PULSE FREQUENCY MODULATION
IN NEURAL SYSTEMS

A RANDOM MODEL

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ABSTRACT   A model is proposed of the pulse frequency modulation process in those neural systems where the neuron discharge is random. The model is characterized by one property, namely input-invariance of the output random process after a time transformation, which, on the one hand, greatly simplifies its analytical treatment, and on the other hand, gives a tool to determine experimentally whether the model describes the external behavior of a given neural system. The main dynamical properties of the model are studied, and the relevance of the results to information transmission by neural systems is discussed.

INTRODUCTION

Recently, those dynamical properties of the pulse generation process in nerve cells which may be relevant to information transmission have been investigated by Bayly (1968). In that study, it was assumed that integral pulse frequency modulation (Li, 1961) is similar to the impulse generation process of those nerve cells which produce impulses at an almost constant frequency (tonic or pacemaker type of cells). Therefore, the output discharge of nerve cells was described by a nonrandom impulse process, namely a train of equally spaced impulses, and the dynamical properties of the integral pulse frequency modulation of this process were derived.

It is well known that in many neural systems the cell discharge is random, and a large amount of work has been done both on experimental analysis and on theoretical models of stationary stochastic activity of single neurons. On the contrary, much less insight exists concerning the dynamical aspects of the signal-processing properties of these cells; preliminary results of a theoretical investigation, based on a model of the diffusion type, are given by Johannesma (1969).

In this paper, a simple model is proposed to investigate the dynamical properties of signal processing in those neural cells where the discharge is random. The model is characterized by one property which, on the one hand, greatly simplifies the analytical treatment, and on the other hand, gives a tool to determine experimentally

whether the model describes the input-output relationship of a given cell having a random discharge.

DEFINITION OF THE MODEL

The definition of any model of the impulse generation process of nerve cells is based on a number of assumptions. Some of the assumptions are common to all models, because they imply cell properties which are widely accepted as general properties of neural activity; other assumptions are more specific, and determine the class of neural cells to which the model is more likely to apply. A discussion of the different assumptions, and of the corresponding experimental support, is given by Moore, Perkel, and Segundo (1966) for a number of earlier models, and by Johannesma (1969) for some recent contributions.

First of all, let us define those basic assumptions of the model which are common to almost all models. It is assumed that the cell is a threshold element, which emits a pulse whenever the magnitude of the somatic potential $y(t)$ reaches the threshold. It also assumed that the output discharge of the cell can be described by a random point process (r.p.p.) $\{t_n\}$, $n = 1, 2, 3, \cdots$. Finally, it is assumed that after an impulse the somatic potential falls immediately to a reset potential y_0.

A more specific assumption is the following. The model belongs to that class, recently discussed by Siebert (1968), in which randomness is intrisinc to the cell: the input to the cell is described by a nonrandom function $m(t)$, the threshold by a random function $k(t)$. The first model of this class is that described by Ten Hoopen, den Hartog, and Reuver, (1963); random phenomena in the excitation of nerve cells are well established, and have been investigated extensively by Verveen (1961). All basic assumptions are illustrated by the block diagram shown in Fig. 1.

Without loss of generality, it is assumed that the reset potential is zero, that the input $m(t)$ and the threshold $k(t)$ are non-negative functions. Furthermore, it is assumed that experiments start at $t = 0$, with the somatic potential set to zero, and only the positive time axis will be considered. For convenience, the input will be divided into two parts:

$$m(t) = m_0 + m_1(t),$$

where m_0 is any given non-negative constant, and $m_1(t)$ any function of t such that $m_0 + m_1(t) \geq 0$ for all t. The constant m_0 can be considered either as a given stationary input taken as reference, or as an internal bias; in the last case, the external input to the cell is represented by $m_1(t)$.

