the effective drive or stimulus. We assume that δ is so small that at most 1 event occurs in each interval of length δ . That is,

$$\begin{aligned} &\text{Pr} [0 \text{ events in } (t, t+\delta) \mid \text{past events at } t_1, t_2, t_3, \dots] \\ &+ \text{Pr} [1 \text{ event in } (t, t+\delta) \mid \text{past events at } t_1, t_2, t_3, \dots] = 1. \end{aligned} \quad (3)$$

Although a great deal can be done with a process as general as this, the most interesting results occur for the particular assumption

$$g[r(t), t_1, t_2, t_3, \dots] = r(t) s \left[\int_{t_1}^t r(u) du \right], \quad (4)$$

for which $r(t)$ is required to be positive. Here, $s[\cdot]$ will be referred to as the recovery function and is intended to reflect the refractory properties of the neural unit. For simplicity we shall assume that $s[\cdot]$ increases monotonically from 0 to 1 as its argument goes from 0 to ∞ . The particular form for the argument shown in (4) assumes that the state of recovery of a neural unit is independent of anything that occurred before the immediately preceding firing, and that the rate of recovery is faster if an effort is being made to stimulate the unit. There is indirect evidence that this is a reasonable assumption, at least for some neurons, but its consequences are somewhat surprising as we shall see.

2. Transformation of the Time Axis

The simplicity of the particular form (4) becomes apparent if we define a new time scale, or clock, by the relationship

$$\tau(t) = \int_{-\infty}^t r(u) du, \quad (5)$$

where t is any time on the original clock, and $\tau(t)$ is the corresponding time on the new clock. In terms of the new clock it can be shown that

$$\Pr [1 \text{ event in } (\tau, \tau+\delta) \mid \text{past events at } \tau(t_1), \tau(t_2), \dots] = s[\tau(t) - \tau(t_1)] \delta. \quad (6)$$

In other words, viewed in terms of the new clock the process is stationary regardless of the time variation of $r(t)$. This property accounts for much of the computational simplicity of this process.

We note that if $s[\mathbf{x}] \equiv 1$, the process considered in terms of the new clock is a stationary Poisson process with rate 1. Actually, for any $s[\cdot]$, we can define a second "clock" (which, however, depends upon the actual event times) in terms of which the original process reduces to a stationary Poisson process with rate 1. Thus, we would expect that much of the analytical simplicity of the Poisson process would also apply to the process defined by (4). This is indeed the case as we shall show by a few examples.

3. Inter-Event Distributions

If we consider a sample function of the process defined by (4) which contains a firing at a particular time t_1 , the conditional probability density function for the interval T to the next firing is easy to calculate. This density function is given by

$$p_r [T | t_1] = r(T+t_1) s \left[\int_{t_1}^{t_1+T} r(u) du \right] \exp \left\{ - \int_{t_1}^{t_1+T} r(x) s \left[\int_{t_1}^x r(u) du \right] dx \right\}. \quad (7)$$

If, in particular, $r(t)$ is a constant and $s[\cdot] \equiv 1$, then $\Pr [T | t_1]$ is exponential, as it should be for a Poisson process. More generally, for $r(t) = r = \text{constant}$

$$p_r [T | t_1] = rs[rT] \exp \left\{ -r \int_0^T s[rx] dx \right\}. \quad (8)$$

The inter-event distribution of (8) has the interesting property that a change in stimulus intensity produces only a change in scale, not in shape. Incidentally, with experimental histograms showing this property, $s[\cdot]$ can be determined from the equation

$$rs[rT] = \frac{p_r [T | t_1]}{\int_T^\infty p_r [T | t_1] dT}. \quad (9)$$

4. Unconditional Probability of an Event

It is easy to show that the probability of a firing in $(t, t+\delta)$, not conditional on the past events, is given by

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$$\Pr [1 \text{ event in } (t, t+\delta)] = \frac{r(t) \delta}{\int_0^\infty \exp\left\{-\int_0^x s(u) du\right\} dx} \quad (10)$$

Since the denominator in (10) is simply a constant scale factor, the unconditional probability of a firing is directly proportional to the stimulus or intensity function $r(t)$. This gives a simple interpretation to the meaning of $r(t)$, independently of $s[\cdot]$. In particular, if the stimulus is periodic and making certain ergodiclike assumptions, we can estimate the form of $r(t)$ from a histogram of event times measured with respect to the beginning of each period; for example, a Post Stimulus Time (PST) histogram. It is interesting that if this model is applicable, individual units may show refractory effects (because $s[\cdot] < 1$ for small values of the argument), whereas populations of such units will show refractory effects only as a diminution in total activity.

5. Interval Distributions

A somewhat more difficult quantity to compute, but one which is of interest for its relation to experimental measurements, is the interval distribution between events in cases in which $r(t)$ is periodic. Letting Δ be the period of $r(t)$, we can show that the fraction of intervals with durations greater than T_o is given by

$$\Pr [T > T_o] = \frac{\int_0^\Delta \frac{r(u)}{\Delta} \exp\left\{-\int_0^{u+T_o} r(z) dz\right\} s(v) dv \, du}{\int_0^\Delta \frac{r(u)}{\Delta} du} \quad (11)$$

6. Applications

Our immediate interest in this random process centers on the possibility of using it to represent the primary auditory unit data of Kiang and others.¹ If this should prove successful (and preliminary efforts indicate that the modeling is at least as satisfactory as that of other models²), then it would be interesting to explore the extent to which the nature of the peripheral coding in the auditory system accounts for certain limitations on discrimination behavior observed psychophysically. For this purpose, it would be necessary to construct the likelihood ratio to test whether particular sets of event times came from one $r(t)$ or another. This seems to be relatively easy to accomplish for the particular random process under discussion. Details of this and other applications will be presented elsewhere.

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B. AUDITORY DISCRIMINATION IN THE BULLFROG

From a phylogenetic standpoint the frog represents a unique evolutionary midstage as life emerged from the sea.¹ To help equip this amphibian for life on land, for the first time, neural mechanisms permitted airborne sound communication and the ability to localize sound.² Within the frog one finds a rudimentary neural auditory system upon which all higher animals have built. To investigators of audition and animal sound communication, it seems fundamental to ask how well this rudimentary system can perform and what types of neural coding are involved. Experimental answers to some of these questions have recently begun to appear.³⁻⁹

The fact that frogs use sound communication seems fairly well established. Anuran vocalizations based on observational and circumstantial evidence are thought to serve primarily for the attraction of a mate.³ The advent of the mating season is signaled by extensive calling of male frogs in chorus and the females of the species are presumably attracted to such calling. During this mating cycle, females are silent.

Spectral and temporal analysis of recorded frog calls have revealed that sympatric species each possess unique calls.⁴⁻⁶ In regions of territorial overlap of two species, the calls of the males diverge in at least one parameter so as to increase their distinction. Biologists and naturalists have argued that species-specific calling serves as an isolation mechanism for the preservation of the species.⁶ Such arguments presume the female to be capable of precise discrimination of calls of her own species from those of other sympatric species. Reliable experimental evidence, however, of auditory discrimination among anurans is lacking. Many clever attempts have been made but, because of the behavioral difficulties encountered in these animals, the results have been inconclusive.

