

## Adaptive Neural Encoder Model with Selfinhibition and Threshold Control

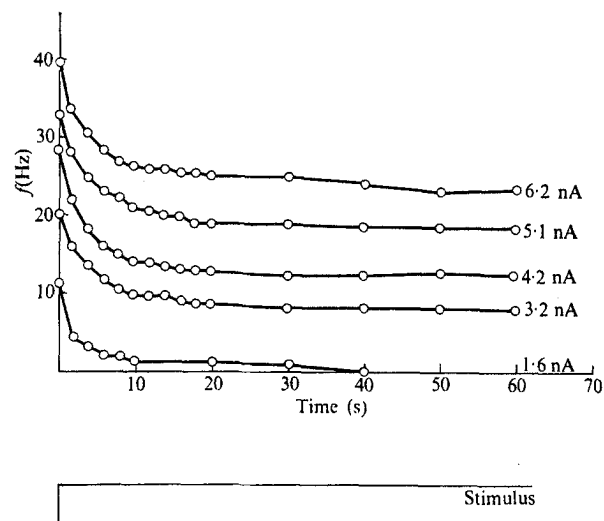
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**Abstract.** A general model for an adaptive neural encoder relating the output firing frequency to input stimulus is presented. The model is based on an “integrate and fire at threshold” scheme and includes cumulative inhibitory feedback as well as output rate dependent threshold control.

### 1. Introduction

Considerable effort has gone into experimental and theoretical investigations concerning adaptation (or accommodation) phenomena in neuronal encoders. In experimental set-ups, neuronal action potential discharges in response to a time-varying excitatory input,  $\lambda(t)$ , are registered and the instantaneous firing rate,  $R(t)$ , is estimated employing some counting or filtering techniques. Although the system under study is known to be nonlinear and as such the responses to simple sets of stimuli do not yield a complete characterization, considerable experimental work has been invested in generating and evaluating step-, ramp-, and sinusoidal responses (Jansen et al., 1970; Sokolove and Cooke, 1971; Grinell, 1977; Jack et al., 1975). The response of an encoder to a step increase in stimulus intensity is an immediate increase in the output firing rate followed by a gradual decline towards a steady state level of activity (Fig. 1). Dynamic step response transients are usually fitted to exponentials, and accommodation time constants can thus be computed. The dependence of the initial and steady state output frequencies as well as that of the adaptation time constants, on the input step amplitude are readily evaluated. Since interspike intervals are essentially random, their variability (second-order statistics) as a function of the firing rate (first-order statistics) is also investigated, with a view to assessing the influence of input or of the output level of activity during the adaptation transients, on firing



**Fig. 1.** Examples of adaptive transient responses to current-step stimuli. (From Sokolove, 1972)

regularity (Bromm and Tagmat, 1977; Sanderson et al., 1979).

Adaptation transients induced by step inputs of amplitude  $\lambda_0$ ,  $\lambda(t) = \lambda_0 u(t)$ , have the following general features:

1. The initial jump is followed by a rapid decay of firing frequency in turn followed by a slower drift towards the steady state (Fig. 2) (Jansen et al., 1970; Sokolove and Cooke, 1971; Grinell, 1977).
2. Both the rapid- and slow-phase adaptation time constants are input-dependent. An increase of the latter is observed as input amplitude increases, while the rapid decay becomes steeper (Sokolove and Cooke, 1971; Sokolove, 1972); in these circumstances there is gradual transition from single-exponential to biexponential accommodation behavior.

