

SELECTIVE INTERACTION MODELS OF EVOKED NEURONAL ACTIVITY

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Abstract

The interaction of two independent Markovian point processes is considered. A pure death process inhibited by a Poisson process is proposed as a model of neuronal activity evoked by transient stimulus. The interaction of a pure birth process with either a Poisson or a pure birth process is suggested for the description of neuronal activity evoked by a continuous stimulus. The Wold's Markov process is used to introduce an after-effect into excitation process. The probabilistic characterizations of response process for these selective interaction schemes are given.

1. Introduction

The selective interaction of two point processes introduced by ten Hoopen and Reuver (1965) has often been used for the description of neuronal spike generation. The neuron has both excitatory and inhibitory inputs represented by two independent point processes. A pulse on the inhibitory input deletes a following pulse on the excitatory input. Non-deleted excitatory pulses form the output of the neuron. The model can be also described as a perfect integrator with reset to zero and threshold one. In this terminology the excitatory pulse produces a change of potential $+1$ and the inhibitory pulse sets the potential to the value -1 .

The original model has been generalized many times and references can be found in several surveys (Fienberg, 1974; Holden, 1976; Sampath and Srinivasan, 1977). As many other applications of the model have been suggested, some of the papers on this topic do not appear in neurophysiological context. The series of papers by Lawrance (1970a,b; 1971a,b; 1979) and the monograph by Råde (1972) give comprehensive characteristic results for the selective interaction of point processes.

The aim of the present contribution is to suggest a new application of selective interaction scheme in neuronal modelling, namely in the field of stimulated activity. As indicated in the above cited surveys, models of evoked activity are rare in comparison with models of spontaneous activity. Such a lack is even more serious if we realize that the situation is the reverse in experimental studies. Furthermore, all previous selective interaction models require steady state conditions.

It is known that a dynamic response, which is usually characterized by the mean spike frequency or the mean interspike interval, varies in time due to adaptation to the maintained stimulus. Examples of statistical methods for description of this phenomenon were introduced by Bromm and Tagmat (1977). Also Tsuchitani (1982) uses very sophisticated statistical methods for experiments with burst stimuli and

first of all the computation of the mean and of the standard deviation for each of the interspike intervals relative to their sequential and temporal order is in connection with presented approach. To achieve certain analogy to experimental situations the results for presented models are also characterized by the interspike interval probability distribution. In addition, some other results are evaluated. The method used for evoked activity modelling is different from that which appeared in the model proposed by Levine and Schefner (1977), but a certain analogy can be found. The system parameters are constant for the duration of each interspike interval in their model and in our case only finite number of changes during any interspike interval may occur. In spite of the fact that some of the analysed problems have already been solved by Basawa (1971) the results achieved are new.

The first part of the paper describes the model for stimuli of short duration, such as tone burst or flash. The influence of long lasting stimuli upon neuronal activity is modelled in the second part of the paper. The adaptation which is one of the main characteristics of stimulated activity (Smith and Zwislocki, 1975; Zeevi and Bruckstein, 1981) is implemented by input point processes with variable intensities.

2. The model of neuronal activity evoked by a transient stimulus

Let us assume that the stochastic process $\{E(t); t \geq 0\}$ representing excitatory activity evoked by a stimulus is a pure death process. We suppose there is a negligible intensity of spontaneous activity relative to evoked activity. The initial state of the excitatory process is proposed to be proportional to the stimulus level, $E(0) = n$, i.e., the stimulus produces n excitatory pulses. We assume that the process of inhibition is a time-homogeneous Poisson process with intensity μ . For the simplicity of notation, it is assumed that the process $\{E(t); t \geq 0\}$ starts at time 0 with a virtual excitatory pulse producing the response pulse. The formal character of this assumption follows from the lack of memory characterizing exponential distribution (e.g. Feller, 1966).

Let $\{X_k, k = 1, \dots, n\}$ and $\{R_k, k = 1, \dots, m \leq n\}$ denote inter-arrival times between $(k-1)$ -th and k -th excitatory pulses and response pulses, respectively, with corresponding cumulative distribution functions (c.d.f.'s) $F_k(t)$ and $H_k(t)$. The symbol T_k denotes the time to the occurrence of the k -th response pulse, thus we have

$$T_k = R_1 + R_2 + \dots + R_k, \quad k = 1, \dots, m$$

and

$$T_0 = 0.$$

The above definitions are illustrated by Fig. 1.