A detailed study of the auditory behavior of one particular frog species, the American Bullfrog (Rana Catesbeiana), has been in progress in this laboratory for several months. The selection of the Bullfrog for study was prompted by recent anatomical⁷ and neurophysiological⁸ investigations into the peripheral mechanisms of audition in this animal. We hope that a behavioral study will, in part, tie these findings together and reveal in what way a complex, meaningful sound is coded in the nervous system of the Bullfrog.

Two large terrariums have housed a colony of adult Bullfrogs in this laboratory since

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last summer. In each terrarium gravel, sand, peat moss, various natural and artificial plants, and shallow ponds were placed in an effort to simulate natural conditions. A small enclosed loudspeaker was put in each terrarium for presentation of selected sounds over a laboratory sound system. A microphone within each terrarium permits monitoring and recording of the activity of the animals during such sound presentations.

By appropriately cycling lighting, temperature, humidity, and feeding conditions, triggered calling has been achieved by playback of Bullfrog choruses. Laboratory males typically answer these playbacks with their well-known mating-croak call. Females also participate in these sessions with "chirps" and "grunts."

It has been observed that the laboratory animals can precisely discriminate calls of their own from those of other related species. For example, a comparison of evoked calling to presentation of Bullfrog, Green Frog (Rana Clamitans) and Southern Bullfrog (R. Grylio) calls shows the following result: significant calling in answer to Bullfrog choruses generally begins approximately 10 seconds after and continues throughout playback. There has never been calling to Green Frog or Southern Bullfrog choruses. Furthermore, all spontaneous vocalizations (resulting from a preceding Bullfrog playback or feeding session) are immediately inhibited by either of these two calls. Upon termination of either the Green Frog or Southern Bullfrog playback, spontaneous calling begins again approximately 45-60 seconds later. These observations are based on approximately 50 separate playbacks of each of the three species and show conclusively that the Bullfrog can indeed discriminate between calls of its own species and those of the sympatric Green Frog and Southern Bullfrog. Similar calling experimentation has revealed that the Bullfrog can also discriminate between its call and those of 27 other closely related species. Calling on the part of the laboratory animals has never accompanied chorus playback of these other species.

Research is now being pursued to reveal exactly what stimulus parameters enable the Bullfrog to uniquely recognize its call. The main aim of this research is the formulation of a model by which discrimination of the Bullfrog croak occurs. To achieve this goal, calling studies involving selected operation on Bullfrog chorus playbacks were made. By tape-recording evoked calling, it was possible to determine the relative amount of calling in answer to filtered Bullfrog choruses. Figure XVI-1 illustrates corresponding croak-calling to a 100-second playback of highpass and lowpass filtered (18 db/octave) Bullfrog croaks (a mating-croak call being defined as a sequence of one or more croaks). The data presented are based on 200 separate trials. The playback level within the terrariums was 30 db above the laboratory background noise level. For highpass filtering, there is a rather steep increase in calling for the cutoff transition of 400-300 cps. Clearly, energy contained in the low frequencies below 400 cps is important to the Bullfrog. A sudden increase in calling is also seen in the lowpass playback as the filter cutoff is increased from 500 cps to 600 cps. For this filtering

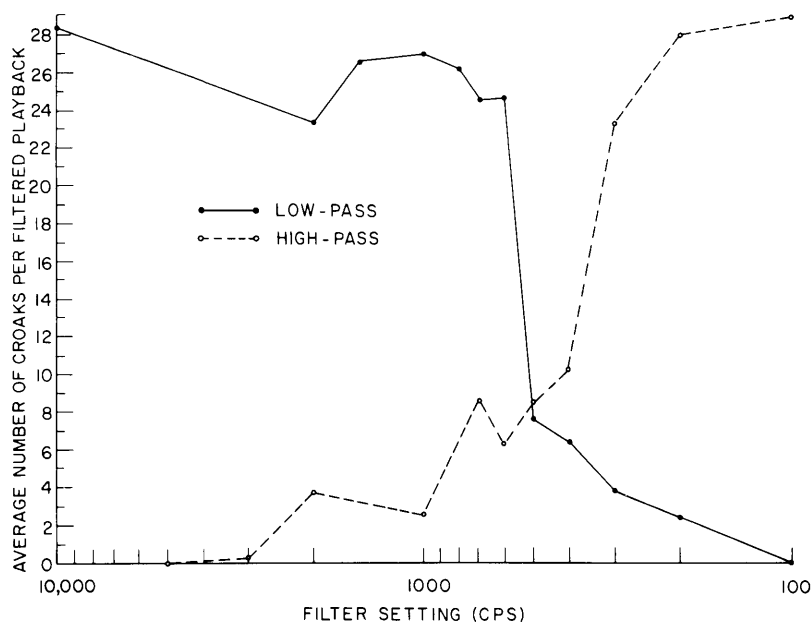


Fig. XVI-1. Evoked calling from laboratory Bullfrogs to playback of highpass and lowpass filtered Bullfrog chorus. Playbacks were filtered by means of an SKL variable electronic filter (Model 302, 18 db/octave). Chorus playbacks lasted for 100 seconds. Data are based on 200 separate trials.

situation, energy above 500 cps is vital.

The filtering employed in Fig. XVI-1 was not very sharp. To obtain a more precise measure of spectral properties of the Bullfrog croak, evoked calling has recently been investigated to a sharply filtered (66 db/octave) 100-cps passband playback of the same Bullfrog chorus (duration: 100 secs). Although this study is not entirely complete, the following conclusions are evident: Considerable calling occurs if the center frequency of the 100-cps wide passband playback lies between 250 cps and 350 cps (the amount of calling approaches that of the unfiltered playback). A lesser degree of calling occurs in the range 1050-1450 cps. No calling has ever been observed to playbacks with center frequency between 50 cps and 150 cps, or 450-650 cps, and only very slight calling between 750 cps and 950 cps. There has been no calling to playbacks above 1500 cps.

The results of calling to filtered Bullfrog playbacks permit an initial step toward a discrimination model. If no other frequencies are present, it appears that only low-frequency energy or high-frequency energy need be present to enable the Bullfrog to recognize its mating call. If, however, energy in the neighborhood of 500-600 cps is present, then both low- and high-frequency energy must be present simultaneously.

Pure tone bursts and pulse trains have also been played back to the colony. Pulse trains of various pulse repetition rates were formed by 0.1-msec pulses. Both pulse

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trains and tone bursts were presented through an electronic switch (Grason-Stadler) with envelope rise and fall times of 25 msec. These stimuli were presented once every 2 seconds with a duration of 0.5 second. Such envelope parameters approximate that of a typical Bullfrog croak.

Pulse trains of 200 pulses per second, or above, and tone bursts of 500-2500 cps cause the animals to seek refuge in the terrarium ponds. Before playback, very few animals will be in the ponds. Most of the laboratory Bullfrogs maintain favorite terrestrial territories. As soon as playback begins, the animals leave their territories and "escape" to the water. Within 15-20 seconds most of them have already entered the ponds. Upon termination of such stimuli presentations, the animals slowly crawl back out of the ponds to resume their territories.