Unfortunately, it is not possible to derive general properties of the model shown in Fig. 1 holding for any random function $k(t)$ and for any relationship between input $m(t)$ and somatic potential $y(t)$. In fact, the crossing problem between a random function and a nonrandom function is not solved in general. In most cases, it is only possible to study the input-output relationship of the model by simulation. If,

however, two further assumptions are made, it is possible to obtain a model which is sufficiently inclusive to admit as output, under a stationary input, any r.p.p., and whose input-output relationship is characterized by one property which greatly simplifies both the analytical treatment and the experimental test. One assumption concerns the relationship between input and somatic potential, the other concerns the threshold.

Concerning the relationship between somatic potential and input, the really basic assumption is that, for any input, the somatic potential is a nondecreasing function of t, except at the reset times. Before considering the general case, however, it is convenient to consider a particular case; therefore, let us first assume that the relationship between input and somatic potential is described by an integral operator:

$$\frac{dy}{dt} = m(t). \tag{1}$$

Of course, the basic assumption is satisfied, because of the condition $m(t) \geq 0$ for all t. The same relationship between input and somatic potential was assumed in the random walk model described by Gerstein and Mandelbrot (1964), and in the non-random model studied by Bayly (1968).

Concerning the threshold, it is assumed that it is described by a random function $k(t)$ defined as follows. Let $\{k_m\}$, $m = 0, 1, 2, \cdots$ be a succession of finite-valued random variables k_m, such that, with probability one, $k_m \geq 0$ for all m. No assumption is made concerning the statistical properties of the random variables k_m; in particular, it is not assumed either that they are independent, or that they are identically distributed. Then:

$$k(t) = k_o \quad \text{for } 0 \leq t \leq t_1$$

$$k(t) = k_i \quad \text{for } t_i < t \leq t_{i+1}, \quad i = 1, 2, 3, \cdots, \tag{2}$$

where $\{t_n\}$, $n = 1, 2, 3, \cdots$, is the output r.p.p.

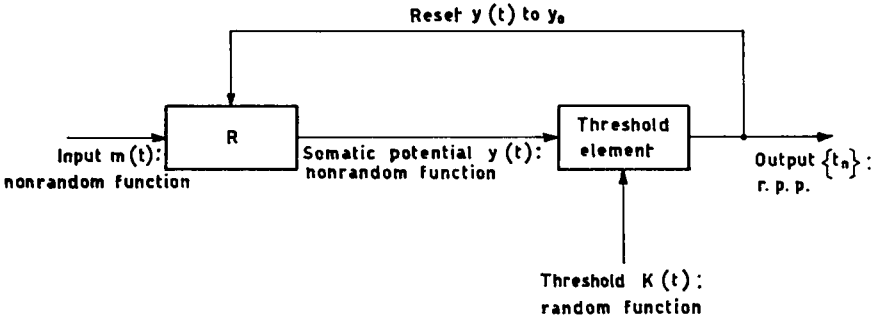The random functions $k(t)$ defined by equation 2 are synchronized with the out-

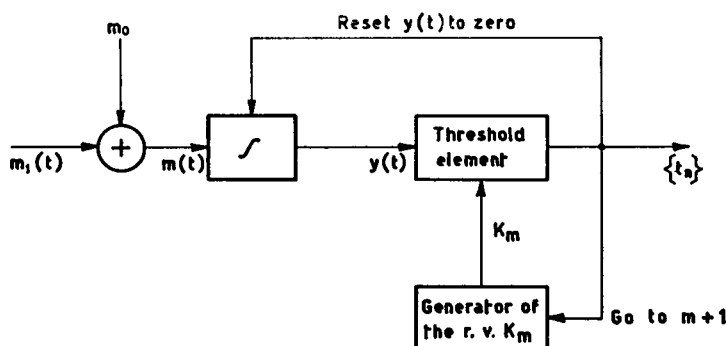FIGURE 1 Block diagram of the basic assumptions.