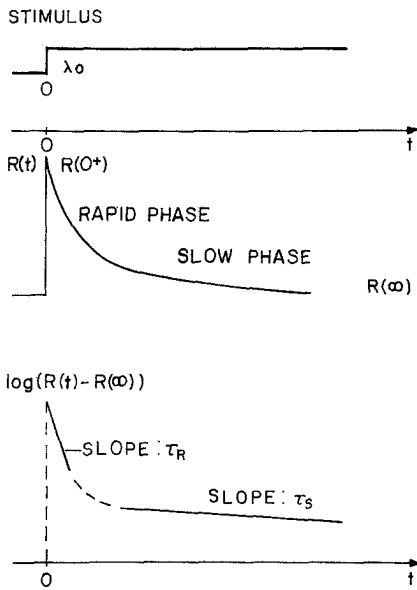


Fig. 2. Time course of two phase adaptive response in firing rate

3. Both initial and steady state rates ( $R(0^+), R(\infty)$ ) increase with  $\lambda_0$  and are subjected to saturation. The ratio  $R(0)/R(\infty)$  remains approximately constant in a certain range of low input intensities and decreases at higher intensities (Jansen et al., 1970; Sokolove, 1972).
4. The firing regularity (the reciprocal of the variability of interspike intervals) decreases in the course of adaptation and depends mainly on the output level of activity (Bromm and Tagmat, 1977; Sanderson et al., 1979).

The intricacy of neural coding calls for the making of models which complement the experimental approach in search for better understanding and parsimonious description of these processes. Models, as Kac (1969) pictorially describes them "... are, for the most part, caricatures of reality, but if they are good then, like good caricatures they portray, though perhaps in distorted manner, some of the features of the real world" and as such help in grasping the essence of the process. Several theoretical models have

been proposed for the neural encoder. While mainly concerned with the experimental input-output behavior, they also attempt to provide insight into, if not possible explanations for, the inner mechanisms of the coding process.

The neuronal membrane integrates ionic currents and discharges an action potential at a certain level of depolarization which defines its threshold. After firing there is an absolute refractory period, followed by one of reduced sensitivity when higher stimuli are needed for discharges to occur. These effects are usually explained by stating that the excitation threshold becomes infinite for some time, then gradually returns to a finite value. This behavior can be modelled as a simple "integrate and fire-at-threshold" scheme defined to perform a cumulative transformation on the stimulus and generate a pulse on reaching a certain threshold. Obviously, if no dynamic influences of input current or output firing on encoder parameters are assumed, the above model cannot account for adaptive effects. In such a case, the frequency of spike discharges depends only on the input intensity and on the fixed encoder parameters, resulting in a simple linear or nonlinear current-to-frequency converter.

There are various possibilities of modifying the integrate-to-threshold models in order to account for adaptive behavior (Fig. 3):

1. Preprocessing of the input stimulus  $\lambda(t)$  may be assumed to yield an output-dependent effective excitatory input,  $\lambda^*(t)$ , driving the spike initiation mechanism.
2. Dynamic influences of the input and/or output on parameters such as encoder threshold, determining the spike initiation, should also be taken into consideration.

Indeed, in the framework of the above possible modifications, several adaptive models were proposed. Considering the neural encoder as a linear current-to-frequency converter, as is, for example, the random integrate-to-threshold model with fixed threshold statistics, Sokolove (1972) introduced a self-inhibitory

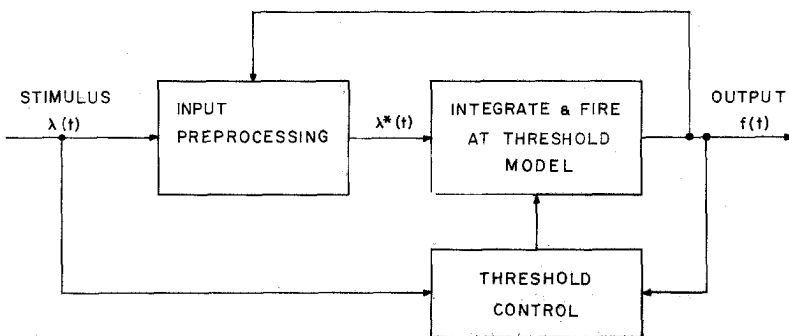


Fig. 3. Possible modifications of basic integrate-to-threshold scheme to obtain adaptive behavior