Playback of pulse trains of 50 and 100 pulses per second and also of 400-cps, and below, tone bursts do not produce a fear reaction. Rather, the animals remain in their territories and, in fact, occasionally call back to these stimuli. Significantly, the temporal structure within the Bullfrog croak is characterized by a repetition rate of approximately 90 per second.⁹

Continued calling experiments involving synthesized Bullfrog croaks are in progress. Attempts at getting the laboratory animals to call back to these synthetic sounds are planned, and we hope they will lead to a more select discrimination model. A study of cardiac conditioning to various classes of sounds in the Bullfrog is also being pursued.

The techniques that are being employed in auditory discrimination studies of the Bullfrog are not believed to be peculiar to this species but rather representative of anuran behavior in general. To insure this conclusion, calling studies are being initiated in the Green Frog. These are expected to parallel and complement the Bullfrog studies.

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C. AN RC MODEL FOR SPONTANEOUS ACTIVITY OF SINGLE NEURONS

Spontaneously active single neurons produce spike trains whose temporal characteristics can be conveniently described in terms of: (a) an interval histogram¹ of the time intervals between successive spikes, and (b) a two-dimensional joint-interval histogram of two successive spike intervals.² These measures can be used to differentiate and characterize various modes of spontaneous activity in actual neurons. Rodieck, Kiang, and Gerstein² computed the histograms of neurons in cochlear nucleus of anesthetized cats, and found typical interval histograms to be: (a) exponential, with a small dead time, (b) approximately Gaussian, or (c) long-tailed, that is, unimodal and asymmetric, with tails longer than exponential.

Various mathematical models have been proposed to explain the observed spontaneous activity of neurons. Kuffler, Fitzhugh, and Barlow³ have suggested that interval histograms of spontaneous spike activity might be described by incomplete Gamma functions. Viernstein and Grossman,⁴ Verveen,⁵ and, more recently, Weiss^{6,7} have examined models based on threshold crossings of a random noise with Gaussian amplitude distribution. Gerstein and Mandelbrot⁸ have discussed a two-parameter model based on a random walk "toward" a firing threshold. Unfortunately, none of these models is able to describe all of the three types of spontaneous activity mentioned above.

In the present report we shall examine another type of model which, in spite of its simplicity, has not been discussed in published work on this subject. This model incorporates the following experimental facts: In its resting state the neuron maintains a constant potential difference across its cell membrane, the internal potential being approximately 70 mv below the external potential. The membrane polarization can be changed by virtue of certain chemicals released by afferent neurons. Such chemicals may either depolarize the membrane – that is, reduce the potential difference – thereby giving rise to what Eccles⁹ terms an excitatory postsynaptic potential (EPSP), or they may hyperpolarize the membrane to produce an inhibitory postsynaptic potential (IPSP). These chemicals are found to be released at the synaptic knobs in quantized amounts, this action causing depolarization and hyperpolarization "pulses" that decay approximately exponentially in time and along the membrane surface.¹⁰ Under certain circumstances these pulses have been observed with microelectrodes.¹¹ The effects of successive pulses are cumulative; if the membrane is depolarized beyond a certain critical value called threshold, a large all-or-nothing action spike which propagates

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without decrement along the neuron's axon, is produced.

These properties of active neurons suggest the following model: The neuron's membrane polarization is assumed to be represented by a single variable called the potential. The potential may change discontinuously by positive or negative steps of size h , representing the EPSP and IPSP pulses. The potential also varies continuously by decaying exponentially toward a fixed value V_0 , called the resting potential. If the potential reaches a positive value V_T , called threshold, the neuron is said to "fire," that is, to produce an action spike, and the potential returns to V_0 .

Under conditions of spontaneous activity, it seems reasonable to assume that the positive and negative pulses are generated by Poisson processes. Hence, the probability density $P_{\pm}(t)$ of time intervals of length t between positive or negative pulses would be exponential:

$$P_{\pm}(t) = R_{\pm} e^{-R_{\pm} t},$$

where R_{\pm} represents the average rate of positive or negative pulses. For successive pulses to be summed, the pulse rates R_{\pm} must exceed the decay rate of the potential

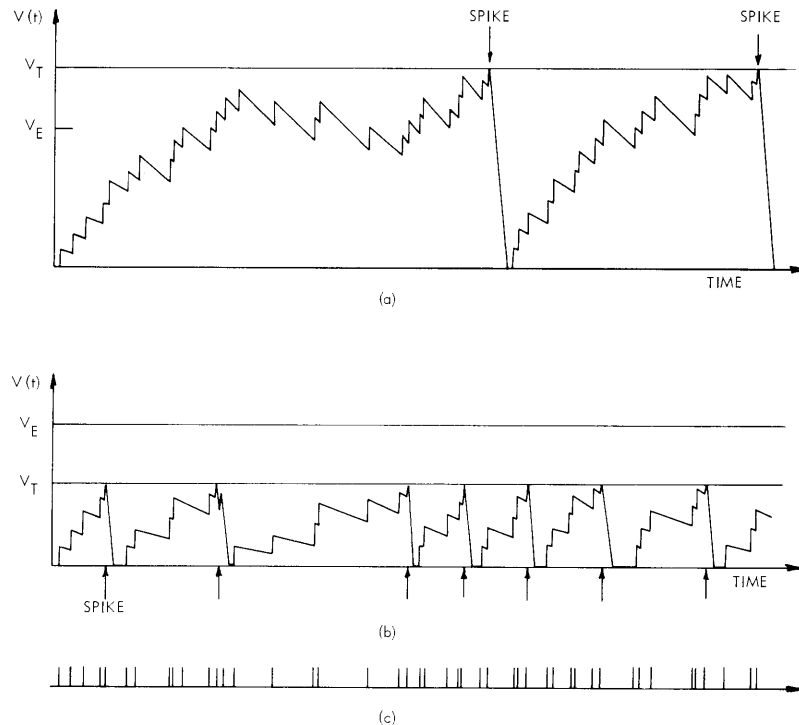


Fig. XVI-2. Neuron potential as a function of time. Neuron time constant $\tau = 7\tau_+$, $\tau_- = \infty$. (a) $V_T > V_E$ mode. (b) $V_T < V_E$ mode. (c) Train of positive pulses producing the potential.

toward its resting state. Figure XVI-2 illustrates a typical path of the potential as a function of time when all pulses are positive (cf. the depolarization of muscle membrane under successive EPSP's observed by Del Castillo and Katz¹²).

This model produces a spike train whose interval histogram is difficult to compute explicitly. The histogram is essentially the probability density of first-passage times from resting potential to threshold.