FIGURE 2   Block diagram of model I. The system starts at t = 0, with the integrator set to zero and the generator of random variables (r.v.) set to random variable k_o .
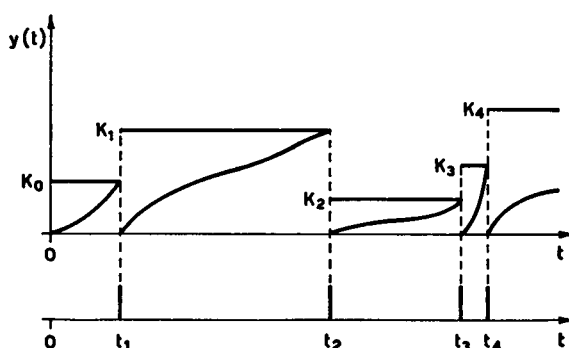

FIGURE 3   Behavior of model I.

put discharge: at any impulse occurrence time t_i the threshold assumes at random a value which holds until t_{i+1}. The block diagram and the behavior of the model corresponding to the relationship of equation 1 and to random functions of the class defined by equation 2 are shown in Figs. 2 and 3, respectively; this model will be denoted by model I.

Physiologically, the random functions defined by equation 2 are very unlikely. On the other hand, too little is known of the internal neural mechanisms to have a realistic model of them. Therefore, it may be convenient to choose a class of random functions leading to a simple model; then, experiments can be performed to see whether the input-output relationship of nerve cells is described by the model. In fact, the validity of the results obtained for the nervous systems does not rest on the validity of the model as a description of the internal neural mechanisms, but on its validity as a model of the external behavior of nerve cells.

THE CHARACTERISTIC PROPERTY OF MODEL I

Let us consider a given system of the class defined by model I, that is to say a given succession of random variables $\{k_m\}$, $m = 0, 1, 2, \cdots$. Clearly, for any input $m(t)$,

the output of the system is the r.p p. $\{t_n\}$, $n = 1, 2, 3, \cdots$, defined as follows: the first point occurrence time t_1 is given by

$$k_0 = \int_0^{t_1} m(t) \, dt, \qquad (3\,a)$$

and, for any i, t_{i+1} is given by

$$k_i = \int_{t_i}^{t_{i+1}} m(t) \, dt. \qquad (3\,b)$$

Let us denote by $\{t_n^0\}$, and let us call carrier, the output of the system when $m(t) = m_0$, for all t. According to equation 3, $\{t_n^0\}$ is defined by

$$t_1^0 = \frac{k_0}{m_0}, \qquad (4\,a)$$

$$t_{i+1}^0 = t_i^0 + \frac{k_i}{m_0}, \quad i = 1, 2, 3, \cdots. \qquad (4\,b)$$

Since no assumption was made concerning the statistical properties of the random variables k_m, the definition of equation 4 shows that $\{t_n^0\}$ can be any r.p.p. (see, for example, the definition of r.p.p. given in Beutler and Leneman, 1966); therefore, model I is sufficiently inclusive to admit as carrier any r.p.p.. The statistical properties of the carrier are determined by the statistical properties of the random variables k_m, and conversely; for example, constraints can be imposed to obtain a stationary carrier. Of course, even if for a given system the carrier is stationary, the output of the system for a nonsteady input will be a nonstationary r.p.p..

Let us denote by $\{t_n^1\}$ the output of the system modulated by a given input signal $m_1(t)$, that is for $m(t) = m_0 + m_1(t)$; furthermore, for the given $m_1(t)$, let us define the change in time:

$$t^1 = \int_0^t \left(\frac{m_0 + m_1(t)}{m_0} \right) dt. \qquad (5)$$

It is immediately verified that, for any $m_1(t)$, t^1 is a nondecreasing function of t. Note that if $m_1(t)$ is stationary, that is if $m_1(t) = m_1$, for all t, the transformation shown in equation 5 is a linear transformation; otherwise, t^1 is a nonlinear transformation of t. Then any system of the class defined by model I satisfies the following:

Property I. For any $m_1(t)$, $\{t_n^1\}$ referred to t^1 is the same r.p.p. as $\{t_n^0\}$ referred to t.