Let us find some properties of the response process $\{R(t); t \geq 0\}$. From the assumption about the nature of the excitatory process we know that random variables $\{X_k, k = 1, \dots, n\}$ are mutually independent with c.d.f.

$$(1) \quad F_k(t) = 1 - e^{-\lambda_{n-k+1}t}.$$

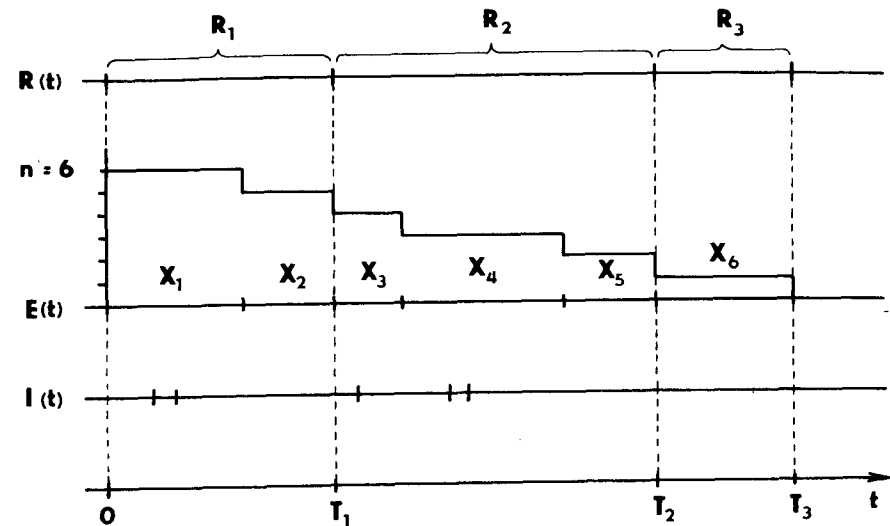


Fig. 1

Similarly, the character of the inhibitory process $\{I(t); t \geq 0\}$ implies that the time to the first inhibitory pulse as well as the following inter-inhibitory intervals are mutually independent random variables with c.d.f.

$$(2) \quad G(t) = 1 - e^{-\mu t}$$

Let us find

$$H_k(t|s) = \text{Prob}(R_k \leq t | E(t_{k-1}) = s),$$

$$(3) \quad k = 1, \dots, m, \quad 1 \leq s \leq n - k + 1$$

which is the conditional c.d.f. of the R_k under the condition that the death process $\{E(t); t \geq 0\}$ is in the state s at the moment of $(k-1)$ -th response pulse. From simple probabilistic considerations follows

$$(4) \quad 1 - H_k(t|s) = e^{-\lambda_s t} + \int_0^t \lambda_s e^{-\lambda_s x} (1 - e^{-\mu x}) (1 - H_k(t-x | E(t_{k-1} + x) = s-1)) dx$$

and

$$H_k(t|0) = 0 \text{ for } t \geq 0.$$

Realizing

$$H_k(t-x | E(t_{k-1} + x) = s-1) = H_k(t | E(t_{k-1}) = s-1)$$

and taking the Laplace-Stieltjes (L.-S.) transformation with respect to t of both sides of (4), we obtain

$$(5) \quad h_k^*(v|s) = \frac{\lambda_s}{\lambda_s + \mu + v} \left[h_k^*(v|s-1) \frac{\mu}{\lambda_s + v} + 1 \right]$$

and

$$h_k^*(v|0) = 0,$$

where symbol * denotes L.-S. transformation of corresponding c.d.f. From this recurrence relationship we can derive a direct formula for $h_k^*(v|s)$,

$$(6) \quad h_k^*(v|s) = \frac{\lambda_s}{\lambda_s + \mu + v} \left[1 + \sum_{j=1}^{s-1} \prod_{i=1}^j \frac{\lambda_{s-i}\mu}{(\lambda_{s-i} + \mu + v)(\lambda_{s-i+1} + v)} \right]$$

We note that R_k can be infinite with positive probability for any $k \geq 1$. The probability of this event is

$$(7) \quad \text{Prob}(R_k = \infty | E(t_{k-1}) = s) = 1 - h_k^*(0|s) = \\ = \frac{\mu}{\lambda_s + \mu} \left(1 - \sum_{j=1}^{s-1} \mu^{j-1} \lambda_{s-j} \prod_{i=1}^j (\lambda_{s-i} + \mu)^{-1} \right)$$

and it is decreasing function of argument s .

