# Threshold Model for Clustered Firing of Neurons

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## Abstract

Two probabilistic threshold models for burst activity of cortical neurons are proposed. In model I every input impulse increases the summed effect of previous input impulses by one unit. The decay of the summed effect takes place in discrete steps of one unit. A response occurs on arrival of an input impulse, when a threshold value is attained.

Although after a response the summed effect is not reset to zero, it cannot exceed the threshold either. The distribution of intervals can be resolved in two components, one for long and one for short intervals. In model II intervals of the short component are terminated by a multiple response instead of one response.

## Introduction

To account for variability in neuronal unitary activity, a class of models has been proposed which is based on the summation of effects brought about by impulses patterned in some way and a response occurring as soon as a minimum amount of summed effect is present. After a response, summation starts anew from zero value. In most studies of an analytical nature, a Poisson arrival of impulses is considered, each having the same unit effect. The effects may last for a fixed time, they may vary in duration or decay as a continuous function of time. If the effects last up to the moment of response, the inter-response durations are gamma distributed. For most other utilized durations of effects, gamma-like distributions are reported, i.e. distributions with a more or less pronounced preferred interval duration.

In addition to the semi-regular discharge with mean interval durations that roughly vary between 10 and 100 msec, particularly cortical neurons frequently exhibit the phenomenon of burst activity when action potentials occur in very short succession, perhaps with a few milliseconds spacing between them. In the interval histograms experimentally obtained by Smith and Smith (1965), two exponential components become apparent: one has a steep slope and is composed of relatively short intervals, and the other is shallower,

representing the longer intervals between action potentials. They have suggested that the clusters of spikes exhibit the characteristic firing pattern of a nerve cell, and that the inter-burst intervals result from a switching or gating process whereby the cell is switched into its standard activity.

The spike train is considered to be composed of a Poisson shower, gated on and off. The durations of on and off periods are exponentially distributed variables with different parameter values. Thomas (1966) described a model based on some known physiological properties of nerve cells, but which is formally similar to the gating model proposed by Smith and Smith (1965) and which has the same type of interval distribution. Ekholm and Hyvärinen (1970) have elaborated a semi-Markov model with intervals belonging to two-component distributions though these distributions need not necessarily be negative exponential functions.

Returning to the threshold model mentioned in the first paragraph, one may wonder whether that model can account for an interval distribution consisting of two negative exponentials. The aim of this paper is to show that this is approximately valid, if a slight modification is accepted. After a response, the summed effect is not destroyed by the occurence of that response, but the summed effect cannot exceed the threshold. It will appear that to account for the steep initial peak in the histogram, the mechanism of multiple responses is indispensable: occasionally one input impulse may give rise to two or more responses. Therefore two models are introduced: I and II, the latter being an extension of the former.

## Model I

The input process is Poisson with parameter $\lambda$. Every input impulse increases the amount of summed effect by one unit, unless the threshold, $k$, has been reached, when input impulses do not increase the

summed effect any further. The decay of the summed effect occurs in steps of one unit and the duration of the unit effect of an input impulse is an exponentially distributed random variable with parameter $\mu$. The resulting curve of the summed effect as a function of time $t$ is a realization of a birth and death process with constant birth rate and linear death rate, having a reflecting barrier at $k$. An input impulse generates an output impulse, or response, if the summed effect at the time of arrival is equal to $k-1$ or $k$. This has been visualized in Fig. 1, with input impulse sequence (a), the summed effect curve (b) and the response sequence (c).
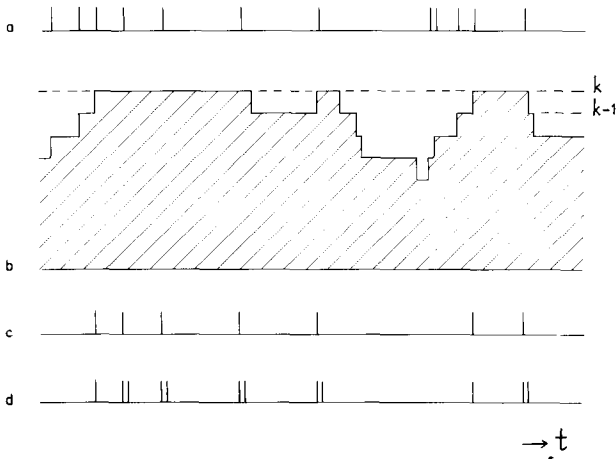


Fig. 1. Input-output relation for models I and II. a input sequence, b summed effect curve, c response sequence for model I and d response sequence for model II

Let $p_1(\tau)$ denote the probability density function of the time intervals $\tau$ between successive responses. Then $p_1(\tau)$ can be decomposed into two distributions, one consisting of intervals during which the summed effect did not fall below $k-1$, the other of intervals with the opposite property. Let $p^d(t)$ denote the conditional probability density function of the time $t$ of the first occurrence of summed effect $k-2$ when the summed effect at time $t=0$ was equal to $k$, given no input impulse has occurred in $(o, t)$. Let $p^f(t)$ denote the probability density function of the time $t$ of the first passage to threshold $k$ when the summed effect at $t=0$ was equal to $k-2$. Let the Laplace transform of a function of $t$ or $\tau$ be denoted by replacing $t$ or $\tau$ by $s$; e.g. the Laplace transform of $p_1(\tau)$ is denoted by $p_1(s)$, where $p_1(s) = \int_0^\infty p_1(\tau)\exp(-s\tau)d\tau$.