Proof. Let $k_0', k_1', k_2', \cdots$ be a given outcome of $\{k_m\}$, $m = 0, 1, 2, \cdots$. Trivially, the member of the random process $\{t_n^0\}$ and the member of the random process $\{t_n^1\}$ corresponding to this outcome are identical, if the change in time defined by equation 5 is performed on the member of $\{t_n^1\}$. Since this is true for any out-

come of $\{k_m\}$, $m = 0$, 1, 2, $\cdots$, then $\{t_n^0\}$ and $\{t_n^1\}$ are the same r.p.p., if $\{t_n^0\}$ is measured in t and $\{t_n^1\}$ is measured in t^1.

In other words, property I states that, for a given system, the time transformation defined by equation 5 makes the output r.p.p. invariant under a change of the input function.

Conversely, given a system whose output is a r.p.p. and whose input is any function $m_1(t)$ of a class of "possible inputs," then, it is easily seen that the external behavior of the system is described by model I if the class of possible inputs is such that a constant m_0 exists for which $m_1(t) + m_0 \geq 0$, for any $m_1(t)$ and all t, and if the system satisfies property I for any $m_1(t)$.

From property I, let us derive first a result showing that the systems of the class defined by model I are good pulse frequency modulators. Let us consider any system of this class such that the carrier $\{t_n^0\}$ is a stationary r.p.p.. Let us denote by ρ_0 the average number of impulses per unit time of $\{t_n^0\}$; ρ_0 is independent of t, since $\{t_n^0\}$ is stationary. Let $\rho_1(t)$ be the average number of impulses per unit time of the r.p.p. $\{t_n^1\}$, corresponding to a given input signal $m_1(t)$, and $\rho_1^1(t^1)$ be the average number of impulses per unit time of the r.p.p. $\{t_n^1\}$ measured in t^1, where t^1 is given by the transformation shown in equation 5. Because of property I,

$$\rho_1^1(t^1) = \rho_0 .$$

Then, since

$$\rho_1(t) = \rho_1^1(t^1) \frac{dt^1}{dt} ,$$

we have:

$$\rho_1(t) = \rho_0 \frac{dt^1}{dt} . \tag{6}$$

From equations 5 and 6, we obtain:

$$\rho_1(t) = \rho_0 \left(\frac{m_0 + m_1(t)}{m_0} \right) . \tag{7}$$

Equation 7 shows that for any system of the class defined by model I, and such that the carrier is a stationary r.p.p., the average number of impulses per unit time is modulated in exactly the same way as the input signal.

By integration of equation 6, it is possible to express t^1 without involving the input function:

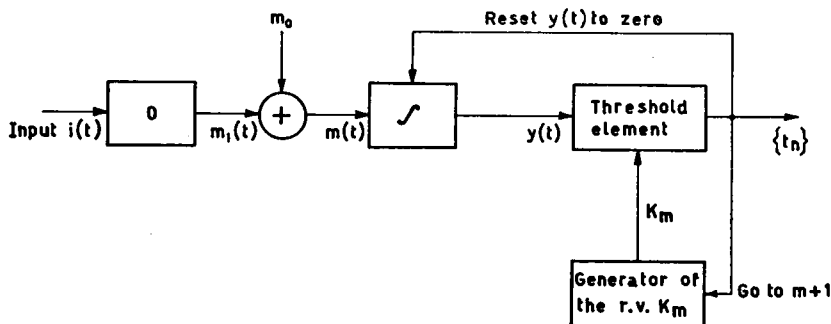$$t^1 = \frac{1}{\rho_0} \int_0^t \rho_1(t)\, dt. \tag{8}$$

FIGURE 4 Block diagram of model G. Model G is obtained by the serial composition of an operator O and of model I.

