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STAP-8: A SUBROUTINE PACKAGE FOR STATISTICAL ONLINE ANALYSIS OF SIMULTANEOUS NEURONAL SPIKE TRAINS*

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STAP-8: A SUBROUTINE PACKAGE FOR STATISTICAL ONLINE ANALYSIS OF SIMULTANEOUS NEURONAL SPIKE TRAINS*

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This paper presents a computer program including a subroutine package for the statistical analysis of neuronal spike trains. Extended use was made of an information display concept, on-line control via teletype intercommunication and the use of a versatile laboratory peripheral, including, among other features, Schmitt-Trigger inputs, multiplexed analog-digital converters, and a variable RC-clock. The software, written exclusively in the system's specific symbolic assembler language, was compiled and tested on a LAB-8 System of DEC**, extended with the Arithmetic Element MP8/1, the Mini-Disk DF32, and the Tektronix Type 601 Storage Oscilloscope, and is available as an assembly listing together with the binary paper tape.

From the neuronal spike trains recorded simultaneously by two Schmitt-Trigger inputs, interspike intervals are counted by the RC-clock counting chain and translated into 12-bit positive integers. These interval data files stored on the disk are available to eight different analysis programs: Interval histogram, autocorrelogram, cumulative distribution function, conditioned probability density, serial correlogram, cross-correlogram, post-stimulus time histogram, and time interval sequence. The results are given as a function or histogram display, or may be punched on paper tape for further analysis.

Neurophysiology Spiketrain analysis Small computer Stochastic point process

1. COMPUTATIONAL METHODS

1.1. STAP-8 does not investigate a new kind of statistical procedure for spike train analysis but rather was designed to give the experimenter an easy-to-control library of well known statistical calculation and display programs which may help to get an instant overview of microelectrode data recording during the experiment. There exist already several off-line analysis programs, e.g. from Lewis [7] for the IBM 7094 and IBM 360 systems, and from Perkel for the IBM 7044 and IBM 360/40 systems (private note). The statistical methods have been suggested by several authors in the last years [8–11] and the list of contributions will further be supplemented [12]. For the related fundamental mathematical theories the reader is referred to the pertinent literature [1–3].

Because of the nearly uniform duration of spikes along a given fiber and their brevity relative to the time intervals between them, the spikes (whose amplitudes are considered to carry no information) are assumed to be point events in time, i.e. the spike train is treated as a stochastic point process [3]. Therefore, it is only the time of occurrence of the spikes (T_i) or the intervals between them (X_i) which are counted and referred to as 'raw data' throughout the following program description. The library is composed of eleven program sequences as described below. They may be called into the core operating area from disk by the use of a three-character code via the teletype keyboard.

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** Digital Equipment Corporation, Maynard, Massachusetts, USA.

1.2. Interval Counter (one channel) (IC1). Interval Counter (two channels) (IC2). These two programs perform digitalization of interspike time intervals X_i in series of 1024 spikes per channel. The Schmitt-Trigger inputs S1 and S2 accept negative spike pulses. The switching thresholds can be varied over the range of 0 to −2.5 V by potentiometers. Input S3 accepts the counter start pulse which enables the RC-clock and initiates the counting procedure. As each spike is recorded, the clock counter value is saved on consecutive train storage locations as a 12-bit unsigned integer representing the number of RC-clock pulses counted during the preceding interval. The counting procedure terminates:

after the digitalization and storage of 1024 or N (see 1.3) intervals;

after the processing of 1024 or N intervals by *one* of the two counters in IC2 mode;

after an OVERFLOW message occurring if any interval exceeds 4095 time units (see 1.3).

Non-required storage locations are set to the value zero and the trains are saved on the disk (see flowchart fig. 3).

1.3. Options (OPT). The program includes output and service subroutines. OPT introduces with label and colon printout and requires the user to specify the option.

OPT:ST. If an input Schmitt-Trigger flip-flop is set to the logic value 1, a standard pulse appears at the digital output S0. The original spike train may then be compared with that recorded by the Schmitt-Trigger, its switching threshold set according to the selected recording level.

OPT:RC. The digital output S0 of the laboratory peripheral is set to −3 V at the RC-clock pulse rate. S0 may be linked to the CRT device and the displayed square wave is then calibrated by the RC-clock control potentiometers. As the results of statistical computation are relative and based upon the time unit, this time base calibration has to be performed very carefully. Throughout the program description, the time unit is assumed to have the value 1 ms (0.001 sec).

OPT:DN. N, the maximum of intervals counted per train, may be specified by the user, but must not exceed 1024!

OPT:P. Either one of the raw data files (spike trains), or the 128 X 3 word array which holds the results of computations, may be punched on paper tape for further analysis.

OPT:L. For each train recorded, five statistical parameters are calculated and listed in floating-point format: N number of intervals of the train specified, T sum of intervals, i.e. total record duration, MU interval mean value, S standard deviation, C estimate of the coefficient of variation, having the value unity for an exponential population.

Formulas of computation:

1.3.1. $$T = \sum_1^N X_i = T_N$$

1.3.2. $$MU = T/N .$$

1.3.3. $$S = \left(\sqrt{N \cdot \sum_1^N X_i^2 - T^2}\right)/N$$

1.3.4. $$C = S/MU .$$

1.4. Histogram Display Subroutine (HST). HST is called into memory either by the user or by the programs AUT, CCR and STH (see below). This sequence begins with a label and parameter request:

Y SCALE FACTOR__

The user has to specify the vertical counting range. If one or more of the 128 histogram classes reach the top of the display area, the user should recall HST and then increase the scale factor by one. The display then is scaled by a factor 2. Histograms are displayed in *storage mode*, i.e. no refreshment sweeps are provided.