Then,

$$p^d(s) = \{k(k-1)\mu^2\}\{s^2+(2k-1)\mu s+k(k-1)\mu^2\}^{-1}.$$

Referring to definitions and formulae, given by Ten Hoopen and Reuver (1965), one has

$$p^f(s) = \lambda^2 A_{k-2}(s)/A_k(s).$$

$A_k(s)$ is given by the recurrence relation

$$A_k(s) = -\{s+\lambda+(k-1)\mu\}A_{k-1}(s)-\{(k-1)\lambda\mu\}A_{k-2}(s)$$

for $k \geq 2$ with $A_0(s) = 1$ and $A_1(s) = -s-\lambda$.

The first component of $p_1(\tau)$ is equal to

$$\lambda \exp(-\lambda\tau) \int_\tau^\infty p^d(t)dt,$$

the second is equal to

$$\int_0^\tau p^d(t)\exp(-\lambda t)p^f(\tau-t)dt.$$

Or, in Laplace transform notation:

$$p_1(s) = \lambda(s+\lambda)^{-1}\{1-p^d(s+\lambda)\} + p^d(s+\lambda)p^f(s).$$

## Model II

The modification consists in the assumption that an interval belonging to the first component of $p_1(\tau)$ is terminated by a pair of output impulses, separated by an interval of duration $\eta$; see Fig. 1d. During the generation of a pair of output impulses, an input impulse has no effect and no decay of effects occurs. In Laplace transform notation, the probability density function of the intervals between responses $p_{II}(\tau)$ is then given by:

$$p_{II}(s) = \exp(-\eta s)\{1-p^d(\lambda)\}\{2-p^d(\lambda)\}^{-1}$$
$$+ p_1(s)\{2-p^d(\lambda)\}^{-1}.$$

## Results

In Fig. 2 has been plotted, on a semi-logarithmic scale, the number of response intervals per second equal to or greater than corresponding values on the abscissa. By definition, this quantity is for $\tau = 0$ equal to the mean frequency, and approaches zero for large values of $\tau$.

The data have been copied from Fig. 2 of Smith and Smith (1965); the points hold for a 216 sec sample of spontaneous firing of a cortical neuron, $\Delta$ for the same cell during stimulation (polarizing by passing electric current through the micro-pipette). The rate of firing amounts to 5.5 and 13.4 per second, respectively.

If one tries to match the experimental data by equating the mean frequency of responses and the slopes of the two approximately exponential regions of each set of points, model I is found to give a poor fit.

On the other hand, model II shows reasonable agreement. Curves in Fig. 2 represent the function:

$$\left\{1 - \int_0^t p_{II}(\bar{\tau})d\bar{\tau}\right\} \times \text{mean frequency} .$$

Curve $a$ holds for spontaneous activity and is obtained by inserting $\lambda = 13.5 \sec^{-1}$, $\mu = 2.37 \sec^{-1}$ and $k = 8$ in the formulae; curve $b$, during stimulation, results from insertion of $\lambda = 33.0 \sec^{-1}$, $\mu = 5.77 \sec^{-1}$ and $k = 8$. It is noted that $k$ as well as $\lambda/\mu$ have the same value, for spontaneous and stimulated activity.
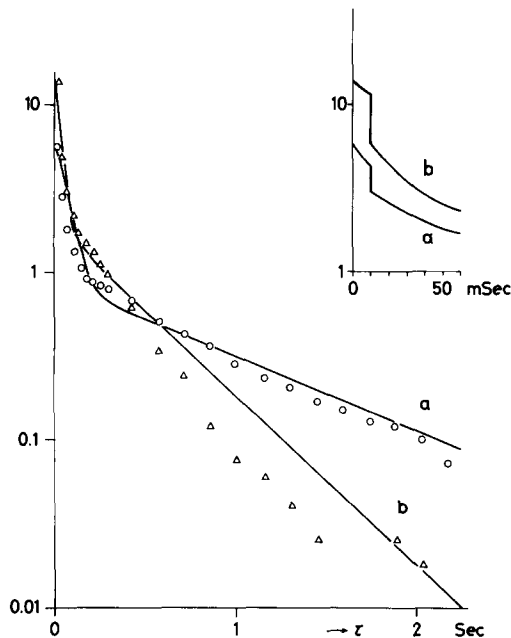


Fig. 2. Number of response intervals per second equal to or greater than $\tau$. Data adopted from Smith and Smith (1965). Curves for model II. For details see text. Inset: curves in more detail up to $\tau = 50$ msec

The actual value of $\eta$ is rather uncritical, at least as long as it is much smaller than the mean interval between responses, as is the case considered here. From sample records, shown in Fig. 6 of the publication cited, $\eta$ was estimated 10 msec.