It is easy to simulate the model with a simple integrating RC circuit. The capacitor voltage into which the positive and negative pulses are fed represents the membrane potential. The incoming pulses are generated by a discriminator whose threshold level is set far above the mean of a random-noise signal; thus the density of pulse intervals will be exponential. These pulses are summed when the RC time constant τ exceeds the mean pulse interval $\tau_{\pm} = 1/R_{\pm}$. When the potential reaches the threshold value V_T , a discriminator produces a neuron "spike," and triggers a large negative pulse that reduces the potential to V_0 . The spike train generated in this way is processed by the same TX-0 program that computes histograms for actual neurons.¹³

We consider first the case in which all incoming pulses are positive (Fig. XVI-2). With the neuron threshold set sufficiently high the potential will increase to an "equilibrium" value V_E , at which the average increase in potential because of incoming pulses equals the average decay — that is, $V_E = \tau/\tau_+$. The potential will fluctuate about V_E because of the fluctuations of pulse intervals about their mean, τ_+ . The neuron threshold can be set above or below this equilibrium level, thereby giving rise to two distinct modes of operation:

(i) Threshold above equilibrium ($V_T > V_E$). The potential rises to V_E and fluctuates about this value until it reaches threshold. This mode would be expected to give rise to rather long intervals between firings (Fig. XVI-2a).

(ii) Threshold below equilibrium ($V_T < V_E$). The potential crosses threshold before reaching V_T . This mode produces more rapid and more regular firings (Fig. XVI-2b).

The interval histograms obtained from the model under these conditions are shown in Figs. XVI-3 and XVI-4, together with their semi-log plots. The circuit's time constant was directly measured to be $\tau = 180$ msec, while the mean interval between incoming pulses was 1.5 msec. With threshold above equilibrium the spike interval histogram is asymmetric, with an exponential tail for long times. With threshold below equilibrium the histogram approximates a Gaussian shape, but remains asymmetric owing to an excess of long intervals.

Figures XVI-5 and XVI-6 show joint-interval histograms for both modes; the intensity of the point (t_1, t_2) is proportional to the number of times interval t_1 is followed by interval t_2 . As would be expected from the fact that successive intervals are statistically independent (since after each firing the potential is reset to the same V_0), both

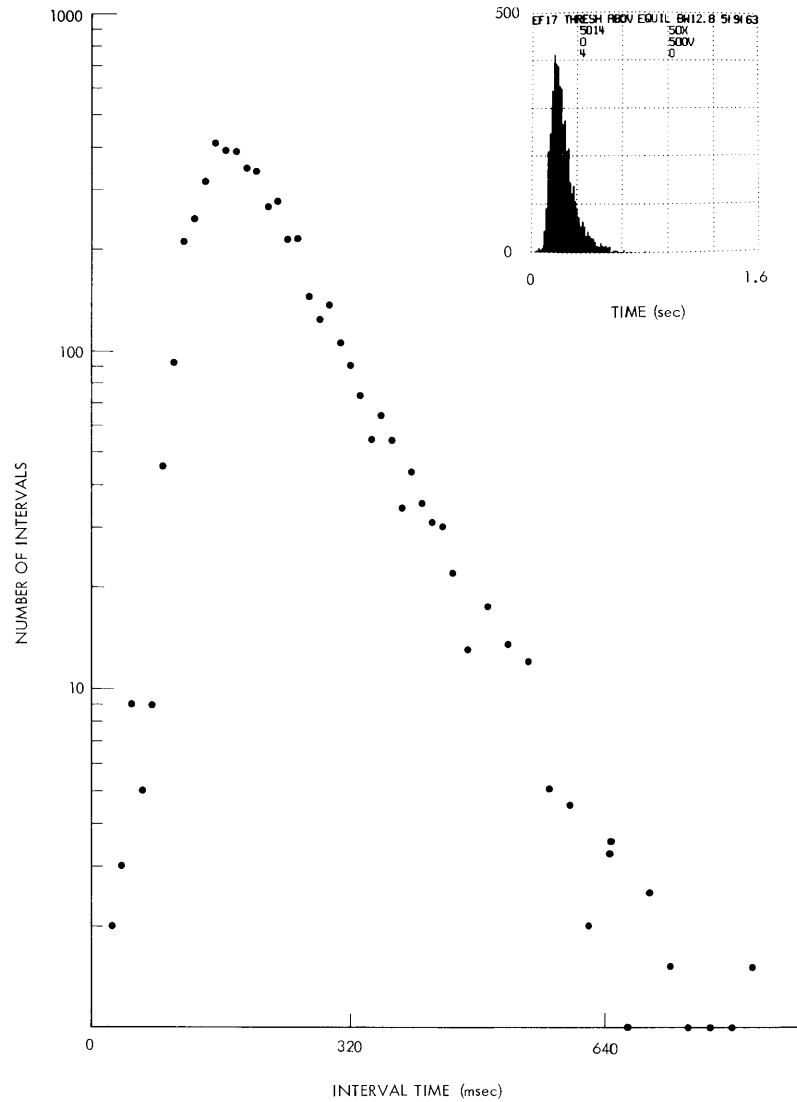


Fig. XVI-3. Interval histogram for $V_T > V_E$. Positive pulses only. $\tau = 180$ msec; $\tau_+ = 1.5$ msec; $\tau_- = \infty$.

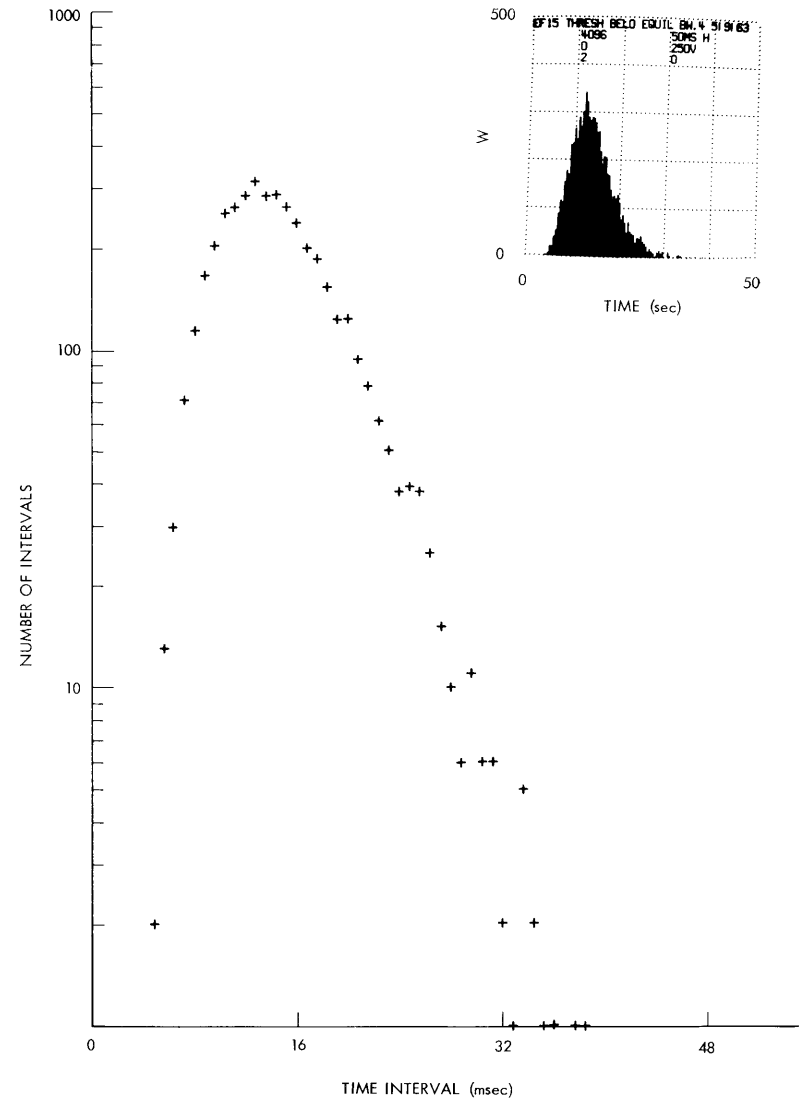


Fig. XVI-4. Interval histogram for $V_T < V_E$. Positive pulses only. $\tau = 180$ msec; $\tau_+ = 1.5$ msec; $\tau_- = \infty$.