1.5. Autocorrelogram (AUT). The autocorrelation is a *probability density* function and specifies the probability of encountering *any* spike as a function of time after a given spike. It is an order-dependent statistical measure and involves time intervals between non-successive spikes:

1.2. Interval Counter (one channel) (IC1). Interval Counter (two channels) (IC2). These two programs perform digitalization of interspike time intervals X_i in series of 1024 spikes per channel. The Schmitt-Trigger inputs S1 and S2 accept negative spike pulses. The switching thresholds can be varied over the range of 0 to −2.5 V by potentiometers. Input S3 accepts the counter start pulse which enables the RC-clock and initiates the counting procedure. As each spike is recorded, the clock counter value is saved on consecutive train storage locations as a 12-bit unsigned integer representing the number of RC-clock pulses counted during the preceding interval. The counting procedure terminates:

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OPT:RC. The digital output S0 of the laboratory peripheral is set to −3 V at the RC-clock pulse rate. S0 may be linked to the CRT device and the displayed square wave is then calibrated by the RC-clock control potentiometers. As the results of statistical computation are relative and based upon the time unit, this time base calibration has to be performed very carefully. Throughout the program description, the time unit is assumed to have the value 1 ms (0.001 sec).

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OPT:P. Either one of the raw data files (spike trains), or the 128 X 3 word array which holds the results of computations, may be punched on paper tape for further analysis.

OPT:L. For each train recorded, five statistical parameters are calculated and listed in floating-point format: N number of intervals of the train specified, T sum of intervals, i.e. total record duration, MU interval mean value, S standard deviation, C estimate of the coefficient of variation, having the value unity for an exponential population.

Formulas of computation:

1.3.1. $$T = \sum_1^N X_i = T_N$$

1.3.2. $$\mathrm{MU} = T/N .$$

1.3.3. $$S = \left(\sqrt{N \cdot \sum_1^N X_i^2 - T^2}\right)/N$$

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1.5. Autocorrelogram (AUT). The autocorrelation is a *probability density* function and specifies the probability of encountering *any* spike as a function of time after a given spike. It is an order-dependent statistical measure and involves time intervals between non-successive spikes:

1.5.1. $$X_i^n = \sum_{k=i}^{i+n-1} X_k\,, \qquad i = 1,\ldots,N-n+1\,.$$

The user specifies the maximum range of observed interval length T_{obs} which is divided into 128 bins of equal class size d. If for the order n the interval X_i^n satisfies the inequality:

1.5.2. $$(j-1)d \leqslant X_i^n < j\cdot d\,,$$

the bin j of the histogram of order n is incremented by one. This histogram is an estimate of the interval density of order n. Since the autocorrelation is the sum of interval densities of all orders, i.e. $N \to \infty$, the histograms are summed up. The estimate error will decrease for increasing n. This rule is contradicted by the fact that higher order histograms flatten out due to the finite number N of the interval sample. The user has to specify the order n. A significant value for n is provided by the lower limit

1.5.3. $$n > \frac{T_{obs}}{\text{MU}}\,,$$

where MU is the interval mean value (see 1.3.2.). For $n = 1$, the *interval histogram* representing the first-order density estimate is computed. It is an order-independent statistical measure and specifies the probability of encountering the subsequent spike as a function of time after a given spike. Computation is performed in unsigned single word arithmetic.

1.6. Cumulative Distribution Function (CMD). This program computes and displays the estimate of the probability distribution:

1.6.1. $$F(t) = \int_0^t f(T)\mathrm{d}T\,,$$

where $f(T)$ is the first-order probability density discussed above (1.5.). It evaluates

1.6.2. $$F_i = \frac{1}{N}\cdot\sum_1^i n_j\,, \qquad i = 1,\ldots,128$$

from the class frequencies n_j computed by AUT (n=1). Computation is performed in unsigned single word arithmetic.

1.7. Conditioned Probability Density (CPD). CPD computes and displays an estimate of the order-independent conditioned probability (postpulse probability, hazard function):

1.7.1. $$\varphi(t) = \frac{f(t)}{1-F(t)}\,.$$

The program evaluates

1.7.2. $$\varphi_i = \frac{n_i}{N - \sum_1^i n_j}\cdot\frac{1}{d}\,, \qquad i = 1,\ldots,128\,.$$

where n_i = interval class frequency, N = number of intervals counted, d = interval class width.

The conditioned density function specifies the probability of encountering a spike at time t, given that there was no spike prior to the time t. Computations are performed in unsigned single word arithmetic.

