The Relation Between Multiple Markov Sequences of Interpoint Intervals and Density Modulated Point Sequences

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Abstract

Markov sequences of interpoint intervals are generated by computer simulation. A kind of rational transitional probability density function is found to be satisfactory to simulate wide varieties of neuronal spike trains. Three examples of the Markov sequences are examined, two of which are to simulate the actual spike trains obtained from the central neurons of the cat. The third one has exponential type interval histogram.

The generated Markov sequences as well as the neuronal spike trains usually show slow fluctuation of point densities. When a point sequence of this kind is smoothed by an appropriate filter, the point density fluctuation is extracted. By an inverse procedure of integral density modulation with this point density as the modulating signal, the point sequence is transfomed into another sequence which has nearly constant point density. It is found that the transformed point sequence can be approximately regarded as a renewal sequence, if the right kind of filter is selected.

1. Introduction

Neuronal spike trains usually have rather complex structure, and cannot be described successfully by simple Poisson point processes or renewal processes.

We previously proposed a density modulated point secuence as a model of the neuronal spike train (Iso, Yanaru and Nakayama, 1971, Yanaru and Iso, 1974). While Nakahama et al. (Nakahama, Ishii and Yamamoto, 1972, 1974) have shown that the neuronal spike trains recorded from the mesencephalic reticular formation (MRF) and the red nucleus (RN) neurons can be regarded as the Markov sequences of interspike intervals. The relation between these two kinds of point sequences is not yet clear. We noticed in the course of previous investigation that the neuronal spike trains obtained by Nakahama et al. showed slow fluctuation of point densities. It will be natural to ask whether these sequences can also be regarded as the point sequences resulted from density modulation of renewal processes.

To investigate this, we choose the following method : 1. A Markov sequence of intervals with known transition probability density function is generated. 2. An approximate point density is obtained by smoothing the point sequence by an appropriate filter. 3. The point sequence is transformed into an another point sequcence, by an inverse procedure of integral density modulation with the approxinate point density as the modulating signal. 4. The transformed sequence is statistically examined.

Three kinds of Markov sequences are generated, two of which are similar to the spike trains of MRF and RN neurons respectively, in the interpoint intervel histograms and in the first order serial correlation coefficients. The third one has an exponenential type interval histogram. The neuronal spike trains are also investigated by the same method.

We will use the following notations to represent five point sequences,

{MRF} : the neuronal spike train of MRF neuron,

{RN} : the neuronal spike train of RN neuron,

{MP−MRF} : the generated Markov point sequence simulating {MRF} ,

{MP−RN} : the generated Markov point sequ-

ence Simulating {RN} ,
{MP−EXP} : the generated Markov point sequence which has exponential type interval histogram.

It is found that all the point sequences examined can be approximately regarded as the modulated point spquences of renewal processes, though the different types of filters are used to smooth the simulated point sequences and the neuronal spike trains : the ideal filter for the simulated point sequences and the Gaussian filter for the neuronal spike trains.

2. Generation of Markov Point Sequence

2.1. General remarks of Morkov process of order k

Let $\zeta = \{x_i\}$ $(x_i > 0,\ i = 0,\ \pm 1,\ \pm 2, \cdots\cdots)$ be a sequence of successive interpoint intervals X_i's and $\{\zeta\}$ be the universe of ζ. Assume that $\{\zeta\}$ forms a stationary stochastic process, i. e. we assume the existence of $(k+1)$ dimensional distribution function,

$$F(x_0,\ x_{-1},\ \cdots,\ x_{-k}) = \mathrm{Prob}(X_0 < x_0,\ \cdots,\ X_{-k} < x_{-k}) = \mathrm{Prob}\,(X_n < x_0,\ \cdots,\ X_{n-k} < x_{-k}), \quad \text{for every } n. \tag{1}$$

A discrete parameter stochastic process $\{\zeta\}$ is said to be a Markov process of order k (wold), if

$$F_{X_0|X_{-1},\cdots,X_{-k}}(x_0|x_{-1},\ \cdots,\ x_{-k}) = F_{X_0|X_{-1},\cdots,X_{-l}}(x_0|x_{-1},\ \cdots,\ x_{-l}), \text{ for all } l > k, \tag{2}$$

where, $F_{X_0|X_{-1},\cdots,X_{-k}}$ and $F_{X_0|X_{-1},\cdots,X_{-l}}$ are conditional distribution functions. We shall call this simply "Markov process", and if we need to indicate explicitly the multiplicity k, we use the term "k-Markov process".

2.2. The method of generation

One of the authors previously reported on a method of generating Markov sequences of intervals with known transition probability densities (Yanaru and Nakahara, 1974). The same method is used here.

Let U be a uniform random number and $F(x)$ be an arbitrary distribution function, then, $X = F^{-1}(U)$, where $F^{-1}(\cdot)$ is the inverse function of $F(\cdot)$, is the random number with the distribution function $F(x)$. If we use the conditional distribution function $F_{X_i|G_{i-1}}(x_i|g_{i-1})(i = 0,\ 1,\ 2,\ \cdots)$ in place of $F(x)$, where G_{i-1} denotes the set of k conditional random numbers, $(X_{i-1},\ \cdots,\ X_{i-k})$, and g_{i-1} is the set of corresponding realizations, $(x_{i-1}, \cdots\cdots, x_{i-k})$, we can generate a k-Markov sequence by the following procedure.

1) Choose an arbitrary set of k initial constans $g_{-1} = (x_{-1},\ \cdots,\ x_{-k})$, for example $x_{-1} = \cdots\cdots = x_{-k} = 1$.