Furthermore, since ρ_0 is a constant, the transformation shown in equation 8 can be expressed in a simpler form, by the change of variable:

$$\theta = \int_0^t \rho_1(t) \, dt. \tag{9}$$

Clearly, input-invariance of the output r.p.p. measured in t^1 and input-invariance of the output r.p.p. measured in θ are equivalent.

The transformations expressed by equations 8 and 9 hold only for those systems where the carrier is stationary; on the other hand, note that they have been obtained from property I but without making use explicitly of the transformation shown in equation 5. In fact, input-invariance of the output r.p.p. after the time transformation, defined by equation 8, or after the change of variable, defined by equation 9, characterizes one class of systems which is wider than the class of systems corresponding to model I, as discussed in the following section.

MODEL G

Let us consider now the model G, shown in Fig. 4, which is obtained by the serial composition of an operator O and of model I, under the following conditions. Let us denote by $i(t)$ the input to model G, that is to say the input to operator O, and by $m_1(t)$ the output of operator O, which is the input to model I. Then, it is assumed that the output $\{t_n\}$ of model I is a stationary r.p.p. when $m_1(t) = 0$, for all t. Concerning the operator O, the only condition to be satisfied is the existence of a constant m_0 such that $m_1(t) + m_0 \geq 0$, for all t, and any input $i(t)$.

In model G, operator O, which fully determines the relationship between input $i(t)$ and average number of output impulses $\rho_1(t)$, represents the processing part, and model I represents the encoding part, which is distortion free, because of equation 7. For instance, if model G is taken as a model of one neural cell, operator O may represent signal processing at the synaptic level (Rall, 1964; 1967); if model G is

taken as a model of one sensory system, operator O may represent the over-all processing from the receptor level to the site of initiation of cell impulses.

Because of property I of model I, for a given operator O, the corresponding model G satisfies property I, where the time transformation which makes input-invariant the output r.p.p. $\{t_n\}$, $n = 1, 2, 3, \cdots$, if expressed in terms of the input $i(t)$, depends on the operator O. For any operator O, however, this time transformation, expressed in terms of the output variable $\rho_1(t)$, is given by equation 8. Therefore, any system of the class defined by model G satisfies the following:

Property G. The output r.p.p. is input-invariant after the time transformation defined by equation 8, or after the change of variable defined by equation 9.

Conversely, it is easily seen that the external behavior of one system is described by one system of the class defined by model G if the system satisfies Property G. In this case, the relationship between $i(t)$ and $\rho_1(t)$ determines operator O, and the statistical properties of the output r.p.p. in any given stationary condition determine model I, namely the random variables $\{k_m\}$, $m = 0, 1, 2, \cdots$.

EXPERIMENTAL TEST OF MODEL G

To determine experimentally whether the external behavior of a given system is described by model G, it is necessary, according to Property G, to test the invariance of the output r.p.p. after the time transformation, equation 8, or the change of variable, equation 9, under a change of the input function. For example, employing interval statistics to describe the output r.p.p., it is necessary to test the invariance of the interval distributions of increasing order. Of course, as usual in statistics, a complete test cannot be obtained, since the analysis can be effectively performed only up to a given-order multivariate distribution of the intervals.

In the transformation shown in equation 8, or equation 9, $\rho_1(t)$ is an ensemble average. In stationary conditions, however, it is possible to evaluate experimentally $\rho_1(t)$ by a time average; this is also possible in dynamic conditions, if a periodic input $i(t)$ is used. In fact, in this case it is possible to evaluate experimentally $\rho_1(t)$ by the number of impulses per unit time averaged on a number of input periods.

As an example, let us consider the cat retinal system, taking as input $i(t)$ the light stimulus, as output $\{t_n\}$ the discharge of one ganglion cell, which is a random discharge (Kuffler, Fitzhugh, and Barlow, 1957). The approximation of the ganglion cell discharge by a r.p.p. is possible because the duration of the cell impulses plus the refractory period is small compared with the interpulse intervals.