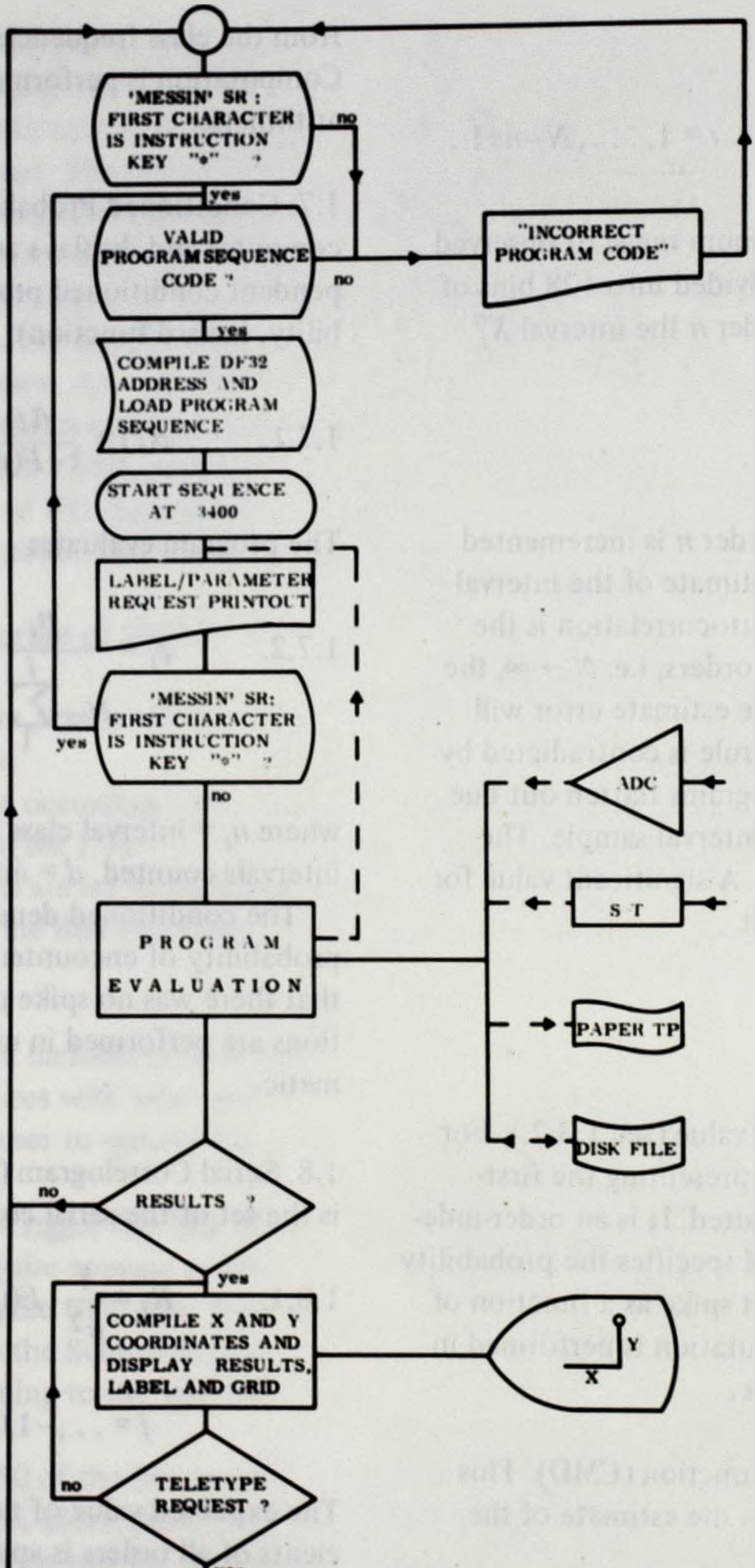
1.8. Serial Correlogram (SCG). The serial correlogram is the set of the serial correlation coefficients

1.8.1. $$R_j = \frac{1}{\sigma^2}\cdot E((X_i-\hat{X})(X_{i+j}-\hat{X}))\,,$$

$$j = \ldots,-1,0,1,\ldots$$

The expected value of the serial correlation coefficients of all orders is approximately zero if the intervals are drawn independently from a common distribution. Positive contributions to serial correlation coefficients are due to long-term trend in data. SCG computes 128 coefficient estimates:

1.8.2. $$R_j = \{\frac{1}{N-j}\sum X_i X_{i+j} - \frac{1}{(N-1)^2} \times (\sum X_i)(\sum X_{i+j})\}$$



1. Standard program flow. The flowchart block identified 'PROGRAM EVALUATION' is a dummy for any of the eleven program sequences mentioned. Two of them are analyzed in detail by the flowcharts of figs. 3 and 4.