2) Take a realization u_0 of a uniform random number $U(0,\ 1)$, and find x_0 satisfying the equation $F_{X_0|G_{-1}}(x_0|g_{-1}) = u_0$, then, x_0 is a realization of the random number with the the distribution function $F_{X_0|G_{-1}}(x_0|g_{-1})$.

3)The condition $g_{-1} = (x_{-1},\ \cdots\cdots,\ x_{-k})$ is replaced by $g_0 = (x_0,\ x_{-1},\ \cdots\cdots,\ x_{-k+1})$, i. e., the oldest of the conditional values, x_{-k}, is removed from the set of condition, and the newly obtained value is added in the latest position.

4) Take the second realization u_1 of the uniform random number $U(0,\ 1)$, and find x_1 which satisfies the relation, $F_{X_1|G_0}(x_1|g_0) = u_1$.

5) Repeat the steps 3) and 4), but each time the condition g_{i-1} is replaced by the new condition g_i.

Thus, the sequence $\{x_i\}(i = 0,\ 1,\ 2,\ \cdots\cdots)$ is obtained. If sufficient numbers of x_i's, which may possibly have the after-effect of the initial values, are discarded, the remaining sequece can be regarded as the stationary k-Markov point sequence.

As the transitional probability density function $T_{X_i|G_{i-1}}(x_i|g_{i-1})$ (for convenience, i=0 is used below), we use Eq. (3),

$$T_{X_0|G_{-1}}(x_0|g_{-1}) = \frac{D\cdot H^{n+(m+1)(k-1)}\cdot x_0^m}{(x_0+H)^{n+(m+1)k}} \tag{3}$$

where,

$$H = x_{-1} + x_{-2} + \cdots\cdots + x_{-k} + C,$$
$$D > 0,\ C > 0,$$
$$x_0,\ x_{-1},\ \cdots,\ x_{-k} \geqq 0\ ,$$
$$m = 0,\ 1,\ 2,\ \cdots, \qquad n = 4,\ 5,\ 6,\ \cdots.$$

Note that an integer larger than or equal to four is used for n, this is necessary for the first and second order moment to exist. The reason why Eq. (3) is used is given in the appendix.

The corresponding conditional distribution function is

$$F_{X_0|G_{-1}}(x_0|g_{-1}) = D\cdot\sum_{j=0}^{m}\binom{m}{j}\cdot\frac{(-1)^j}{n+2m+2+j}\cdot\left\{1-\left(\frac{H}{x_0+H}\right)^{n+2m+2+j}\right\}. \tag{4}$$

The following three types of sequences are generated.

Type 1, {MP−MRF} : $k = 3,\ n = 39,\ m = 9,\ c = 2.8$.

$$D = 2.908\times10^{12}$$

Type 2, {MP-RN} : $k = 3,\ n = 21,\ m = 3,\ c = 4.0$

$$D = 1.438\times10^{5}$$

Type 3, {MP-EXP} : $k = 3,\ n = 4,\ m = 0,\ c = 2.0$

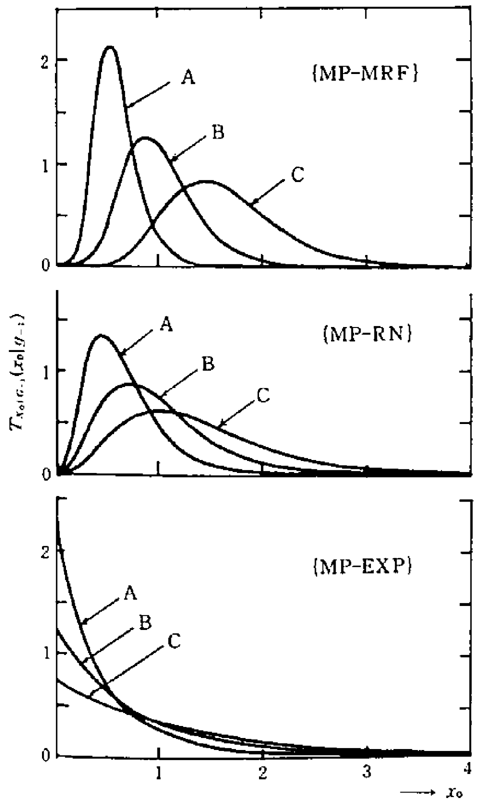
$$D = 6.000$$

As mentioned in the introduction, the sequences of type 1 and 2 are intended for simulating the neuronal spike trains obtained from the MRF and RN neurons respectively. The sequence of type 3 has the exponential type interval histogram.

For the type 1 and 2 sequences, the parameter values are determined so as to satisfy the following conditions.

(i) The order of multiplicity k is equal to three.

(ii)The probability density functions of intervals should resemble in shape the interval histograms of the corresponding neuronal spike trains, as closely as possible.



Examples of the transitional probability density functions of intervals of three types of sequences.

curve A : $x_{-1} = x_{-2} = x_{-3} = 0.2$,
curve B : $x_{-1} = x_{-2} = x_{-3} = 1.0$,
curve C : $x_{-1} = x_{-2} = x_{-3} = 2.0$

Fig. 1

(iii) The first order correlation coefficients of intervals should be nearly equal to those of the corresponding neuronal spike trains.

Fig. 1 shows examples of the transitional probability density function of three types of sequences. The conditional values are as follows, curve A : $x_{-1}= x_{-2} = x_{-3} = 0.2$, curve B : $x_{-1} = x_{-2} = x_{-3} = 1.0$, curve C : $x_{-1} = x_{-2} = x_{-3} = 2.0$.