The action of the light stimulus on the distribution of the interpulse intervals has been studied both for different stationary conditions and for different dynamic situations, using a light stimulus sinusoidally modulated. The results, described by Gestri, Maffei, and Petracchi (1966) and by Gestri and Petracchi (1970), have shown that the interval distribution is input-invariant if the intervals are measured in θ, as given by equation 9. Then, at least for what concerns the action of the input

of single intervals of the discharge, the input-output relationship of the cat retinal system is described by model G. The relationship between light stimulus and $\rho_1(t)$, which in model G determines operator O, ha; been studied by Hughes and Maffei (1966).

Some other experimental evidence exists of the input-invariance of the statistical properties of the neural discharge after the time transformation, equation 8, or the change of variable, equation 9. In the auditory system, Siebert (1965) has shown that the distribution of the interpulse intervals of primary auditory neurons is, for different stationary conditions of stimulus, invariant after one linear time transformation, which is the form assumed by equation 8 in stationary conditions. Knox (1968) has shown that the same property is true for primary receptor neurons in the statocyst organ of the lobster (*Homarus americanus*), under low frequencies of sinusoidal stimulation.

POWER DENSITY SPECTRUM OF THE MODULATED OUTPUT PROCESS

One general property of the systems corresponding to model I as pulse frequency modulators is given by equation 7. Another important evaluation tool for pulse frequency modulators is the study of the spectral properties of the modulated output discharge. Although it is not easy to derive directly from property I a property of the power density spectrum holding for any system of the class defined by model I, property I greatly simplifies the study of the spectral properties of any given system of the class.

For example, let us consider the system defined by model I where the carrier $\{t_n^0\}$ is a stationary Poisson r.p.p.. The system was chosen both because it is the simplest and because it can be considered as the opposite limiting case of the system considered by Bayly (1968), where the carrier consisted of equally spaced impulses. In fact, to investigate the functional significance of the randomness of the cell discharge in many nervous systems, it may be useful to compare the results obtained assuming a periodic carrier with the results obtained assuming a Poisson carrier. Note that the comparison makes sense because the same impulse generation process is assumed in both cases.

To derive, for a given system, the spectral properties of the output r.p.p. for a given modulating signal $m_1(t)$, it is not necessary to specify the definition shown in equation 3 and then to make use of it; in fact, the system is completely defined by the value of m_0, by the carrier $\{t_n^0\}$, and by property I. Therefore the definition expressed by equation 3 will be specified only for the sake of completeness.

The carrier $\{t_n^0\}$ is a stationary Poisson r.p.p. if, and only if, the random variables k_m of the definition, equation 3, are independent, equally distributed, and their distribution is:

$$p(k_m') = \alpha e^{-\alpha k' m},$$

where α is a constant, independent of m (Blanc-Lapierre and Fortet, 1965, Chapt. 4, Sect. 7). The two constants m_0 and α determine the average number of impulses per unit time ρ_0 of the carrier; in fact, it is:

$$\rho_0 = \alpha m_0 .$$

The choice of the value of one of these constants, for example the choice of m_0, is arbitrary, but determines the class of the signals which can be transmitted, because of the condition $m_0 + m_1(t) \geq 0$ for all t.

Let us derive now the spectrum of the output process $\{t_n^1\}$, when a sinusoidal signal is applied. Without loss of generality, let $m_0 = 1$ and $m_1(t) = m_1 \sin \omega_1 t$, where $m_1 \leq m_0$. Because of property I, $\{t_n^1\}$ will be a nonstationary Poission process (clearly, this is the crucial point); according to equation 7, the average number of impulses per unit time $\rho_1(t)$ will be:

$$\rho_1(t) = \rho_0(1 + m_1 \sin \omega_1 t) \tag{10}$$

The autocorrelation function $R_1(h)$ and the power density spectrum $\phi_1(\omega)$ of a nonstationary Poisson process are well known (for example, see Blanc-Lapierre and Fortet, 1965, Chapt. 5, Sect. 10). For a nonstationary Poission r.p.p. $\{t_n^1\}$ whose average number of impulses per unit time is given by equation 10, it is:

$$R_1(h) = \rho_0^2 + \frac{\rho_0^2 m_1^2}{2} \cos \omega_1 h + \rho_0 \delta(h), \tag{11}$$

$$\phi_1(\omega) = \frac{\rho_0}{2} + \rho_0^2 \delta(\omega) + \frac{\rho_0^2 m_1^2}{2} \delta(\omega - \omega_1), \tag{12}$$

where δ is the Dirac function.