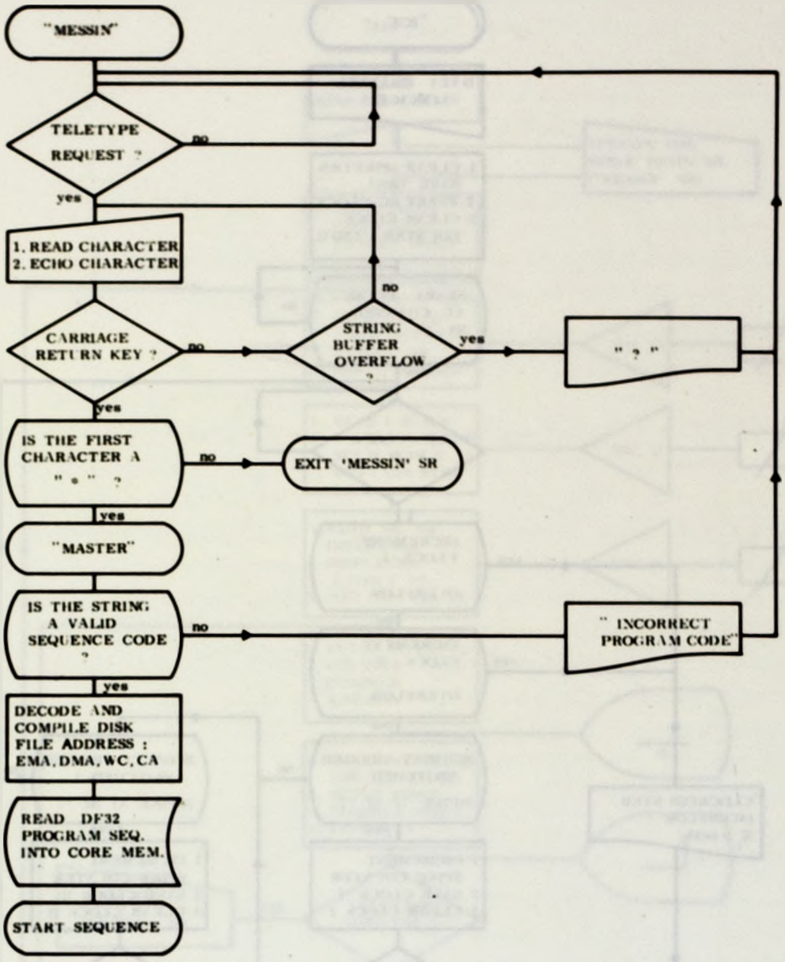
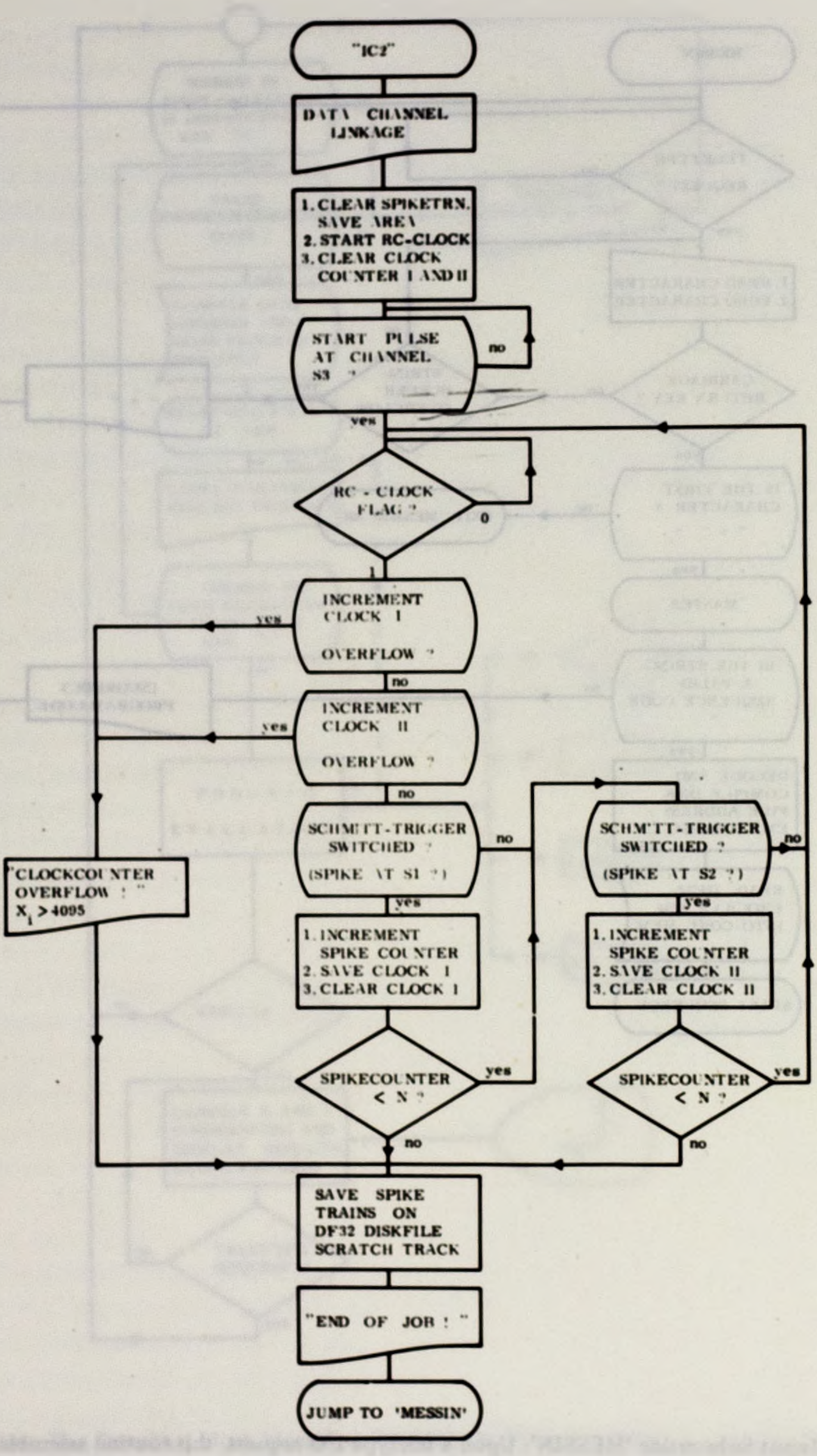


Fig. 2. Character String Input Subroutine 'MESSIN'. Upon a teletype I/O request, this routine assembles and stores ASCII character code strings. Strings of less than 16 characters are recognized, the RETURN key interpreted as the string terminal. When a "*" symbol is encountered in the first location, the string is interpreted as a user's request for program sequence retrieval. The program code is recognized and, if valid, decoded in subroutine 'MASTER'. Otherwise control returns to the background program, and a reference to the string may be made by the means of a pointer in page zero.



nterval Counter (two channels). Digitalization of interspike intervals is performed by the means of a variable RC-
le-precision counters, labeled CLOCK I and CLOCK II respectively. This allows counting up 4095 time units per
The time unit usually is set to 0.001 sec, higher values are optional for slow discharge rates.