The relation (7) can be simplified when taking into account that the probability that the i -th excitatory pulse fails to elicit a response is

$$(8) \quad P_i = \int_0^t (1 - e^{-\mu t}) \lambda_{n-i+1} e^{-\lambda_{n-i+1} t} dt = \frac{\mu}{\lambda_{n-i+1} + \mu},$$

from which it immediately follows that

$$(9) \quad \text{Prob}(R_k = \infty | E(t_{k-1}) = s) = \prod_{i=1}^s \frac{\mu}{\lambda_{s-i+1} + \mu}.$$

Thus the unconditional probability that the stimulus fails to elicit a response is clearly equal to $\prod_{i=1}^n \mu(\lambda_{n-i+1} + \mu)^{-1}$. This value can be related to stimulus strength and in this way the type of dependency of λ_i on i can be roughly estimated.

Similarly the probability that the given stimulus produces exactly j response pulses can be calculated as the number of successes in n independent Bernoulli trials, with the probability of success in the i -th trial equal to $1 - P_i$.

Realizing that the probability of the event $\{R_i = \infty\}$ is positive for any i we know that the expected value of R_i is infinite. Let us derive the conditional expectation for inter-response time intervals under the condition the interval is finite. Using (5), the conditional moments can be computed and the following recurrence formula is obtained:

$$(10) \quad M(R_k|s, R_k < \infty) = \int_0^{\infty} t dH_k(t|s, R_k < \infty) = \\ = \frac{1}{\lambda_s} + M(R_k|s-1, R_k < \infty) \frac{\mu}{\lambda_s + \mu}.$$

Since $M(R_k|1, R_k < \infty) = \frac{1}{\lambda_1}$ the relation (10) can be written in the form

$$(11) \quad M(R_k|s, R_k < \infty) = \sum_{i=1}^s \frac{1}{\lambda_{s-i+1}} \prod_{j=1}^{i-1} \frac{\mu}{\lambda_{s-j+1} + \mu}$$

The conditional moments of higher order can similarly be evaluated.

The results (6), (9) and (11) are valid under the condition that $E(t_{k-1}) = s$. To remove this condition the probability of this event has to be found. It is $P(E(0) = n) = 1$ and $P(E(0) = j) = 0$ for $j \neq n$, however, it is obvious that a non-degenerate probability distribution can also be considered. We can easily deduce that

$$P(E(t_1) = s) = P_1 P_2 \dots P_{n-s-1} (1 - P_{n-s}), \quad s = 0, 1, \dots, n-1$$

where P_i is given by relation (8), by computing the probability that $n-s$ Bernoulli trials are necessary for the first success. Generally, we get

$$(12) \quad P(E(t_k) = s) = (1 - P_{n-s}) \sum (1 - P_{i_1}) \dots (1 - P_{i_{k-1}}) P_{i_k} \dots P_{i_{n-s-1}}, \\ s = 0, 1, \dots, n-k,$$

where the sum is over the all combinations of the numbers

$\{1, \dots, n-s-1\}$ and $P(E(t_k) = s) = 0$, $s = n-k+1, \dots, n$.

Thus using (12), the condition that we know the state of the excitation process can be removed from (6), (9) and (11).

Example 1. Let us illustrate the derived results on an example where stimulus produces a finite size excitatory discharge with constant intensity $\lambda_1 = \lambda_2 = \dots = \lambda_n = \lambda$, i.e. the sequence $\{x_k\}$ is formed by n pulses generated in accordance with Poisson process with parameter λ . In this case we have

$$(6') \quad h^*(v|s) = \frac{\lambda(\lambda + \mu)}{(\lambda + \mu)(\lambda + \mu + v) - \lambda\mu} \left[1 - \left(\frac{\lambda\mu}{(\lambda + \mu + v)(\lambda + \mu)} \right)^s \right],$$

$$(9') \quad \text{Prob}(R_k = \infty|s) = \left(\frac{\mu}{\lambda + \mu} \right)^s = p^s$$

and the moment relationship (11) takes the form

$$(11') \quad M(R_k|s, R_k < \infty) = \frac{\lambda + \mu}{\lambda^2} \left[1 - \left(\frac{\mu}{\lambda + \mu} \right)^s \right] = \\ = \frac{\lambda + \mu}{\lambda^2} (1 - p^s),$$

where $s = 1, \dots, n$, denoting the probability that the next excitatory pulse elicits no response by

$$P = \frac{\mu}{\mu + \lambda}. \text{ For the excitatory process we get}$$

$$(12') \quad P(E(T_k)=s) = \binom{n-s-1}{k-1} (1-p)^k p^{n-s-k},$$

$$s=0, 1, \dots, n-k$$

$$k=1, \dots, m,$$

which can be identified with Pascal distribution (e.g. Hahn and Shapiro, 1967); and thus we obtain

$$(13) \quad P(R_k=\infty) = \sum_{s=1}^{n-k+1} \left(\frac{\mu}{\lambda+\mu}\right)^s \binom{n-s-1}{k-2} (1-p)^{k-1} p^{n-2-k+1} = \\ = \binom{n-1}{k-1} (1-p)^{k-1} p^{n-k+1}.$$