If desirable, $\eta$ may be thought of as a random variable with the same mean value. For the conditions presented through curve $a$, and those of curve $b$, about 40% of the intervals belong to the very short burst intervals of 10 msec duration. A nearly equal part consists of moderately short intervals, i.e. with a duration of the order of 100 msec, while the remaining 20% have durations in the range of 1 second. The theory implies that, in Fig. 2, curve $a$ starts at $5.67 \sec^{-1}$ for $t = 0$, changes continuously to $5.25 \sec^{-1}$ up to

$t = 10$ msec, at this point changes abruptly to $2.95 \sec^{-1}$ and thereafter decreases monotonically to zero. Curve $b$ starts at $13.4 \sec^{-1}$, while changing stepwise at $t = 10$ msec from $11.2 \sec^{-1}$ to $5.78 \sec^{-1}$.

## Discussion

We have tried to give a formal description of neural spike trains in which short periods of burst activity alternate with relatively silent periods, a property which manifests itself in the interspike interval distribution in the form of two roughly exponential regions. To this end we resorted to a modification of a model that had been used in other neuronal activity studies.

It is based on the summation of elementary effects, a threshold for discharge and a reset of the summed effect after a response. In model I it is assumed that, after a response, the summed effect is not reset but remains equal to threshold value $k$ as long as no decay of effects occurs. Differently stated, input impulses give a response at the moment of arrival, unless the summed effect due to previous input impulses has fallen below a critical value, $k - 1$. The arrival of input impulses is assumed Poisson and the duration of the effect of each input impulse is distributed exponentially. Both assumptions are fairly common in theoretical studies, and very desirable if one wants to attack problems analytically.

Model I does not meet the requirements with regard to the interval histogram. Therefore, in model II, an extra assumption has been introduced in that an output impulse may be followed by another one after a short time of 10 msec, depending on whether or not the summed effect has been below value $k - 1$ since the last output impulse. This dependence on the past history makes the process non-Markovian, though not much.

Estimation and comparison of the system parameters for spontaneous and stimulated activity reveals that in model II quantity $k$ possess the same value for both types of activity. The values for input frequency $\lambda$ and rate of decay $\mu$ have changed, but by the same factor, denoted by $\varrho$; thus $\lambda/\mu$ has not changed.

In general, threshold models have the property of shape invariance for a given value of $k$ and given ratio of input frequency and rate of decay. So, for models I and II, when $\lambda_1/\mu_1 = \lambda_2/\mu_2$, and $\lambda_1/\lambda_2 = \varrho$, then $p_2(t) = p_1(t/\varrho)/\varrho$, where $p_1(t)$ and $p_2(t)$ denote the respective probability density functions of response intervals, except at $t = \eta$ and $t = \eta/\varrho$ for model II. This amounts to a transformation of the $t$-coordinate.

This peculiarity had been noticed before. It appears, from data of Goldberg *et al.* (1964) on spontaneous and

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stimulated activity of neurons in the superior olivary complex in cat, that the interspike interval histograms would have similar shapes after appropriate scaling. In more detail, the property of shape-invariance had been investigated in cat cochlear nucleus cells by Pfeiffer and Kiang (1965). They concluded that, when the time scales of histograms for responses to low and moderate levels of acoustic stimulation are expanded by a factor equal to the ratio of the average rate of stimulated and spontaneous activity, the shapes of the histograms for both spontaneous and stimulated conditions are very similar. The similarity in shape of inter-spike interval distributions for spontaneous and stimulated activity holds for any particular shape of the four classes of distributions, according to a tentative classification of interval distributions.

The shapes of histograms remain similar even in cases for which the rates of stimulated activity are tenfold greater than the rates of spontaneous activity.

It can be deduced from the formulae that $p_{II}(\tau)$ equals the sum of $k + 2$ negative exponentials. Properly speaking, when, as we concluded, $k = 8$, $p_{II}(\tau)$ is composed of 10 exponential components. However, the resulting curves can be fairly well approximated by two exponentials as Fig. 2 shows.

The structure of impulse trains can also be analyzed by estimating the probability of occurrence of $n$ impulses within a given time interval. Smith and Smith (1965) computed this quantity in their Fig. 7 for durations of 50 msec when $n$ ranges from 0—7.

Comparison of their experimental data with results of our model II shows that a slight modification of this model is required. A preliminary investigation indicates that, instead of a pair of output pulses, one input impulse may give rise to two or more output impulses, according to some probability distribution. This has not been pursued here, because it does not affect much our main conclusions.

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