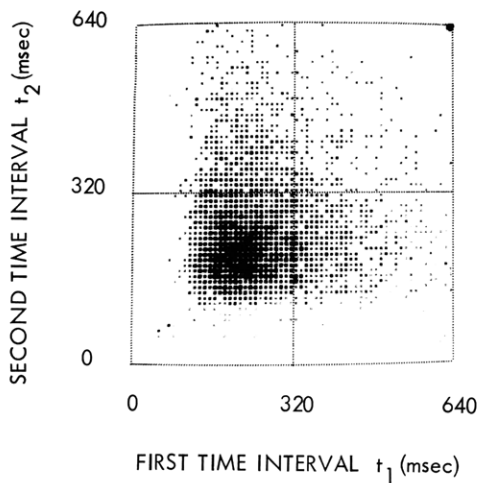


Fig. XVI-5. Joint-interval histogram for $V_T > V_E$. (Same time constants as in Fig. XVI-3.)

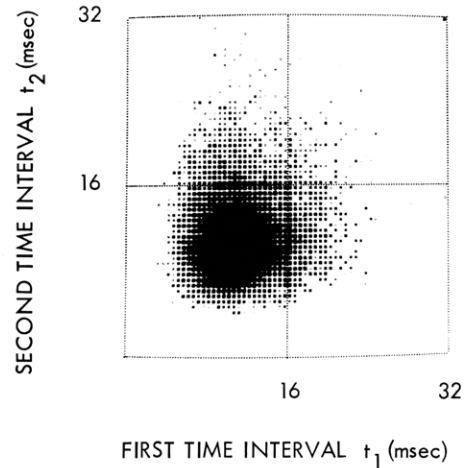


Fig. XVI-6. Joint-interval histogram for $V_T < V_E$. (Same time constants as in Fig. XVI-4.)

joint-interval histograms are symmetric about 45° . The $V_T > V_E$ plot shows that for intervals exceeding the mean, lines of equal joint probability density are approximately straight lines parallel to $t_1 + t_2 = 0$ — as would be expected for Poisson events. The $V_T < V_E$ mode has almost circular lines of equal probability density, which is characteristic of Gaussian interval densities. Thus with positive pulses the model gives exponential and almost Gaussian interval histograms, but not those with longer-than-exponential tails.

A more general situation involves both positive and negative pulses of equal magnitude h (Fig. XVI-7). We consider first the situation when the mean rate of positive

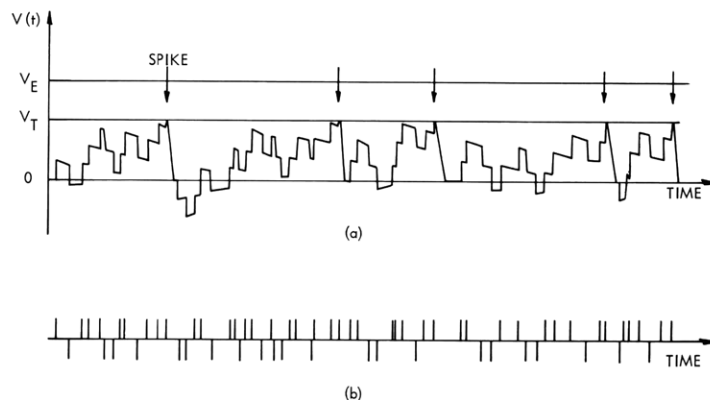


Fig. XVI-7. (a) Neuron potential as a function of time for positive and negative pulses. $R_+ > R_-$. (b) Train of positive and negative pulses producing the potential.

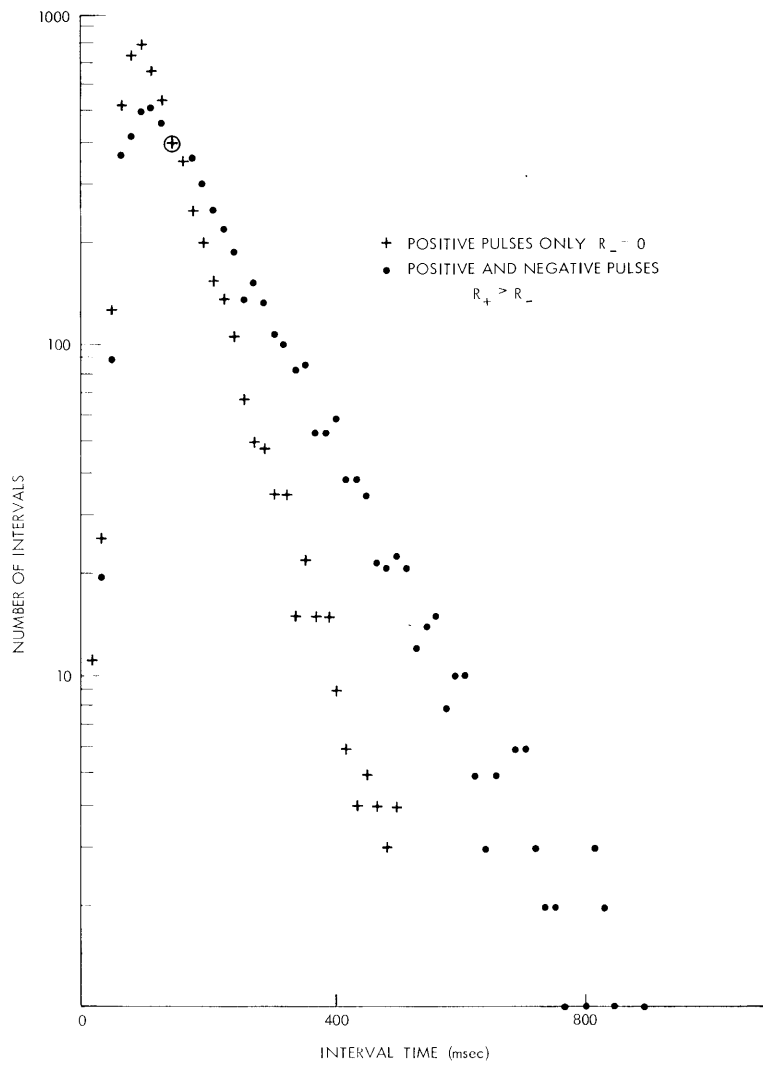


Fig. XVI-8. Interval histogram for $V_T > V_E$, with and without negative pulses.