Example 2. More relevant seems to be the case when the intensity of the excitatory process depends on n . Let us assume that the excitatory process is a linear death process, $\lambda_i = i\lambda$ and that $\mu = K\lambda$. It follows from (8) that immediately after the stimulus the output activity for large n is only negligibly affected by the inhibition. On the other hand at the moment when λ_{n-i+1} is small relatively to μ the effect of inhibition prevails. Using (9) we get

$$\text{Prob}(R_k=\infty|s) = \prod_{i=1}^s \frac{K}{(i+K)}$$

$$\text{and for natural } K \text{ it is } \text{Prob}(R_k=\infty|s) = \frac{K^s K!}{(s+K)!}$$

from which the type of dependency between stimulus intensity represented by n and probability of no response to this stimulus can be seen. Similarly, it holds for the conditional mean response interval that

$$M(R_k|s, R_k < \infty) = \frac{K!}{\lambda} \sum_{i=1}^s \frac{K^{i-1}}{(s-i+1)(i-1+K)}.$$

3. A model of neuronal activity evoked by a continuous stimulus

Let us suppose that $\{E(t), t \geq 0\}$ is a pure birth process with parameters

$$\lambda_k, k=1, \dots, \sum_{k=1}^{\infty} \frac{1}{\lambda_k} = \infty$$

and let the other assumptions be retained from the previous model. This assumption aims to describe the influence of a long lasting stimulus on the excitatory activity. In our situation one may expect $\lambda_k \rightarrow \lambda$ for $k \rightarrow \infty$ and thus the introduced assumption about the honesty of the birth process is only formal. The random variables X_k are mutually independent with c.d.f.

$$(14) \quad F_k(t) = 1 - e^{-\lambda_k t}, k=1, \dots$$

Defining conditional c.d.f. of R_k by (3) for $k=1, \dots$ and $s \geq n+k$, we get by analogous reasoning the following result

$$(15) \quad h^*(v|s) = \frac{\lambda_s}{\lambda_s + \mu + v} \left[h_k^*(v|s+1) \frac{\mu}{\lambda_s + v} + 1 \right].$$

Thus

$$(16) \quad h^*(v|s) = \frac{\lambda_s}{\lambda_s + \mu + v} \left(1 + \sum_{j=1}^{\infty} \prod_{i=1}^j \frac{\mu}{(\lambda_{s+i-1} + v)} \frac{\lambda_{s+i}}{(\lambda_{s+i} + \mu + v)} \right)$$

and for unconditional L.-S. transformation we use the relation

$$(17) \quad h_k^*(v) = \sum_{s=n+k-1}^{\infty} h_k^*(v|s) P(T_{k-1}=s).$$

$$\text{We have } P(T_0=i) = \begin{cases} 1, & i=n, \\ 0, & i \neq n, \end{cases}$$

$$P(T_1=s) = \frac{\lambda_{s-1}}{\lambda_{s-1} + \mu} \prod_{j=n}^{s-2} \frac{\mu}{\lambda_j + \mu},$$

for $s \geq n+1$

and as the probability that i -th excitatory pulse fails to elicit a response is analogous to (8)

$$P_i = \frac{\mu}{\lambda_i + \mu}, i=1, \dots$$

the probability of the event $\{T_{k-1}=s\}$ can be computed also for $k > 2$ and substituted into the relation (17). The character of P_i also implies that

$$P(R_k=\infty|s) = \prod_{i=s-n+1}^{\infty} \frac{\mu}{\lambda_i + \mu} = 0$$

and similarly to (10) and (11)

$$(18) \quad M(R_k|s) = \frac{1}{\lambda_s} + M(R_k|s+1) \frac{\mu}{\lambda_s + \mu} = \\ = \sum_{i=0}^{\infty} \frac{1}{\lambda_{s+i}} \prod_{j=0}^{i-1} \frac{\mu}{\lambda_{s+j} + \mu}.$$