3. Inverse Density Modulation

We want to know what kind of point sequence results from a Markov sequence of intervals, when its slow fluctuation of point density is eliminated. In this section we first describe the method to obtain an approximate point density. Next, the processes of density modulation and inverse density modulation are briefly surveyed. We then apply the above methods to the simulated point sequences and neuronal spike trains, that is, we obtain the approximate point densities from these sequences, and using this approximate point densities and inverse modulation procedure, we transform the original point sequences to new point sequences which have nearly constant point densities. The original sequences, their approximate point densities, and the inverse modulated point sequences are statistically examined.

3.1. Approximate point density

Let $t_i(i = 1, 2, \cdots\cdots, N)$ be the occurrence times of points, then,

$$R(t) = \sum_{i=1}^{N}\delta(t-t_i), \tag{5}$$

where $\delta(t)$ is the delta function, repesents the pulse train. When this pulse train is smoothed by an appropriate filter, the approximate point density is obtained. We try two kinds of filters : an ideal filter, which has an impulse response or a time weighting function $W_I(t)$, and a Gaussian filter with an impulse response $W_G(t)$. The ideal filter has the rectangular shape in frequency domain, with the central frequency F_0 and the frequency bandwidth F_w. The Gaussian filter has the shape of normal probaility density function in both frequency domain and time domain.

The smoothed signal $\lambda_1(t)$ is given by

$$\lambda_1(t) = \sum_{i=1}^{N} W_j(t-t_i) \qquad (j = I \text{ or } G) \tag{6}$$

When the filter is an ideal type, $\lambda_1(t)$ can take negative value. But, since the point density must be nonnegative, $\lambda_1(t)$ is shifted uniformly in the positive direction as follows,

$$\lambda_2(t) = \lambda_1(t) - \lambda_{1min} \tag{7}$$

where λ_{1min} is the minimum value of $\lambda_1(t)$. To avoid the edge effect, we discard the sufficient length of parts, $\varepsilon \cdot M_X$, where ε is a positive integer, and M_X is the mean interval, from the both ends of $\lambda_2(t)$. Finally, normalizing $\lambda_2(t)$ to haye unit mean value, we obtain the approximate point density,

$$\lambda_a(t) = \frac{(t_2 - t_1)\cdot\lambda_2(t)}{\int_{t_1}^{t_2} \lambda_2(t)dt}. \tag{8}$$

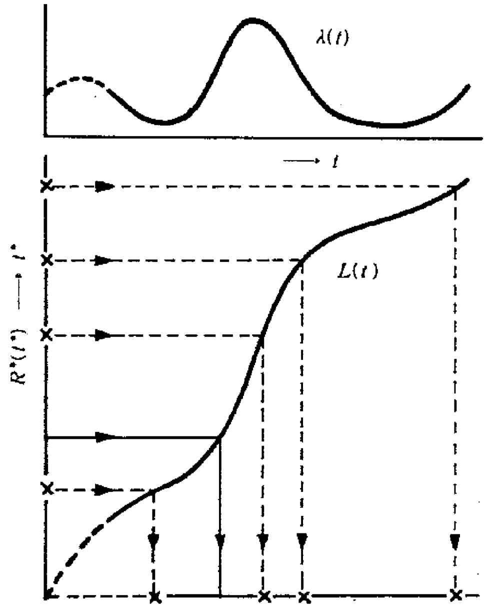
where, $t_1 = \varepsilon \cdot M_X$, $t_2 = (N-\varepsilon)\cdot M_X$.

3.2. Density modulation and inverse density modulation

As reported previously (Yanaru and Iso 1974), density modulation is carried out as follows. Fig. 2 shows the mudulation procedure. $R^*(t^*)$ is the unmodulated point sequence, $\lambda(t)$ is the modulating signal, $L(t)$ is the integral of $\lambda(t)$, i. e.,

$$L(t) = \int_0^t \lambda(u)du. \tag{9}$$

$R(t)$ is the modulated point sequence.



The modulation procedure. $R^*(t^*)$: the unmodulated point sequence, $R(t)$: the modulated point sequence, $\lambda(t)$: the modulating signal, $L(t)$: the integral of $\lambda(t)$

Fig. 2

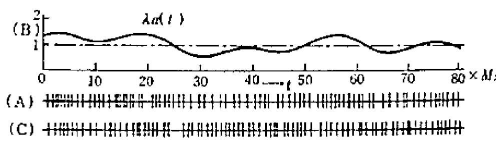
If a certain point sequence with a point density fluctuation is given, we can extract the approximate point density $\lambda_a(t)$ as described in the last setion. Further, using as the modulating signal, we can obtain the inverse modulated point sequence $R_a^*(t^*)$ by the inverse procedure of the density modulation.

3.3. Results

Five kind of point sequences are examined : {MP-MRF} , {MRF} , {MP-RN} , {RN} , {MP-EXP}, each of which consists of 2000 interpoint intenals. The duration of the corresponding approximate point density is 1600 M_X, i. e., the values of N and ε in Eq. (8) are 2000 and 200 respectively.

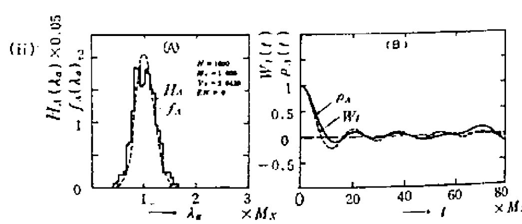
The results obtained by statistically processing these point sequences {MP-MRF}, {MRF} and {MP-EXP} are shown in Fig. 3, Fig. 4 and Fig. 5 respectively. (As for the point sequences {MP-RN} and {RN} the results are not illustrated to save the space, but we come to the similar conclusions to those for the point sequences {MP-MRF} and {MRF})

Fig. 3. The results of point sequence {MP-MRF}



(A) : a part of original point sequence, (B) : the approximate point density, (C) : the inverse modulated point pequence.