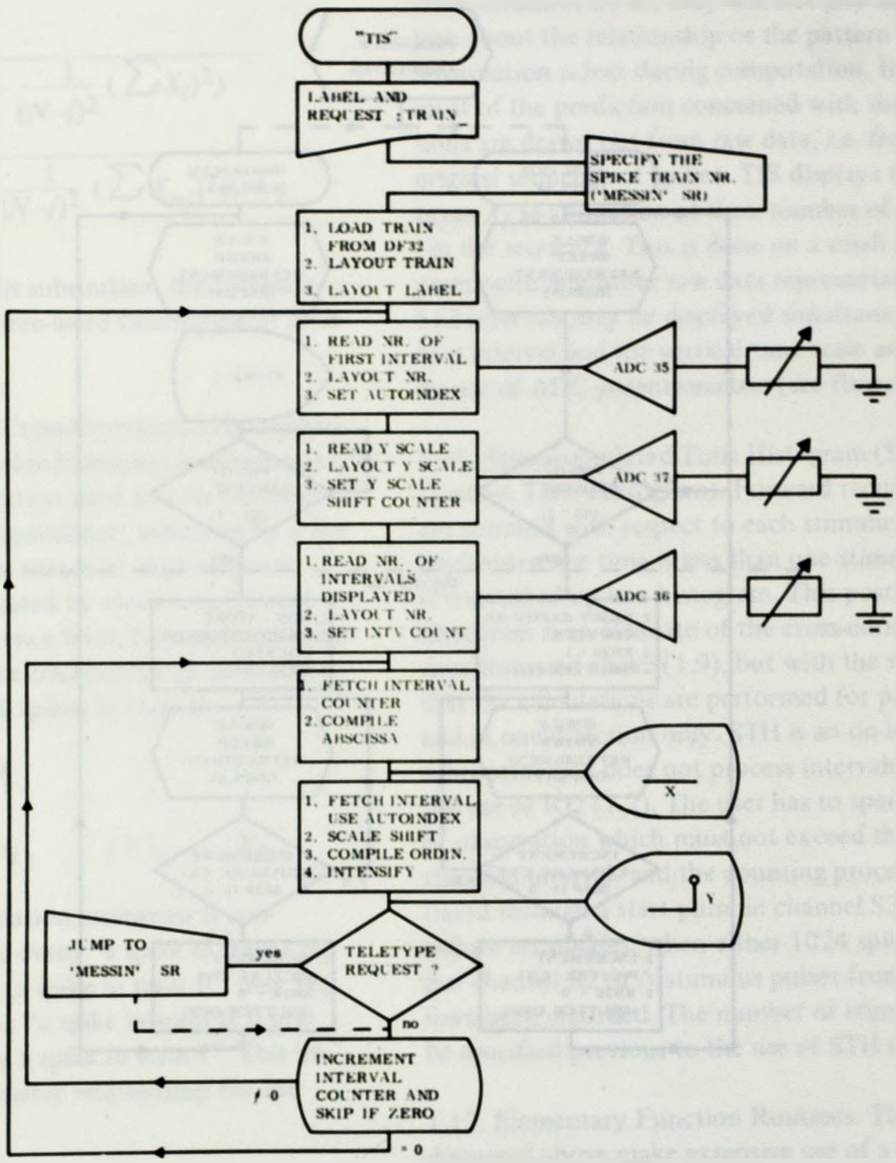


Fig. 4. Time Interval Sequence. This flowchart illustrates the option offered by small computers: Instant interaction between the user and program flow which is required when a 'trial-and-error' analysis is recommended.

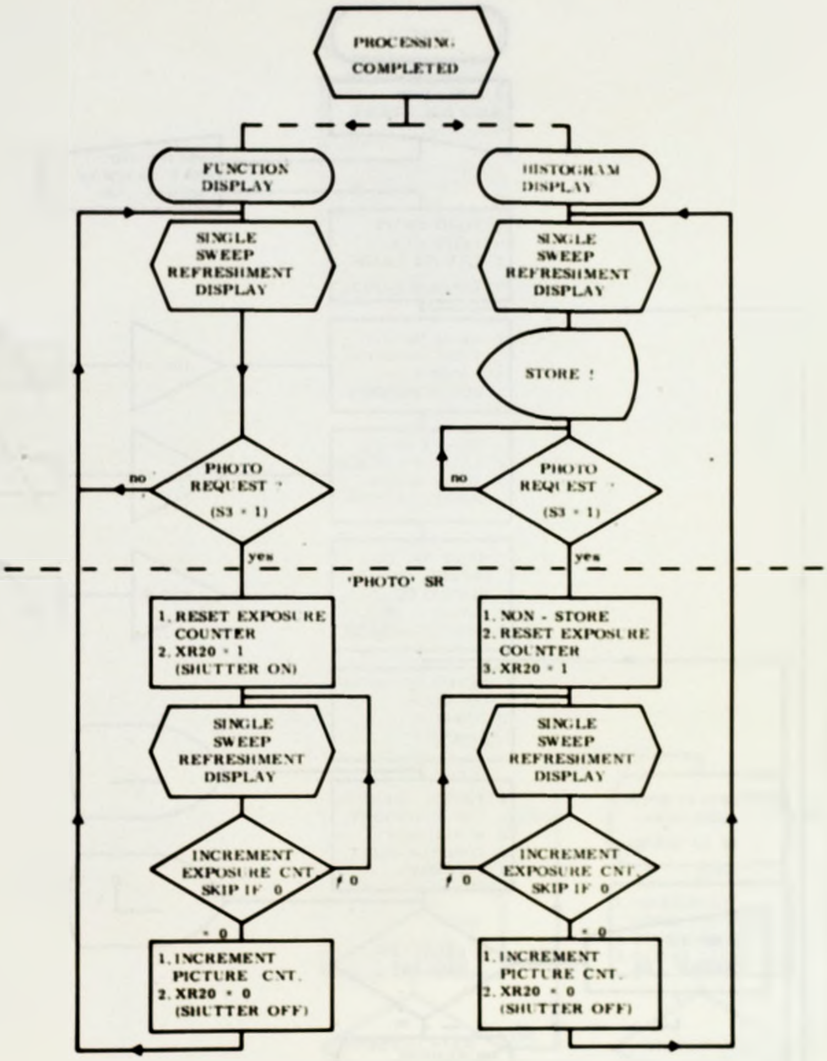


Fig. 5. CRT and Photo Remote Control Logic: The long refreshment intervals (0.3 – 0.5 sec) for histogram display imply the use of a storage oscilloscope to provide flicker-free pictures. However, photo records may be taken during a non-store sequence to provide well-focused copies. This sequence is initiated through sense line S3, its duration controlled by the exposure counter. The picture counter is incremented for each sequence and its value displayed in the top right corner of the display label for additional record identification.

$$\times \{\sqrt{\left(\frac{1}{N-j}\sum X_i^2 - \frac{1}{(N-j)^2}\left(\sum X_i\right)^2\right)} \cdots$$

$$\cdots \overline{\times \left(\frac{1}{N-j}\sum X_{i+j}^2 - \frac{1}{(N-j)^2}\left(\sum X_{i+j}\right)^2\right)}\}^{-1},$$

for $j = 1, \ldots, 128$. In this subroutine, the computations are performed in three-word floating-point arithmetic.