Obviously, under the steady-state conditions when $\lambda_k \rightarrow \lambda$, we get $M(R_k|s) \rightarrow M(R) = (\lambda + \mu) \lambda^{-2}$. Then assuming that λ is proportional to stimulus intensity and $\lambda \gg \mu$, the approximately linear relation between the input intensity level and the output firing rate is valid. This fact corresponds to experimental results in many receptor neurones (Angelini *et al.*, 1982). On the other hand, the lower part of the sigmoid stimulus-response curve described, e.g. by Nillson (1975) can be approximated by $M^{-1}(R)$ for $\lambda < \mu$.

Up to this point, this model of neuronal activity evoked by a continuous stimulus only formally differs from the previous model. To include adaptive character of the

$$(12') \quad P(E(T_k)=s) = \binom{n-s-1}{k-1} (1-p)^k p^{n-s-k},$$

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Obviously, under the steady-state conditions when $\lambda_k \rightarrow \lambda$, we get $M(R_k|s) \rightarrow M(R) = (\lambda + \mu) \lambda^{-2}$. Then assuming that λ is proportional to stimulus intensity and $\lambda \gg \mu$, the approximately linear relation between the input intensity level and the output firing rate is valid. This fact corresponds to experimental results in many receptor neurones (Angelini *et al.*, 1982). On the other hand, the lower part of the sigmoid stimulus-response curve described, e.g. by Nillson (1975) can be approximated by $M^{-1}(R)$ for $\lambda < \mu$.

Up to this point, this model of neuronal activity evoked by a continuous stimulus only formally differs from the previous model. To include adaptive character of the

inhibitory process, let us assume that the process of inhibition $\{I(t), t \geq 0\}$ is also a pure birth process with parameters

$$\mu_k, k = 1, \dots, \sum_{k=1}^{\infty} \frac{1}{\mu_k} = \infty \text{ and } I(0) = 1.$$

The intervals between inhibitory pulses are mutually independent random variables with c.d.f.

$$(19) \quad G_k(t) = 1 - e^{-\mu_k t}.$$

Let us find

$$H_k(t|s, i) = P(R_k \leq t | E_{(k-1)} = s, I(t_{k-1}) = i),$$

$$k = 1, \dots, \quad s \geq n + k + 1, i \geq 1.$$

Using the same approach as previously we get

$$(20) \quad 1 - H_k(t|s, i) = e^{-\lambda_s t} + \sum_{j=1}^{\infty} \int_0^t \lambda_s e^{-\lambda_s x} P(i+j, x|i) \times \\ \times (1 - H_k(t-x | E(t_{k-1}+x) = s+1, I(t_{k-1}+x) = i+j)) dx = \\ = e^{-\lambda_s t} + \int_0^t \lambda_s e^{-\lambda_s x} (1 - e^{-\mu_i x}) dx - \\ - \sum_{j=1}^{\infty} \int_0^t \lambda_s e^{-\lambda_s x} P(i+j, x|i) H_k(t-x | E(t_{k-1}+x) = \\ = s+1, I(t_{k-1}+x) = i+j) dx,$$

where $P(i+j, x|i)$ denotes the transition probabilities from the state i at time zero to the state $i+j$ at time x for the inhibitory process $\{I(t), t \geq 0\}$.

For the considered pure birth process $\{I(t), t \geq 0\}$, $P(i+j, x|i)$ can be computed using the recurrence relationship (e.g. Bharucha-Reid, 1960)

$$(21) \quad P(i+j, x|i) = \mu_{i+j-1} e^{-\mu_{i+j} x} \int_0^x e^{\mu_{i+j} z} P(i+j-1, z|i) dz$$

for $i \geq 1$,

$$P(i, x|i) = e^{-\mu_i x}.$$

Taking L.-S. transformation of both sides in (20), we get

$$(22) \quad h_k^*(v|s, i) = \frac{\lambda_s}{\lambda_s + \mu_i + v} + \sum_{j=1}^{\infty} \lambda_s P^*(i+j, \lambda_s + v|i) h_k^*(v|s+1, i+j)$$

$$\text{where } P^*(i+j, \lambda_s + v|i) = \int_0^{\infty} e^{-(\lambda_s + v)t} P(i+j, t|i) dt.$$