Fig.3 ——(i)

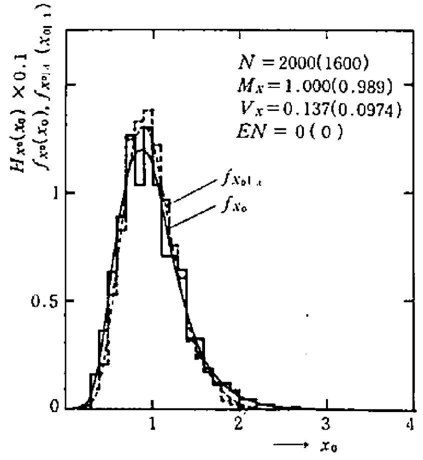


(A) : the histogram $H_A(\lambda_a)$ of the approximate point density (solid line), and the theoretical probability density function

$f_A(\lambda_a)\left\{= \frac{29^{29}}{28!}\lambda_a^{28}\cdot\exp(-29\lambda_a)\right\}$ (broken curve).

(B) : the autocorrelation function $\rho_A(t)$ of the approximate point density (solid curve), and the shape of the time weighting function $W_t(t)$ (broken curve).

Fig. 3 ——(ii)



The probability density function

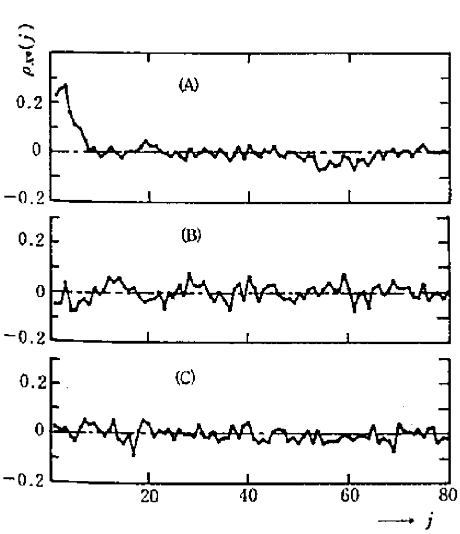
$f_{X_0}(x_0)\left\{=\frac{4.387\times10^{22}\cdot x_0^8}{(x_0+2.8)^{39}}\right\}$ (solid curve),

and the conditional probability density function

$f_{X_0|A}(x_0|1)\left\{=\frac{10^{10}}{9!}\cdot x_0^9\cdot\exp(-10x_0)\right\}$ (broken curve).

The interval histogram $H_{X_0}(x_0)$ of the original sequence {MP-MRF} (solid line), and that of the inverse modulated point sequence $\{\text{MP-MRF}\}_{inv}$ (broke line).

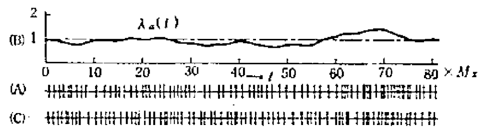
Fig. 3 ——(iii)



(A): the serial correlation coefficients of intervals, $\rho_{X_0}(j)$ of the original point sequence {MP-MRF}, (B): $\rho_{X_0}(j)$ of the inverse modulated point sequence $\{\text{MP-MRF}\}_{inv}$ (C): $\rho_{X_0}(j)$ of the point sequence $\{\text{MP-MRF}\}_{inv\text{-}shuff}$

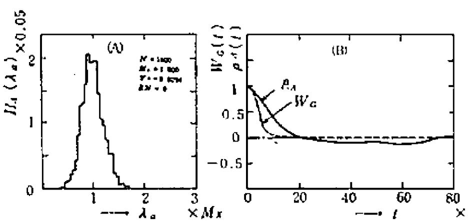
Fig. 3 ——(iV)

Fig.4. The results of point sequence {MRF}



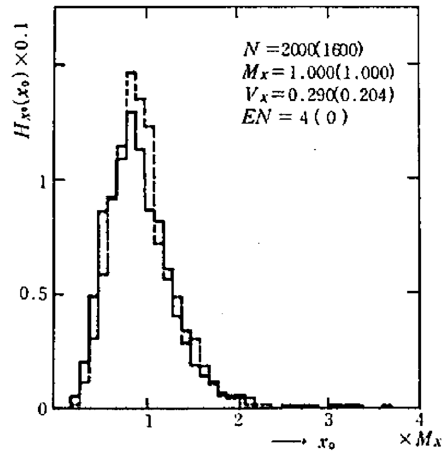
(A): a part of the original point sequence, (B): the approximate point density, (C): the inverse modulated point sequence.

Fig. 4 -(i)



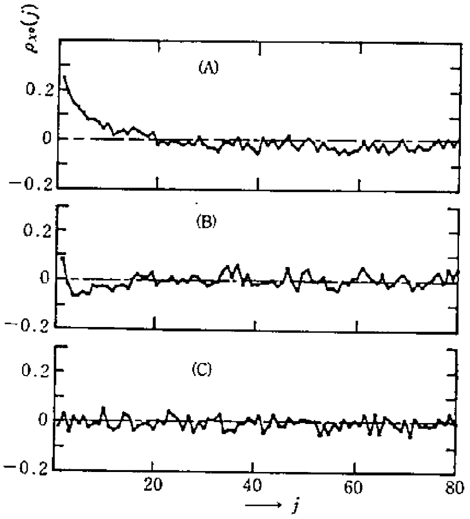
(A): the histogram $H_A(\lambda_a)$ of the approximate density, (B): the autocorrelation function $\rho_A(t)$ of the approximate point density (solid curve), and the shape of the time weghting function $W_C(t)$ (broken curve).