1.9. Cross-Correlogram (Cross-Correlation Histogram) (CCR). The cross-correlation histogram is an estimate of the cross-correlation function used as a corroboration of the hypothesis of independence, indicated by a flat cross-correlogram, or as a means of exploring suspected interactions indicated by elevations (peaks) with respect to the reference level. Forward and backward recurrence times are counted for all spikes in train I with respect to all spikes in train II

1.9.1. $$T_i^j = T_j^{\mathrm{II}} - T_i^{\mathrm{I}}, \quad i = 1, \ldots, N_{\mathrm{I}}, \quad j = 1, \ldots, N_{\mathrm{II}},$$

of which the cross-correlation histogram is constructed. The compound event "a spike in train I is followed at a time T_i^j by a spike in train II" may be described equivalently as "a spike in train II is pre-preceded at a time T_i^j by a spike in train I". This implies the following symmetry relationship for the cross-correlation

1.9.2. $$\frac{\xi_{\mathrm{I}\to\mathrm{II}}}{\mu_{\mathrm{I}}} = \frac{\xi_{\mathrm{II}\to\mathrm{I}}}{\mu_{\mathrm{II}}},$$

where μ_{I} and μ_{II} are the mean intervals between spikes. Therefore, the cross-correlation estimate is measured in one direction, from train I to train II, but for both positive and negative values of T_i^j. Computations are performed in signed double-precision arithmetic.

1.10. Time Interval Sequence (TIS). Most of the statistical analysis done will deny the 'null hypothesis' but rather leads to the prediction of 'dependence', 'functional relationship', or 'significant patterns'. Although these measures do so, they will not give any information about the relationship or the pattern itself. This information is lost during computation. In practice most of the prediction concerned with these questions are drawn out from raw data, i.e. from the original sequence of spikes: TIS displays the interval times X_i as a function of their number of occurrence i in the sequence. This is done on a small area compared with any other raw data representation. Up to 512 intervals may be displayed simultaneously, the first interval and the vertical time scale are controlled by use of ADC potentiometers (see flowchart fig. 4).

1.11. Stimulus-related Time Histogram (STH) (Post-stimulus Time Histogram). Forward recurrence times are counted with respect to each stimulus pulse. If any recurrence time is less than one stimulus interval it is counted up in a histogram. This post-stimulus tim histogram is an estimate of the cross-correlation function discussed above (1.9), but with the restrictions that the calculations are performed for positive times and in one direction only. STH is an on-line analysis subroutine and does not process intervals counted by the use of IC2 (1.2). The user has to specify the time of observation which must not exceed the length of the stimulus interval, and the counting procedure is initiated through a start pulse in channel S3. The procedure terminates, when either 1024 spikes from input channel S2 or N stimulus pulses from input S1 have been recorded. The number of stimuli, N, must be specified previous to the use of STH (see 1.3).

1.12. Elementary Function Routines. The programs discussed above make extensive use of a set of subroutines stored in the lower core memory. Most of them are modified versions of the system's original software. For a general review, they are listed below:

MESAGE	Character String Type-out Subroutine
MESSIN	Character String Input Subroutine
MASTER	Program Control Master Subroutine
BINDEC	Binary to BCD Conversion
DECBIN	BCD to Binary Conversion
BINDUM	Binary Dump Subroutine

OCTDUM	Octal Dump Subroutine
PUNCH	Binary Punch Dubroutine
WRT/RDD	Disk Write/Read Subroutine
LOADTR/SAVETR	Interval Data File Load/Save Subroutine
GRID1/GRID2	CRT Scale Grid Display Subroutine
LABEL	CRT Label Layout Array
CHDSC	CRT Character Display Subroutine
READC	Analog-to-Digital Conversion
PHOTO	Photo Remote Control Subroutine
DFERR/ICPC OFLOW/ZERON	Error Message Subroutine

2. SAMPLE RUN

The spike trains were obtained from experiments with cats under chloralose anesthesia. The pyramidal tract (PT) and the lateral reticular nucleus (LRN) were exposed by a ventral approach and action potentials from single neurons recorded with tungsten microelectrodes.

PROGRAM LOADED/SELECT SUBROUTINE:
TYPE "*" AND CODE:

OPT IC1 IC2 HST AUT CMD TIS CPD SCG CCR	Initial dialogue following the loading procedures (In all examples, user response is underlined for clarity)
STH	End of initial dialogue
* OPT	
'OPT': RC	RC-clock calibration: Time base set to 0.001 sec
'OPT': ST	Schmitt-Trigger switching thresholds is varied to provide selective spike recording
S: 1	
'OPT': DN	Specify interval file length!
N: 1024	
'OPT': *IC1	Record and digitalize spike train!
'IC1' LINK DATA SIGNAL TO S1 START PULSE TO S3!	(Initial dialogue terminated: IC1 requires start pulse!)
EOJ!	Processing terminated!
*OPT	Start statistical parameters!
'OPT': L	
T: 1	(Input file: train I)
N + 0.1024000 E + 04 T + 0.3894170 E + 06 MU + 0.3802900 E + 03 S + 0.4564290 E + 03 C + 0.1200212 E + 01	1024 intervals have been counted over a period of 389.417 sec (6.5 min). Interval mean is 0.380 sec with standard deviation 0.456 sec. Estimate of the coefficient of variation is 1.2
'OPT': *TIS	To make out the source of the unusual variation the interval times are displayed sequentially (fig. 6A)
68-175 PT5	Record label: Experiment and unit identifier
*AUT	
'AUT' TRAIN 1 LAG ORDER 1 X SCALE FACTOR 4 'HST' Y SCALE FACTOR 1	A interval histogram (fig. 6B) is computed to show the probability density of the two populations indicated by fig. 6A
*SCG	
'SCG' TRAIN 1	The serial correlogram is used to test the sequential independence of the action potentials (fig. 7A)