Substituting Laplace transformation of (21) into (22) we have

$$(23) \quad h^*(v|s, i) = \frac{\lambda_s}{\lambda_s + \mu_i + v} + \\ + \sum_{j=1}^{\infty} \lambda_s h_k^*(v|s+1, i+j) \frac{1}{\mu_i + \lambda_s + v} \prod_{n=1}^j \frac{\mu_{i+n-1}}{\mu_{i+n} + \lambda_s + v}.$$

Differentiating both sides of (23) we get the formula for mean interspike intervals:

$$(24) \quad M_k(s, i) = \frac{\lambda_s}{(\lambda_s + \mu_i)^2} - \sum_{j=1}^{\infty} \lambda_s \left(\frac{\partial P^*(i+j, \lambda_s + v|i)}{\partial v} \right) \Big|_{v=0} - \\ - M_k(s+1, i+j) P^*(i+j, \lambda_s|i) = \\ = \frac{1}{\lambda_s} + \sum_{j=1}^{\infty} \lambda_s M_k(s+1, i+j) \frac{1}{\mu_i + \lambda_s} \prod_{n=1}^j \frac{\mu_{i+n-1}}{\mu_{i+n} + \lambda_s}.$$

A natural way to generalize a renewal process is to assume that the sequence of intervals forms a time-homogeneous first order Markov chain — Wold's Markov process. Let us use this to introduce an after-effect into the excitation process $\{E(t), t \geq 0\}$. So we retain the whole scheme of Poissonian inhibition with the only change that the excitation process is Wold's Markov process with conditional density function $f(x|y)$. Obviously, for the stationary process the marginal density functions $f(x)$ satisfy the equation

$$f(x) = \int_0^{\infty} f(x|y) f(y) dy.$$

In spite of the fact that this type of process has been extensively studied, the only case for which the solution of this equation was found in closed form is the reversible counter introduced by Lampard (1968). It should be pointed out that this system has been used as stimulating source in neurophysiological experiments.

Let us denote $H(y|x)$ the conditional c.d.f. of inter-response interval under the condition that the previous interval equals x , and for formal reasons assume that this interval ends at time zero.

Then we have

$$(25) \quad 1 - H(y|x) = \\ = e^{-\mu x} \left[1 - F(y|x) + \int_0^y (1 - e^{-\mu \tau}) f(\tau|x) (1 - H(y - \tau|x)) d\tau \right] + \\ + \int_0^x \mu e^{-\mu z} \left[(1 - F(y|w) + \int_0^y (1 - e^{-\mu \tau}) f(\tau|w) (1 - H(y - \tau|x)) d\tau \right] dw dz$$

where

$$g(w|z) dw = \text{Prob}(\text{the last excitatory pulse before time zero occurs at time } [-w, -w+dw) \text{ under the conditions that it occurs in the time interval } [-z, 0)).$$

Thus

$$h^*(v|x) = e^{-\mu x} \left[f^*(\mu + v|x) + f^*(v|x)h^*(v|x) - f^*(v + \mu|x)h^*(v|x) \right] + \int_0^x \mu e^{-\mu z} \int_0^z \left[f^*(\mu + v|w) + f^*(v|w)h^*(v|x) - f^*(v + \mu|w)h^*(v|x) \right] g(w|z) dw dz$$

and finally
(26)

$$h^*(v|x) = \frac{e^{-\mu x} f^*(\mu + v|x) + \int_0^x \mu e^{-\mu z} \int_0^z f(\mu + v|w) g(w|z) dw dz}{1 - (f^*(v|x) - f^*(v + \mu|x)) - \int_0^x \mu e^{-\mu z} \int_0^z (f^*(v|w) - f^*(v + \mu|w)) g(w|z) dw dz}$$

Substitution of specific types of $f(y|x)$ into this relationship as well as evaluation of conditional moments does not lead to tractable formulas. The same applies for the equation for marginal density function.

4. Conclusions

We can easily realize that the selective interaction models of neuronal activity ignore a lot of the phenomena of real neurones. On the other side the output behaviour of this model of evoked activity does not disagree with reality and Sampath and Srinivasan (1977, p. 65) also suggest the use of this type of model for the description of the sensory system. The comparison for different intensity transient stimuli and their probabilities of response follows from the first part of the paper. For comparison with experiment, with transient as well as continuous stimuli, the commonly used PSTH could be complemented with histograms of the firsts, the seconds and so on poststimulus intervals separately. Then a comparison of the model with the experimental data seems to be feasible. The present paper contains only results on the inter-response time. Using them and those of point process theory the other properties of the process $\{R(t); t \geq 0\}$ can be derived.

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