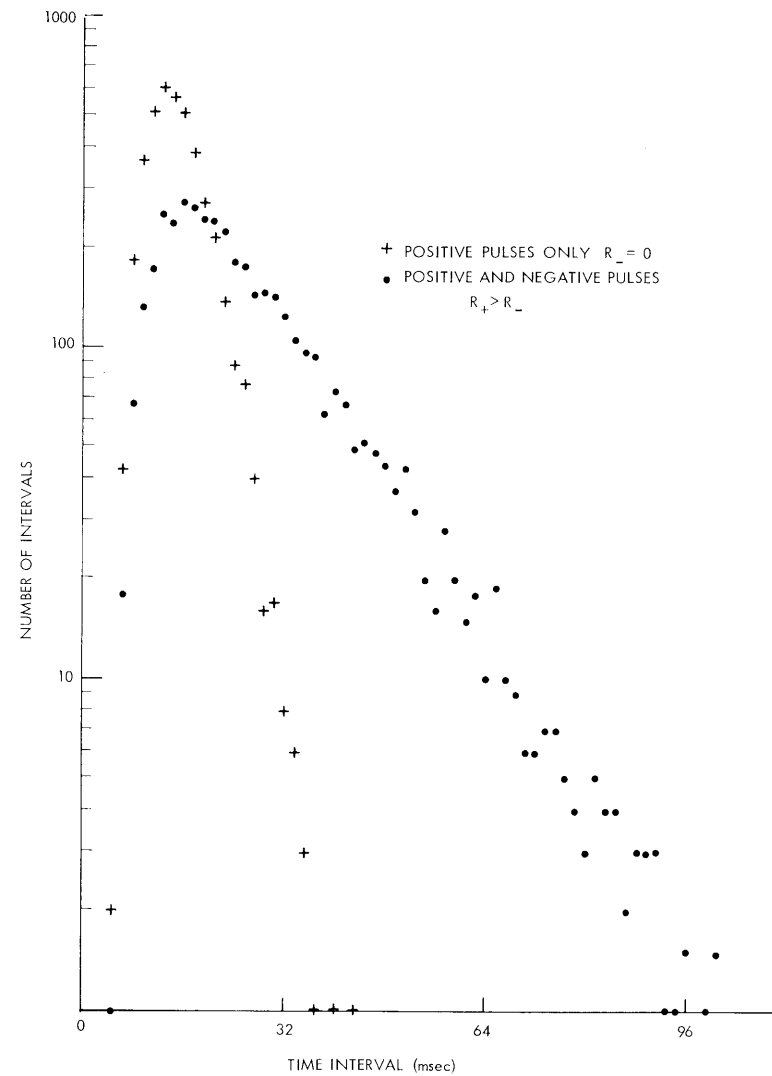


Fig. XVI-9. Interval histogram for $V_T < V_E$, with and without negative pulses.

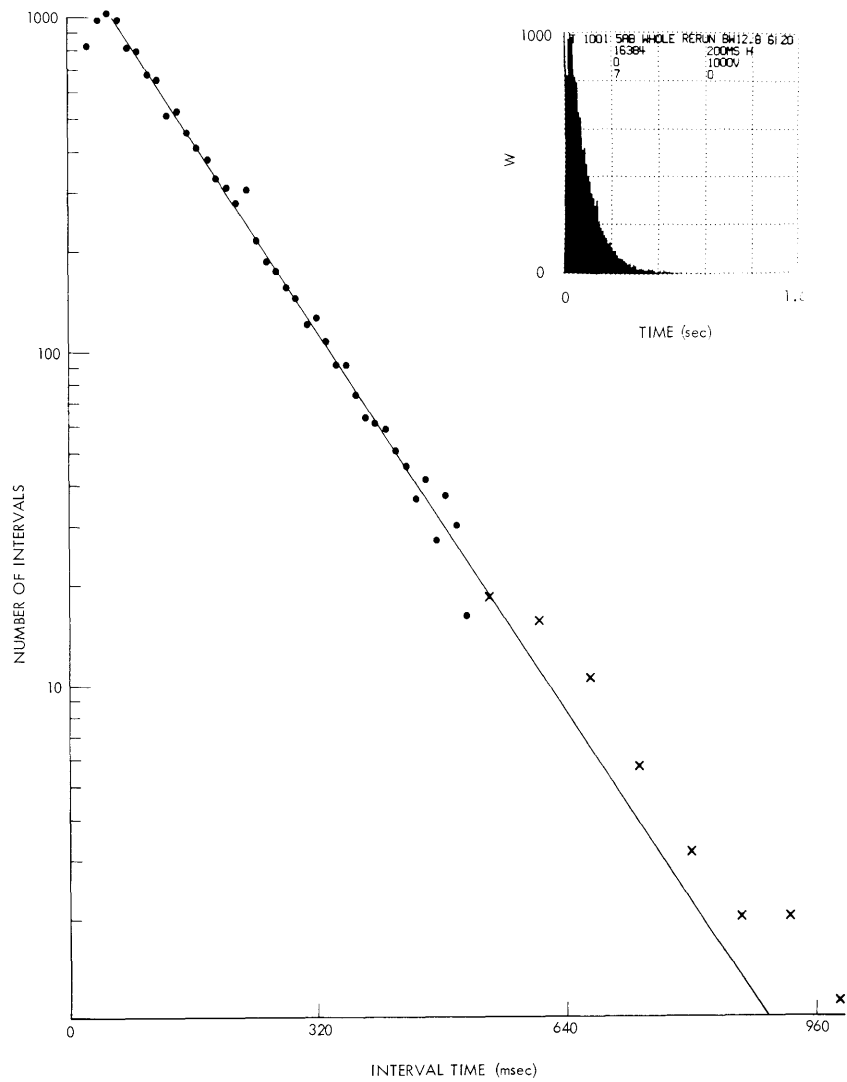


Fig. XVI-10. Interval histogram for approximately equal positive and negative pulse rates ($V_T \approx 0$). $\tau = 50$ msec; $\tau_+ = \tau_- = 1.2$ msec. (X signifies lumped data.)

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pulses, R_+ , exceeds that of negative pulses R_- ; in this case the potential will again have a positive equilibrium value, $V_T = h \frac{(R_+ - R_-)}{1/\tau}$. Figure XVI-8 shows a comparison of the histograms for $V_T > V_E$ with and without negative pulses; the negative pulses are seen to extend the histogram but not to alter its shape; the tail remains exponential. Similarly, Fig. XVI-9 shows a histogram for $V_T < V_E$ before and after negative pulses are introduced; with the addition of negative pulses the histogram's tail approaches an exponential – probably due to the fact that the negative pulses reduce the equilibrium level and bring threshold effectively closer to equilibrium. Thus, when R_+ is considerably larger than R_- , introducing negative pulses does not result in any new histograms.

The model can also be operated with the rates of positive and negative pulses approximately equal; in this case the equilibrium potential $V_T = 0$. Figure XVI-10 shows an interval histogram obtained for $\tau_+ = \tau_- = 1-2$ msec and $\tau = 50$ msec. The semi-log plot shows a slight deviation from exponential, in the direction that is characteristic of long-tailed histograms. This deviation could probably be made more pronounced by further adjustments of the time constants and perhaps by revision of certain assumptions (as stated below).

Thus, under the various conditions that we have investigated, the RC model seems capable of simulating most of the spontaneous spike trains observed in actual neurons. Within these limitations the results suggest that neurons with quasi-Gaussian histograms have a higher rate of incoming EPSP's – or a greater predominance of EPSP's over IPSP's – than those with exponential histograms (if equal threshold levels are assumed).