Fig. 4 ——(ii)



The interval histogram $H_{X_0}(x_0)$ of the original sequence {MRF} (solid line), and that of the inverse modulated point sequence $\{\text{MRF}\}_{inv}$ (broken line).

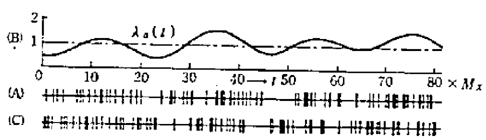
Fig. 4 ——(iii)



(A): the serial correlation coefficients of intervals, $\rho_{x_0}(j)$ of the original point sequence $\{MRF\}$, (B): $\rho_{x_0}(j)$ of the inverse modulated point sequence $\{MRF\}_{inv}$ (C): $\rho_{x_0}(j)$ of the point sequence $\{MRF\}_{inv\text{-}shuff}$

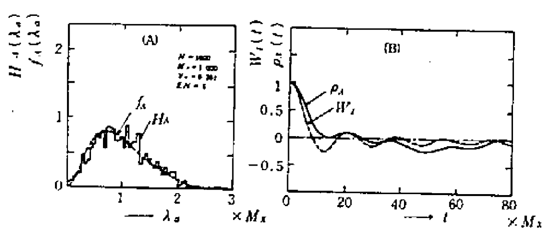
Fig. 4——(iv)

Fig. 5. The results of point sequence {MP-EXP}



(A): a part of original point sequence, (B): the approximate point density, (C): the inverse modulated point sequence.

Fig. 5 ——(i)

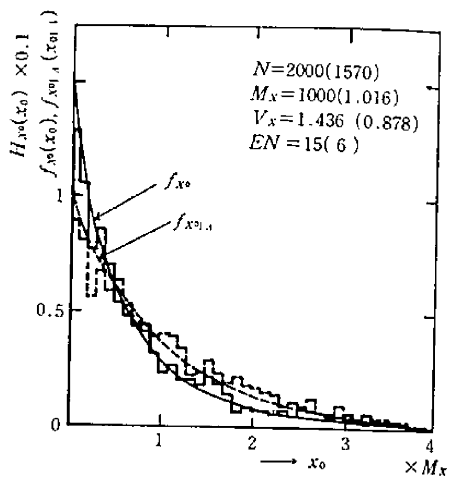


(A): the histogram $H_A(\lambda_a)$ of the approximate point density (solid line), and the theoretical probability density function

$f_A(\lambda_a)\left\{=\frac{3^3}{2!}\lambda_a^2\exp(-3\lambda_a)\right\}$ (broken curve).

(B): the autocorrelation function $\rho_A(t)$ of the approximate point density (solid curve), and the shape of the time weighting function $W_t(t)$ (broken curve).

Fig. 5——(ii)



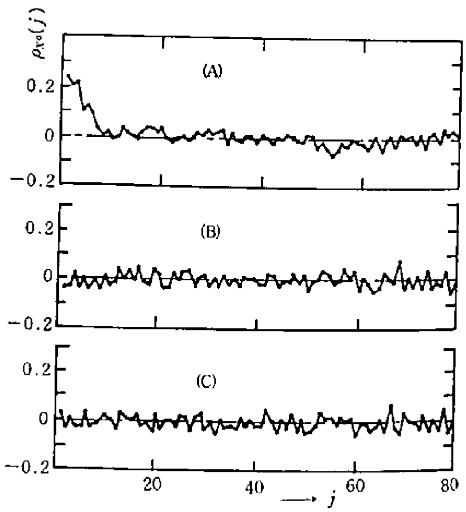
The probability density function

$f_{x_0}(x_0)\left\{=\frac{24}{(x_0+2)^4}\right\}$ (solid curve),

and the conditional probability density function $f_{x_0|A}(x_0|1)\{=\exp(-x_0)\}$ (broken curve).

The interval histogram $H_{x_0}(x_0)$ of the original sequence {MP-EXP} (solid line), and that of the inverse modulated point pequence $\{MP\text{-}EXP\}_{inv}$ (broken line).

Fig. 5 ——(iii)



(A): the serial correlation cofficents of intervals $\rho_{x_0}(j)$ of the original point sequence {MP-EXP}, (B): $\rho_{x_0}(j)$ of the inverse modulated point sequence $\{MP\text{-}EXP\}_{inv}$ (C): $\rho_{x_0}(j)$ of the point sequence $\{MP\text{-}EXP\}_{inv\text{-}shuff}$

Fig. 5——(iv)

Each of these figures contains four parts (i) ~(iv) as follows.

(i), (A), A part of the original point sequence, the point of occurrences are marked by vertical bars.

(B), The approximate point density of the point sequence.

(C), The inverse modulated point sequence.

The time scale is common to all figures, and the mean interval is taken as the unit.

(ii), (A), The The histogram $H_\Lambda(\lambda_a)$ of the approximate point density $\lambda_a(t)$ (solid line), and the theoretical probability function $f_\Lambda(\lambda_a)$ of Eq. (23) (broken curve). The binwidth for $H_\Lambda(\lambda_a)$ is 0.05. N is the total number of samples. EN is the number of samples whose values exceed the maximum value of the abscissa. V_Λ is the variance of Λ.