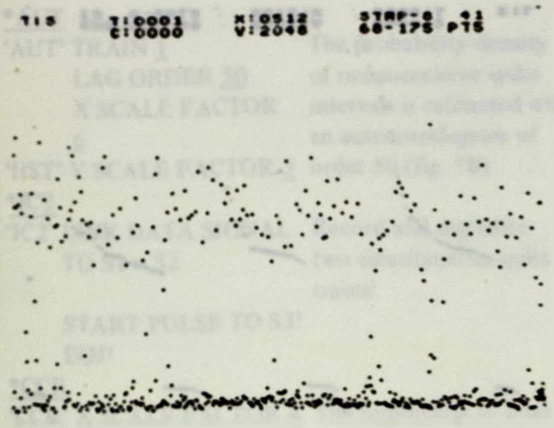


Fig. 6A. Spontaneous activity of a pyramidal tract unit (PT 5). INTERVAL SEQUENCE: 512 consecutive interval times are displayed on the ordinate. The vertical range covers 2048 mSEC. Two distinctive populations of long and short intervals are indicating a 'burst' pattern.

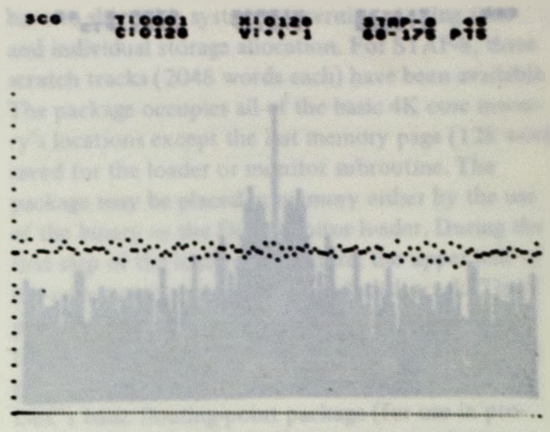


Fig. 7A. Spontaneous activity of unit PT 5. SERIAL CORRELOGRAM: The first 128 serial correlation coefficients do not show positive contributions above the significant level. The intervals are assumed to be drawn independently from the populations mentioned in fig. 6A, i.e. the number of spikes per 'burst' may vary at random.

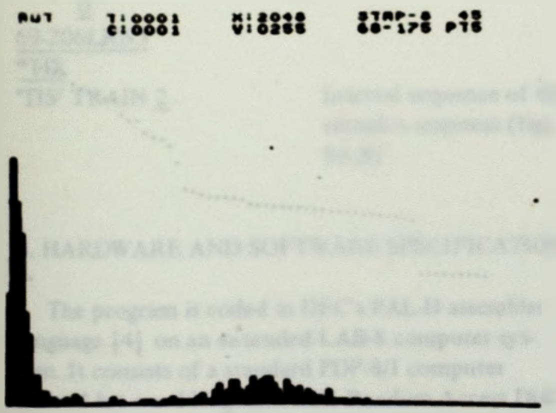


Fig. 6B. Same spike train as in fig. 6A. INTERVAL HISTOGRAM. Bimodal distribution with modes at 100 msec and at 1000 msec. Long and short intervals occur at a ratio of 1:2 respectively. The sample contains 1024 intervals.

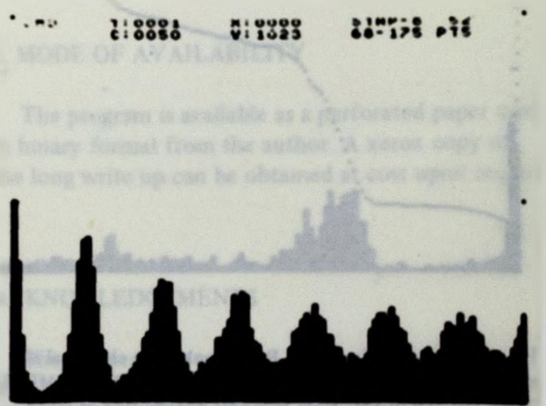


Fig. 7B. Same spike train as in fig. 7A. AUTOCORRELOGRAM: Discrete intervals of low and high expectation density are due to the narrow interspike-interval distributions shown in fig. 6B (time of observation 8 sec!).

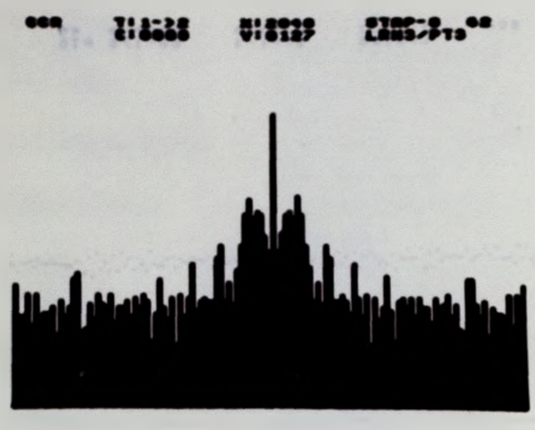


Fig. 8A. Spontaneous activity of a unit in the lateral reticular nucleus (LRN3 = spike train I) and of a unit of the pyramidal tract (PT3 = spike train II). CROSS-CORRELOGRAM: Recurrence times were displayed from – 1024 msec to + 1024 msec. Mutual interaction is indicated by significant peaks with interaction delay times varying from 0 to 16 msec and from 96 msec to 112 msec.