feedback reducing the effective excitatory input. The result, obviously oversimplified, was a simple linear dynamic system with high-pass filter properties, which adapted as such to step stimuli but did not predict input-dependent time constants. Recently the authors introduced a model postulating output-rate-dependent threshold control in pulse frequency modulation (Bruckstein and Zeevi, 1979a). This model, exhibiting characteristics of an automatic gain control mechanism, reproduces the fast phase behavior featuring steeper decline of the output firing rate at larger step stimuli amplitudes. To account for both the rapid and slow phases of adaptation, the model was further elaborated by adding a self-inhibitory loop to a pulse frequency modulation (PFM) system with output-dependent threshold control. At first approximation, this rather sophisticated scheme reduces to a simple nonlinear model and predicts the experimental findings concerning the two phases of adaptation, reproducing the correct dependence of response dynamics on stimulus conditions.

## 2. The Neural Encoder Model

The neural encoder responds to an excitatory input current of time-varying intensity,  $\lambda(t) > 0$ , with a sequence of essentially identical spikes or action potentials. Denoting the shape of the action potential by  $p(t)$ , the output of the encoder is given by:

$$f_p(t) \triangleq \sum_k p(t - t_k) = p(t) \circledast \sum_k \delta(t - t_k), \quad (1)$$

where  $\delta(t)$  is the Dirac impulse and  $\circledast$  denotes the convolution operator.

The stochastic "integrate and fire-at-threshold" or "integral pulse-frequency-modulation" (IPFM) scheme defines, in terms of the input  $\lambda(t)$ , the set of spike-occurrence-times  $\{t_k\}$  (Gestri, 1971; Bruckstein and Zeevi, 1979a) as:

$$\int_{t_k}^{t_{k+1}} x(\xi) d\xi = a_k, \quad k \in N \quad (2)$$

with  $t_0 = 0$  as an arbitrary time origin. Here the  $a_k$ 's are random threshold values – successive, independent realizations – at times  $t_k$  – of a threshold random variable  $A(t)$  with a generally time-dependent density  $p_A(a, t)$ . Accordingly the output pulses of the encoder model occur at times specified by a random point process hereinafter to be called the "output point process".

It should be emphasized that alternative estimators may be defined for the *level of activity* of a randomly discharging neural encoder at a certain moment  $T$ , a few of which are:

(a) The *expected number of occurrences* may be evaluated over a short interval  $(T, T + \Delta T)$ ,  $N(T, T + \Delta T)$ , yielding the *point density*  $D(T)$  of the output random point process at  $T$  (on the assumption that no significant changes occur in  $\lambda(t)$  or in threshold statistics over such an interval).

By definition, thus:

$$D(T) \triangleq E \left[ \frac{N(T, T + \Delta T)}{\Delta T} \right]. \quad (3)$$

(b) The *expected value of the instantaneous frequency*  $F(T)$  at the moment  $T$ , taken as the inverse of the duration of the interspike interval containing  $T$ ,  $I(T) = (t_{k+1}, t_k)$ , may also be considered. (Here  $k$  is a chance parameter):

$$F(T) \triangleq E[\|I(T)\|^{-1} | T \in I(T)], \quad (4)$$

where  $\|I\| \triangleq t_{k+1} - t_k$ .

(c) The inverse of the *expected value of the interoccurrence interval duration*,  $\|I(T)\|$ , may likewise be regarded as a measure of activity:

$$S(T) \triangleq E^{-1}[\|I(T)\| | T \in I(T)]. \quad (5)$$

Since the levels of activity defined by these estimators are obviously not identical, they have to be proven well defined and consistent. (For example, doubling the activity in terms of one of the estimators will double the activity in all others; this will be done later.) It is also advisable to confine oneself to a specific estimation technique for comparison purposes.

The density of the output point process relating to the output of one neural encoder was shown to be the biologically relevant parameter (Terzuolo, 1970), whereas the above definitions involve ensemble averaging that is valid only when dealing with large populations of identically driven stochastic encoders. [For a very good insight-providing discussion of this problem, see Knight's work (Knight, 1972).] An estimate of the density of the output process is however obtainable by considering the output of one encoder, from the number of occurrences over a period of time  $\Delta T$ , assumed to be small compared to changes in the very low frequency input  $\lambda(t)$ . Hereinafter,  $R(T)$  will denote the encoder level of activity at the time  $T$ , and we shall call it the expected spike discharge rate.