(B), The autocorrelation function $\rho_\Lambda(t)$ of the approximate point density $\lambda_a(t)$ (solid curve), and the shape of the time weighting function $W_j(t)$ ($j = I$ or G) (broken curve).

(iii), The probability density function $f_{X_0}(x_0)$ given by Eq. (22) (solid curve), and the conditional probability density function $f_{X_0|\Lambda}(x_0|1)$ given by Eq. (25) (broken curve).

The interval histogram $H_{X_0}(x_0)$ of the original point sequence {・} (solid line), and that of the inverse modulated point sequence $\{\cdot\}_{inv}$ (broken line). The time binwidth is $0.1M_X$, N is the total number of sample intervals. EN is the number of sample intervals whose values exceed the maximum value of the abscissa. V_X is the variance of intervals. The values of these numbers in parentheses are for the inverse modulated point sequence $\{\cdot\}_{inv}$.

(iv), (A), The serial correlation coefficients of intervals, $\rho_{X_0}(j)$ of the original pointsequence {・}

(B), $\rho_{X_0}(j)$ of the inverse modulated point sequence $\{\cdot\}_{inv}$.

(C), $\rho_{X_0}(j)$ of the point sequence $\{\cdot\}_{inv\text{-}Shuff}$ which is obtained by shuffling the inverse modulated point sequence. The shuffling is carried out as follows. Two numbers i and j are drawn from the integer uniform random number $U(1, 1600)$, the i-th and j-th intervals are interchanged, this procedure is repeated 2000 times.

The shuffled sequence thus obtained may be regarded as the homogeneous renewal point sequence. The comparison between the curves (B) and (C) helps us to find how close the inverse modulated point sequence is to the homogeneous renewal point sequence.

To minimize the serial correlation coefficient of intervals, we need to adjust the filter shape, i. e., the central frequency F_0 and the frequency bandwidth F_w for the ideal filter, and the frequency bandwidth for the Gaussian filter. Each of the above figures shows the best result of several trials.

We observe the following from these figures.

1) The approximate point densities $\lambda_a(t)$, of (i)−(B) represent fairly well the slow flutuations of (i)−(A).

2) The slow fluctuations are greatly decreased in the inverse modulated point sequences $\{\cdot\}_{inv}$ as shown in (i)−(C).

3) The autocorrelation functions of the approximate point densities, $\rho_\Lambda(t)$ of the simulated point sequences and the time weighting functions $W_I(t)$ show fairly similar shapes, but the functions $\rho_\Lambda(t)$ are somewhat wider than the corresponding time weighting functions $W_G(t)$ for the case of neuronal point sequences.

4) There is sufficient similarity between the shapes of the histograms of the approximate point densities, $H_\Lambda(\lambda_a)$, and those of the probability density function $f_\Lambda(\lambda_a)$ given by Eq.(23) in the appendix.

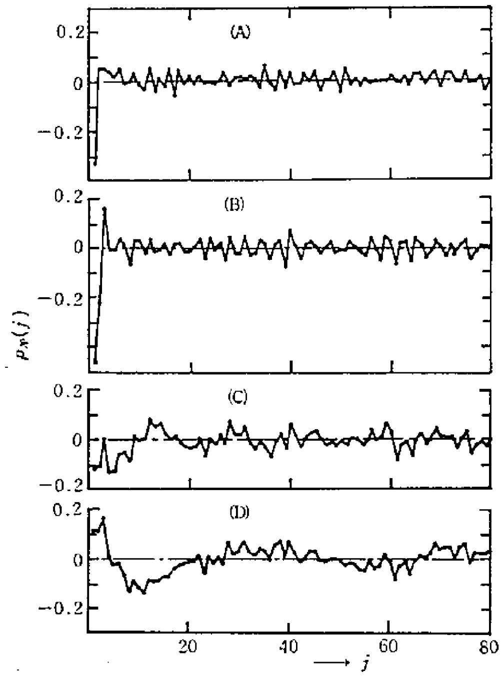
5)There is close resemblance between the interval histograms $H_{X_0}(x_0)$ of the inverse modulated point sequence $\{\cdot\}_{inv}$ and the conditional probability density functions $f_{X_0|\Lambda}(x_0|1)$ of Eq. (25) in the appendix.

4) and 5) show that an approach adopted in the appendix is adequate.

6) By comparing the curves in (iv)−(B), the serial correlation coefficient of intervals, $\rho_{X_0}(j)$ of inverse modulated point sequence $\{\cdot\}_{inv}$, with the curves of (iv)−(C), those of the shuffled sequences $\{\cdot\}_{inv\text{-}Shuff}$, we notice slight residuals of correlations at small j values in $\rho_{X_0}(j)$ of $\{\cdot\}_{inv}$. Thus we may roughly regard the inverse modulated point sequences as homogeneous renewal point sequences, In other words, some Markov sequences of intervals can also be regarded as density modulated renewal point sequences.

7)There is fairly close similarity between the neuronal point sequence {MRF} and its simulated point sequence {MP-MRF} or between {RN} and {MP-RN} . But it should be noted that the Gaussian filter is used to smooth the neuronal point

sequence because it leads to smaller correlation coefficients than the ideal filter does.



Variation of the serial correlation coefficients of intervals, $\rho_{x_0}(j)$ of the point sequence {MP-MRF}$_{inv}$, when the frequency bandwidth of the ideal filter is changed.

(A) : $F_0 = F_w = 0.5$ (B) : $F_0 = F_w = 0.1$,
(C) : $F_0 = F_w = 0.03$, (D) : $F_0 = F_w = 0.01$.