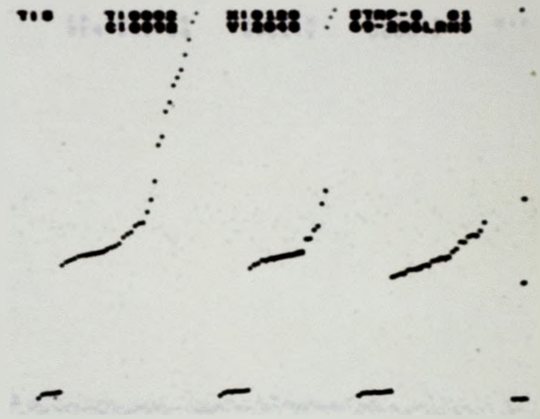


Fig. 9A. Activity of unit LRN3 evoked by electrical stimulation of the cat's contralateral forepaw. INTERVAL SEQUENCE: The post-stimulus time intervals are displayed sequentially. The stimulus artifact is immediately followed by early discharge-intervals and later by the after-discharge-intervals. Vertical time range: 2048 msec; sequence of 128 intervals after three consecutive stimuli.

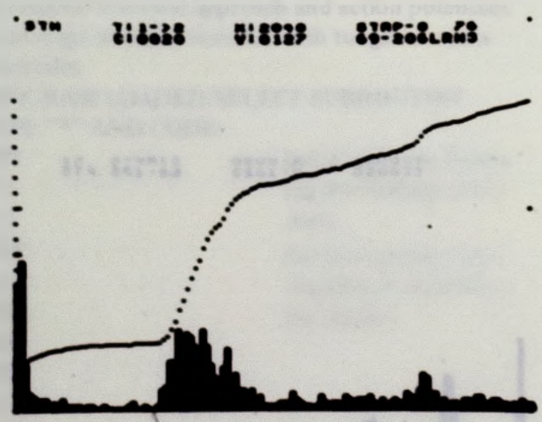


Fig. 8B. Activity of a unit (LRN3) evoked by electrical stimulation of the cat's contralateral forepaw. POST-STIMULUS TIME HISTOGRAM: Note trimodal distribution of recurrence times: An early-discharge (mode: 16 msec – 32 msec) and two after-discharges (modes: 688 msec – 704 msec and 1584 msec – 1600 msec). The double exposure shows the post-stimulus time histrogram together with the CUMULATIVE DISTRIBUTION FUNCTION. The sample contains 1024 stimulus-related spikes with respect to 20 stimuli.

Fig. 9B. Same spike train as in fig. 9A. INTERVAL SEQUENCE: Vertical time range: 4096 msec; sequence of 64 intervals after one single stimulus.

*AUT	
'AUT' TRAIN 1 LAG ORDER 50 X SCALE FACTOR 6	The probability density of nonsuccessive spike intervals is estimated with an autocorrelogram of
'HST' Y SCALE FACTOR 3	order 50 (fig. 7B)
*IC2	
'IC2' LINK DATA SIGNAL TO S1 + S2	Record and digitalize two simultaneous spike trains!
START PULSE TO S3! EOJ!	
*CCR	
'CCR' X SCALE FACTOR 4 'HST' Y SCALE FACTOR 0	The hypothesis of interaction is verified by a cross-correlogram (fig. 8A)
LRN3/PT3	Record identifier: Train I from LRN unit 3 Train II from PT unit 3
*STH	
'STH' X SCALE FACTOR 4 CHECK: STIMULUS TO S1? SIGNAL TO S2? START PULSE TO S3?	The stimulus related response of the LRN unit 3 is checked by a post-stimulus time histogram (fig. 8B)
'HST' Y SCALE FACTOR 0	
69-206LRN3	
*TIS	
'TIS' TRAIN 2	Interval sequence of the stimulus response (figs. 9A,B)

3. HARDWARE AND SOFTWARE SPECIFICATIONS

The program is coded in DEC's PAL-D assembler language [4] on an extended LAB-8 computer system. It consists of a standard PDP-8/I computer (4K/12-bit word length), a 32K Random Access Disk File DF32 [6], the Extended Arithmetic Element MP8/I, the AX08 Laboratory Peripheral [5], and a Tektronix 601 Storage Oscilloscope*. Several users have to share this system concerning running time and individual storage allocation. For STAP-8, three scratch tracks (2048 words each) have been available. The package occupies all of the basic 4K core memory's locations except the last memory page (128 words) saved for the loader or monitor subroutine. The package may be placed in memory either by the use of the binary or the Disk Monitor loader. During the first step of the loading procedure, the upper half of the core memory is saved on a full disk track. This part includes the eleven sequences discussed in section 1. Only the service and I/O routines rest in core permanently. Saved core space is then loaded with DEC's basic floating-point package (for use in programs OPT and SCG), and again saved on the lower half of the second disk track available. A phantom routine which monitors the initial load-and-save procedure is located at the resident sequence operating area and will be lost when the first sequence is called into core. The disadvantage of this concept becomes evident when package extensions for additional analysis programs should be implemented. However, as the equipment provides use of the Disk Monitor System, a user with high-priority access may compile an open ended library by the use of the storage and retrieval facilities of the monitor system. This program may also be adapted to a LINC-8 or a PDP-12 system.

* This system is part of the equipment of the EEG Laboratory, Department of Pediatrics, University of Zürich.

5. MODE OF AVAILABILITY

The program is available as a perforated paper tape in binary format from the author. A xerox copy of the long write up can be obtained at cost upon request

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