Similarly, a neuron with a long-tailed interval density would have approximately equal rates of incoming EPSP and IPSP.

The RC model may be able to generate other histogram shapes – and perhaps produce more pronounced long-tailed densities – if some of the following assumptions are revised.

(a) A crucial assumption thus far has been that the interval density of incoming pulses will be exponential. Other density shapes such as Gaussian have not yet been investigated, and, when they are, they may yield different histograms.

(b) The sizes of the positive and negative pulses have been assumed to be constant and equal. Neurophysiological experiments indicate that the effect of a single IPSP depends strongly on the degree of membrane polarization.¹³

(c) The assumption of independence of successive intervals – implicit in the automatic return to V_0 after firing – might be relaxed in order to produce different interval and joint-interval histograms.

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D. EXPERIMENTS ON MACHINE RECOGNITION OF CONNECTED HANDWRITTEN WORDS

1. Introduction

Handwriting recognition, considered as a sample problem in recognition of widely variable patterns by automata, has received previous consideration¹⁻³; however, error rates previously achieved have been rather high. We approach the problem of searching for invariants of the handwritten patterns by consideration of the intrinsic movements that execute the handwriting activity. Recognition is performed on three different levels by taking into account at each of the higher levels the additional constraints that are observed.

In this report results are presented for recognition experiments conducted under various conditions of machine learning for test data consisting of 100 words written by 4 subjects. The test vocabulary consisted of 12 words generated from 9 letters. The

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words were selected so as to form a group in which knowledge of one letter of the word supplies little information about the other letters. A dictionary consisting of those 59 words that were considered to be likely products of misrecognition was used to eliminate any nonwords that might be generated by the program.

The program presented identifies handwritten words written with the aid of special apparatus that enables the recording of the writing as a two-dimensional vector displacement function of time. The words are analyzed, first, by segmenting them into strokes that are considered to represent the basic units of handwriting movement and, second, by applying a transformation to convert the stroke description from a vector function of time to a multidimensional parameter vector. In the space of all possible stroke vectors some clustering of points is found which corresponds to the particular strokes of every letter. With the aid of appropriate estimates of the multivariate probability distributions of stroke parameters conditioned by a particular stroke group, the likelihood of an unknown stroke belonging to that group can be estimated. Constraints among the various strokes of a word are found to occur on two levels – within individual letters and among the letters that are known to form a word of the language. The intraword stroke constraints are used to select, from the set of all possible sequences of strokes that correspond with some minimum likelihood to the experimentally determined strokes, those that constitute possible letter sequences. If a dictionary of the words of the language is available to the machine, it can eliminate nonwords and thereby arrive at the word that it considers most likely to be represented by the handwritten word.

2. Methodology

a. Segmentation

A representation of handwritten words by means of the spatial coordinates x and y was first suggested by Frishkopf.² It has been shown previously by Eden and Halle⁴ that handwriting can be characterized as a sequence of basic strokes connected according to a rule. That formalization, however, did not specify algorithmic procedures for recovery of the basic strokes from handwritten words. This deficiency can be overcome by the formulation of an operational definition of a stroke or the segmentation points between strokes. Under the assumption that the pen velocity is a continuous vector function of time, a segmentation point is defined as one for which the velocity component along the y coordinate has zero value. The segments so delimited can be considered as meaningful units of the handwriting if replacement of individual segments by using different input samples does not distort the word so formed beyond human recognition. A word is taken to mean a connected sequence of letters with an interpretation in a particular natural language. Obviously, such words must be in the vocabulary of the human observer. Another significant advantage is that the segmentation of a word into a stroke

sequence is a refinement of the segmentation of the word into letters, an operation successfully executed by humans, but one for which no acceptable algorithmic solutions have been presented.

b. Stroke Identification

In order to classify individual strokes into categories so that the information of membership in the respective categories for the strokes constituting the word is sufficient to recover the letter sequence, we transform the topological description of the stroke into a numerical representation. Such a representation may be obtained by means of a set of parameters that, on the basis of an appropriate model of the generating system, can serve to regenerate the stroke under consideration. The particular model utilized in this work was described as Model B in our previous report.⁵

Strokes are classified into their respective categories by means of maximum-likelihood estimates based on the assumption that the individual parameters describing members of any stroke category have multivariate normal distributions with possibly unequal covariance matrices for the different categories. Mathematically, the probability density $p_i(\bar{X})$, where \bar{X} is from the category π_i , is given by

$$p_i(\bar{X}) = \frac{1}{(2\pi)^{p/2} |\bar{V}_i|^{1/2}} \exp\left[-\frac{1}{2}(\bar{X}-\bar{\mu}_i)' \bar{V}_i^{-1}(\bar{X}-\bar{\mu}_i)\right],$$

where p is the number of dimensions of the parameter vector \bar{X} , \bar{V}_i is the covariance matrix of the parameters for the category π_i , and $\bar{\mu}_i$ is the vector of parameter means for the category π_i . Subject to these assumptions, it can be shown⁶ that the optimal recognition procedure is to calculate the likelihood function

$$l_i(\bar{X}) = -(\bar{X}-\bar{\mu}_i)' \bar{V}_i^{-1}(\bar{X}-\bar{\mu}_i) - \log_e |\bar{V}_i|$$

for each stroke category and select that category for which this function is maximized. Since at this level of the recognition program we expect a rather high probability of classification error, we establish a likelihood threshold level, eliminating from further consideration only those stroke categories that fall below this level.

In order to reduce the number of possible abstract stroke sequences corresponding to any handwritten word which are preserved for further consideration, it is important to minimize the number of different stroke categories. This minimization is carried out by starting with the finest possible partition of the stroke space that would be obtained by assigning each stroke of each letter to a different category and merging all topologically similar categories while preserving the unique decodability of stroke sequence into letter sequences. Where different forms of particular letters are found

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to consist of different numbers of strokes, such variations are recognized by the representation of the letter by several variants having different abstract stroke representations.

c. Letter Identification

By constructing a table of letter variants with their corresponding stroke sequences, we permit the mechanization of the stroke-to-letter sequence transformation, as well as eliminate from further consideration all stroke sequences to which no letter sequences correspond. No information about constraints between successive strokes is available to the program other than the information about which strokes may follow each other within any letter. In calculating the letter likelihood estimates, the conditional probability that the stroke s_j follows the stroke s_i is assumed to be proportional to the probability of the stroke s_j , given only the parametric representation of that stroke, if, in fact, such a sequence is possible, and zero otherwise. The exact probabilities are obtained by renormalization over the stroke sequences with nonzero probability.

Letter sequences are generated by considering, in turn, all possible ordered stroke sequences that may be generated from the stroke categories exceeding the likelihood threshold. The strategy used is to start with the first member of the first stroke set, attempt a continuation with the first member of the second set, and continue until either an uncontinuable sequence is found or the last stroke of the word is reached. For uncontinuable sequences the last stroke selected is dropped and the next member, if there is any, of the same stroke set is considered. If no continuation is found, one more stroke is deleted and the process is continued from that point.

d. Word Recognition

The letter sequences found by the above-mentioned procedures in most cases will specify nonwords. Our attention is focused on misreading one word for another and, therefore, the information that all possible inputs are words of the language is made available to the computer. This step is also essential if comparison is to be made with human performance in such recognition tasks.