Fig. 6.

Fig. 6 shows how the serial correlation coefficients, $\rho_{x_0}(j)$ of the inverse modulated point sequence {MP-MRF}$_{inv}$, vary when the frequency bandwidth of the ideal filter is changed. The wider the bandwidth is, the more enhanced is the negative values of the lower order correlation.

We have found that the serial correlation coefficient curve which is very similar to curve (A) or (B) is obtained, when several renewal point sequences are superposed (Yanaru, Oda and Iso, 1975). In the nervous system, the supersosition of spike trains is widely observed. Therefore, it will be worthwhile to study the density modulation of the superposed renewal point sequence.

4. Conclutions

1) When a given point sequence has slow fluctuation of point density, we can find a class of probability density functions, which are convenient to represent the histograms of the point density values and those of intervals of this point sequence, and are easy to manipulate.

2) From one of these probability density functions, we can derive the transitional probability density function of Markov process of order k, which can be used to generate a Markov sequence of intervals by means of computer simulation.

3) Some of Markov sequences of intervals, both simulated sequences and neuronal spike trains, can be regarded as point sequences which are obtained by density by density modulation of renewal processes.

Appendix

Derivation of Equation (3)

Assume that a given sequence of intervals has large positive serial correlation coefficients of intervals extending over considerable serial numbers. The point sequnce usually shows slow fluctuation of the point density. It the fluctuation is so slow that the point denstiy does not change its value appreciably during the period equal to the mean interval, then we can approximate the point density by a steplike signal as shown in Fig. 7.

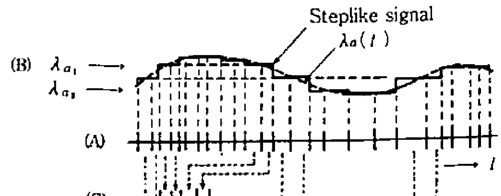


Diagram showing the derivation of Eq.(10).
(A): original point sequence, (B): the corresponding steplike signal, (C): the point sequence obtained by arranging the intervals which have the same value λ_{a_1}, (D): the point sequence obtained by arranging the intervals which have the same value λ_{a_2}.

Fig. 7.

The steplike signal is composed as follows : A step width is equal to the sum of two successive intervals, and the value of the signal is equal to the mean value of the point density in the interval of the step.

By considering all the steps which have the same value $\Lambda = \lambda_a$ together, the conditional probability density function $f_{X_0,X_{-1}|\Lambda}(x_0, x_{-1}|\lambda_a)$ of (X_0, X_{-1}), given $\Lambda = \lambda_a$, can be obtained. From the definition of the conditional probacility density function,

$$f_{X_0,X_{-1}|\Lambda}(x_0, x_{-1}|\lambda_0) = \frac{f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_a)}{f_\Lambda(\lambda_a)}, \quad (10)$$

where, $f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_a)$ is the three dimensional probability density function of (X_0, X_{-1}, Λ) and $f_\Lambda(\lambda_a)$ is the marginal probability density function of Λ.

From the joint probability density function, we can derive various marginal probability density functions

$$f_{X_0,X_{-1}}(x_0, x_{-1}) = \int_0^\infty f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_a)d\lambda_a, \quad (11)$$

$$f_{X_i}(x_i) = \int_0^\infty\int_0^\infty f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_a)dx_jd\lambda_a, \quad (12)$$

where, $(i, j) = (0, -1)$ or $(-1, 0)$,

$$f_\Lambda(\lambda_a) = \int_0^\infty\int_0^\infty f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_a)dx_0dx_{-1}. \quad (13)$$

We previously reported that when a renewal process is density modulated, the local independence is preserved between successive interpoint intervals, i. e.

$$\begin{aligned} &f_{X_0,X_{-1}|\Lambda(t)}(x_0, x_{-1}|\lambda(t), t\epsilon T) \\ &= f_{X_0|\Lambda(t)}(x_0|\lambda(t), t\epsilon T) \\ &\cdot f_{X_{-1}|\Lambda(t)}(x_{-1}|\lambda(t), t\epsilon T). \end{aligned} \quad (14)$$

If a Markov sequence of intervals can be regarded as the density modulated renewal sequence, the same relation must hold for an appropriate signal $\lambda_a(t)$.

If the steplike signal is used for $\lambda(t)$, Eq.(14) assumes the form,

$$f_{X_0,X_{-1}|\Lambda}(x_0, x_{-1}|\lambda_a) = f_{X_0|\Lambda}(x_0|\lambda_a)\cdot f_{X_{-1}|\Lambda}(x_{-1}|\lambda_a) \quad (15)$$

From Eqs. (10) and (15),

$$f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_a) = \eta_0(x_0, \lambda_a)\cdot\eta_{-1}(x_{-1}, \lambda_a),$$

where, $\eta_i(x_i, \lambda_a) = \{f_\Lambda(\lambda_a)\}^{\frac{1}{2}} f_{X_i|\Lambda}(x_i|\lambda_a)$ $(i = 0$ or $-1)$ (16)

Assume the following function for η_i,

$$\eta_i(x_i, \lambda_a) = b_i(a\lambda_a)^{\frac{n+m}{2}}\cdot x_i^m\cdot\exp\{-a\lambda_a(x_i+\frac{c}{2})\}, \quad (i = 0 \text{ or } -1). \quad (17)$$