The power density spectrum, equation 12, of the modulated output r.p.p. $\{t_n^1\}$ is given by the spectrum $\phi_0(\omega)$ of the carrier $\{t_n^0\}$:

$$\phi_0(\omega) = \frac{\rho_0}{2} + \rho_0^2 \delta(\omega),$$

plus the spectrum $\phi_s(\omega)$ of the output signal $\rho_1(t)$:

$$\phi_s(\omega) = \frac{\rho_0^2 m_1^2}{2} \delta(\omega - \omega_1),$$

without cross-terms. If this spectrum is compared with the spectrum of a sinusoidally modulated nonrandom carrier of equally spaced impulses (Bayly, 1968), it is seen that the efficiency of the second system is limited by the presence of discrete spectral components at the carrier frequency and its multiples, and by the presence of spec-

tral cross-terms (sidebands). This limitation does not exist for that system defined by model I which has a random carrier of the Poisson type.

CONCLUSIONS AND COMMENTS

It has been shown that the encoding part of model G, namely model I, is a good pulse frequency modulator. Therefore model G is more likely to apply to those neural systems, especially sensory systems, where there is some evidence of the fact that neural information is transmitted by pulse frequency modulation.

Property G gives a simple tool for testing the validity of model G as a description of the dynamical behavior of neural systems. Assuming that, for a given neural system, the input-output relationship is described by model G, the following conclusions can be derived.

(a) The information-carrying parameter is given by the average number of impulses per unit time $\rho_1(t)$. In fact, property G and the transformation shown in equation 8, or equation 9, show that $\rho_1(t)$ contains the whole information on the input $i(t)$ carried by the output r.p.p. $\{t_n^1\}$, since the knowledge of $\{t_n^0\}$ and of $\rho_1(t)$ implies the knowledge of $\{t_n^1\}$, for any $i(t)$.

(b) The randomness of the carrier improves the efficiency of the system. In fact, comparison of the power density spectrum of the modulated output process for the two opposite limiting cases, namely the carrier of equally spaced impulses and the Poisson carrier, shows that the Poisson carrier is the optimum.

Concerning point a, let us recall that $\rho_1(t)$ is an ensemble average. It is true that, using a periodic stimulus, $\rho_1(t)$ can be estimated experimentally by a time average, namely by the number of impulses per unit time averaged on a number of stimulus periods. On the one hand, it is very unlikely that this is actually performed at the reception level in neural systems; on the other hand, this holds only for periodic stimuli. Therefore, point a implies a parallel organization, where a number of nerve cells, whose discharges are in the best case statistically independent, transmit the same signal (Gestri et al., 1966; Maffei, 1968); an estimate of $\rho_1(t)$ can in this case be obtained by averaging the discharges of these cells, which seems a reasonable operation for a nerve cell.

Point b may be relevant to information transmission in neural systems, especially because it is known that many neural systems transmit information also at frequencies of stimulation of the same order as, or greater than, the average impulse frequency of the corresponding neural cells.

Of course, to derive more specific conclusions for a given neural system, for instance to see if the power density spectrum of the modulated neural discharge of the system is predicted by the model, it is necessary to study that system defined by model I where the carrier $\{t_n^0\}$ is specified according to the statistical properties of the stationary activity of the corresponding neural cells. This can always be done, because it has been shown that model I is sufficiently inclusive to admit as carrier any r.p.p..

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