Nonwords are eliminated as they are generated by allowing the letter-sequence generator program continuous access to a dictionary. This facility speeds up the recognition program considerably by preventing the complete development of letter sequences that are determined to be nonwords by consideration of the first few letters. If more than one word can be generated from the strokes that are found to exceed the likelihood threshold, the likelihood of each is determined from the letter-sequence likelihood by renormalization over all words so generated. This procedure implicitly assumes an a priori probability distribution for the input words such that the word probability is equal to the reciprocal of the number of dictionary entries if the word is listed in the

dictionary, and zero otherwise.

The experiments described here were carried out with a limited dictionary containing only those words that the experimenter thought would be likely results of misrecognition. Other experiments are now being carried out with words generated from the complete lower-case alphabet and a dictionary of the 10,000 most frequently used words in the English language.

3. Results and Conclusions

The experimental system for the study of handwriting data has been described previously.⁵ The 100 handwriting samples were segmented into strokes and these strokes were classified manually into 42 categories according to the letters from which they



Fig. XVI-11. Sample of handwritten word used in the recognition experiment.

originated. A typical handwriting sample is illustrated in Fig. XVI-11. Groups of topologically similar categories within which differentiation was not necessary for unique letter specification were merged so that the final partition consisted of 24 stroke categories, 12 upstrokes and 12 downstrokes. Special categories were assigned to writing segments found connected onto, but not forming part of, the first and last letters of many words. Twelve component parameter vectors were used for all experiments except one, the eight previously discussed⁵ being

augmented by parameters giving the total x displacement, the total y displacement, and initial and final x velocities. The variables were selected without any a priori information about their relative usefulness in an attempt to provide the system with as much useful information as possible about the strokes. In Experiment 1C, in order to examine the effects of a reduced parameter set, recognition was attempted by using only 5 parameters corresponding to the variables of Model A of our previous report.⁵

A partial test showed no significant improvements if the complete covariance matrix was used instead of the variances alone. For this reason, and also to save storage and computation time, all covariances were arbitrarily assumed to be zero.

Six experiments were carried out with the recognition rates given in Table XVI-1. A composite confusion matrix for all experiments is given in Table XVI-2.

We observe that although Experiments 1A and 1B result in identical recognition rates, the set of words incorrectly identified is not the same. This shows that in a few cases the use of upstrokes may help or hinder correct recognition. Theoretically, since each letter can be assigned a unique sequence consisting of downstrokes only, the

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Table XVI-1. Results of handwriting recognition experiments.

Experiment Number	Learning Set	Test Set	Strokes used for recognition	Percentage correctly recognized
1A	all strokes	all strokes	all strokes	91
1B	all downstrokes	all downstrokes	all downstrokes	91
1C	all downstrokes	all downstrokes	all downstrokes 5 parameters only	68
2A	subjects A, B subjects C, D	subjects C, D subjects A, B	all strokes	69
2B	subjects A, B subjects C, D	subjects C, D subjects A, B	all downstrokes	56
3	50 samples – all subjects and words	50 different samples – all subjects and words	all downstrokes	83

information contained in the upstrokes is redundant once the downstrokes are specified. However, if the downstrokes are not known with certainty, the use of upstrokes as well may improve recognition. By considering the results of Experiments 2A and 2B in comparison with those of Experiments 1A and 1B, we see that the relative usefulness of the upstrokes depends on the extent of our ability to recognize the downstrokes reliably. The significant saving in computation time resulting from the sole use of downstrokes led us to use them alone in further studies of the behavior of the recognition system.

Significant differences among the various subjects' writing, such as size, slope, speed of execution, and shape of letters, prevent a ready generalization of parameters over the writings of different subjects. A comparison of the results of Experiments 2B and 3 shows the importance of exposing the machine in the learning phase to samples written by the people whose writing it will encounter in the test phase. In the absence of such learning, recognition, of course, will deteriorate. We may note that the appropriate parameter statistics do give a numerical representation to a subject's handwriting and therefore, given the parameters of a particular handwriting sample and the statistics for a number of subjects including the writer, the machine presumably can identify the writer of the sample. Other experiments are now being carried out to test how well the machine can adapt its representation of the strokes to those of a new subject if it is given initial statistics compiled from the writing of others and tested with a sample sequence written by the new subject.

The information obtained about the strokes by using the complete set of 12 parameters

Table XVI-2. Confusion matrix for recognition experiment errors.

	Fail	Fall	Feel	Fell	Fill	Foal	Foil	Fool	Fowl	Full	Furl	Fair	Fare	File	Filer	Fire	Flail	Flee	Flue	Fore	Four	Free	Frill	Froe	Fuel	Furor	**	
Fail (8)*		1 1 1									1 1 2 1		1							1		1			1 2			
Fail (8)					1					1 1 1 3 2 1													1 1					
Feel (10)				1 2 1 1 1	1																							
Fell (9)					1									1 1 1 1 1				1										
Fill (6)				1 1 3 3 1																								
Foal (9)								1 1 3 3 1	1 1 1 2 2 1 1																		1 1	
Foil (8)	1		1 2								1																	1
Fool (9)						1 1	1 1												1									1
Fowl (8)						1 1 3 1		1 1 1 2 1														1 1						
Fowl (8)								1 1 1														1						
Full (8)		2 1 1											1		1													2
Furl (9)	1 1	1					1				1 1					1 1 1	2		1	1								1 1 1

Entries in rectangles refer to several experiments as follows

1A	1B	1C
2A	2B	3

*Numbers in parentheses give number of different samples of that word in input data.

** No word recognized.

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is somewhat redundant. From Experiment 1C we observe that using less than one-half of the parameters results in only a 25 per cent deterioration of the recognition rate. Clearly, not all parameters are equally useful, but since the contributions from the several parameters are not additive, any simplification by a reduction in the number of parameters would require an exhaustive search procedure. The variances serve as normalizing factors in calculating the contribution of each parameter to the stroke likelihood measure, but other than that all parameters are weighted equally. This procedure, although valuable in general, may fail to resolve particular confusions such as those between the letters l and ℓ correctly. In such cases it may be useful to have a list of likely confusions, together with information about which parameters would be most useful in resolving them.

We may note that the test vocabulary was intentionally selected to limit the information supplied by the word context. These words are particularly difficult to recognize because the misrecognition of one letter is likely to generate a different word. The complete dictionary is on the average much less clustered, that is, a substitution for one letter is less likely to generate a new word, and therefore recognition rates for more general data should be higher.

The main aspect in which the program's performance now differs from that of humans is that it does not use any form of "Gestalt" recognition of complete characters. One may say that it occasionally fails to see the whole word by looking at it only one stroke at a time. The program indicates the places where possible ambiguities may exist by likelihood ratios of the most likely words which are nearly one. It has not been endowed with facilities to locate the source of the confusion and attempt to resolve it. In other respects the results of misrecognition by the machine are precisely the same as those of humans when further deterioration of the writing samples takes place.

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