Where, n and m are positive integers satisfying the conditions $n \geq m+4$, $n+m = 2\xi$ $(\xi = 2, 3, \cdots\cdots)$. a, b and c are also positive integers and are determined so as to satisfy the relation,

$$\int_0^\infty\int_0^\infty\int_0^\infty f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_a)dx_0dx_{-1}d\lambda_a = 1 \quad (18)$$

Eq. (18) reduces to

$$\frac{b_0b_{-1}(m!)^2\cdot(n-m-2)!}{a\cdot c^{n-m-1}} = 1 \quad (19)$$

Thus, various probability density functions are derived as follows,

$$f_{X_0,X_{-1},\Lambda}(x_0, x_{-1}, \lambda_0) = b_0b_{-1}\cdot(a\lambda_a)^{n+m}\cdot x_0^m\cdot x_{-1}^m \cdot\exp\{-a\lambda_a(x_0+x_{-1}+c)\}, \quad (20)$$

$$f_{X_0,X_{-1}}(x_0, x_{-1}) = \left\{\frac{b_0b_{-1}(n+m)!}{a}\right\} \cdot\frac{x_0^m x_{-1}^m}{(x_0+x_{-1}+c)^{n+m+1}}, \quad (21)$$

$$f_{X_i}(x_i) = \left\{\frac{b_0b_{-1}(n+m)!}{a}\cdot\sum_{r=0}^m\binom{m}{r}\cdot\frac{(-1)^r}{(n+r)}\right\} \cdot\frac{x_i^m}{(x_i+c)^n}, \quad (i = 0 \text{ or } -1) \quad (22)$$

$$f_\Lambda(\lambda_a) = b_0b_{-1}(m!)^2\cdot(a\lambda_a)^{n-m-2}\cdot\exp(-ac\lambda_a), \quad (23)$$

$$f_{X_0,X_{-1}|\Lambda}(x_0, x_{-1}|\lambda_a) = \frac{(a\lambda_a)^{2(m+1)}}{(m!)^2}\cdot x_0^m\cdot x_{-1}^m\exp\{-a\lambda_a(x_0+x_{-1})\}, \quad (24)$$

$$f_{X_i|\Lambda}(x_i|\lambda_a) = \frac{(a\lambda_a)^{m+1}}{m!}\cdot x_i^m\cdot\exp(-a\lambda_a x_i) \quad (i = 0 \text{ or } -1). \quad (25)$$

Further, we add the normalization conditions, $\bar{X}_i = 1$ and $\bar{\Lambda} = 1$, (where, $\bar{X}_i$ and $\bar{\Lambda}$ are the mean values of intervals and steplike signal respectively), i. e.,

$$a = \frac{\sum_{r=0}^{m}\binom{m}{r}(-1)^r/(n+r-m-1)}{\sum_{r=0}^{m+1}\binom{m+1}{r}(-1)^r/(n+r-m-2)}, \quad (26)$$

$$a\cdot c = n-m-1. \quad (27)$$

Consequently, all the probability density functions of Eqs. (20)~(25) are perfectly characterized by the two parameters n and m.

Note that some of these probability density functions are rational functions, and the others are the special Erlangean types. Further, they can take sufficiently wide varieties of shases, and can be fitted to various interval histograms of actual neuronal point sequences.

To generate the k-Markov sequence, we need the joint probability density functions of successive intervals, whose two dimensional and one dimensional marginal probability density functions are expressed by Eqs. (21) and (22) respectively.

Consider the $(i+1)$ dimensional extension of

Eq. (21),

$$f_{X_0,X_{-1},\cdots,X_{-i}}(x_0,\ x_{-1},\ \cdots,\ x_{-i}) = \frac{a_i x_0^m x_{-1}^m \cdots x_{-i}^m}{(x_0+x_{-1}+\cdots+x_{-i}+c)^{n+(m+1)i}} \tag{28}$$

where, $a_0 = \frac{b_0 b_{-1}(n+m)!}{a} \cdot \sum_{r=0}^{m} \binom{m}{r} \frac{(-1)^r}{(n+r)}$,

$$a_i = \frac{a_{i-1}}{\sum_{r=0}^{\infty} \binom{m}{r} \Big/ \{n+r+(m+1)(i-1)\}} \quad (i = 1, 2, \cdots),$$

then the conditional probability density function of X_0, given the i intervals imediately preceding X_0, $X_{-1} = x_{-1}$, $X_{-2} = x_{-2}$, $\cdots$, $X_{-i} = x_{-i}$ is given by

$$f_{X_0|X_{-1},\cdots,X_{-i}}(x_0|x_{-1},\ \cdots,\ x_{-i}) = \frac{f_{X_0,X_{-1},\cdots X_{-i}}(x_0,\ x_{-1},\ \cdots,\ x_{-i})}{f_{X_{-1},X_{-2},\cdots,X_{-i}}(x_{-1},\ x_{-2},\ \cdots,\ x_{-i})} = \frac{D \cdot H^{n+(m+1)(i-1)}}{(x_0+H)^{n+(m+1)i}} , \tag{29}$$

where, $D = \frac{a_i}{a_{i-1}} = 1 \Big/ \left\{ \sum_{r=0}^{m} \frac{\binom{m}{r}}{n+r+(m+1)(i-1)} \right\}$,

$H = x_0 + x_{-1} + \cdots x_{-i} + c$,

$$C = \frac{(n-m-1) \cdot \sum_{r=0}^{m+1} \binom{m+1}{r} \cdot (-1)^r / (n+r-m-2)}{\sum_{r=0}^{\infty} \binom{m}{r} (-1)^r \Big/ (n+r-m-1)}$$

When i is replaced by k, this agrees with Eq. (3).

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