The integrate and fire at threshold spike initiation model provides for the  $k$ -th occurrence time the following implicit formula:

$$\int_0^{t_k} \lambda(\xi) d\xi = x_k, \quad (6)$$

where

$$x_k \triangleq \sum_{k=1}^k a_k. \quad (6a)$$

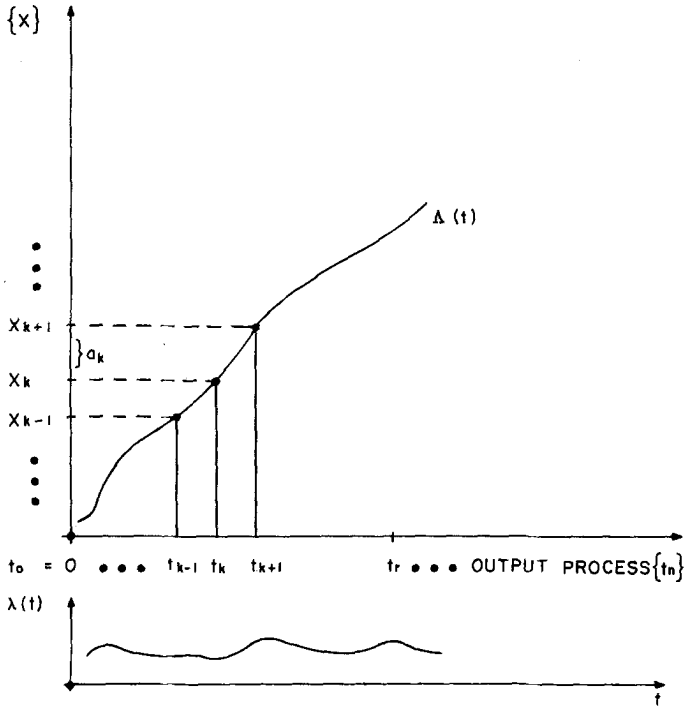


Fig. 4. Relationship between firing output process  $\{t_k\}$  and threshold process  $\{x_k\}$ , as mapped by input [integral density modulation (Yanaru and Iso, 1974)]

Accordingly the  $t_k$ 's may obviously be regarded as the moments at which the nondecreasing function  $x(t) = \int_0^t \lambda(\xi) d\xi$  crosses the levels  $x_k$ , (clearly  $x_{k+1} > x_k$  for all  $k$ ). Now, referring to Fig. 4, the  $x_k$ 's also define a random point process  $\{x_k\}$  (on the  $x$ -axis) with interval statistics determined by those of the random variable  $A$ .

In analogy to the definitions of  $D(T)$ ,  $F(T)$ , and  $S(T)$ , we have for the process  $\{x_k\}$ :

$$D_x(X) \triangleq E \left[ \frac{N_x(x + \Delta x)}{\Delta x} \right], \quad (7)$$

$$F_x(X) \triangleq E[\|I_x(X)\| | X \in I_x(X)], \quad (8)$$

and

$$S_x(X) = E^{-1}[\|I_x(X)\| | X \in I_x(X)]. \quad (9)$$

Let's find the relations between  $D_x$ ,  $F_x$ ,  $S_x$  and corresponding estimators for the level of activity. It is obviously true that

$$N_x(x(T), x(T + \Delta T)) \equiv N(T, T + \Delta T)$$

therefore we can write

$$\begin{aligned} D(T) &= E \left[ \frac{N_x(x(T), x(T + \Delta T))}{\Delta T} \right] \\ &= E \left[ \frac{N_x(x(T), x(T + \Delta T))}{x(T + \Delta T) - x(T)} \cdot \frac{x(T + \Delta T) - x(T)}{\Delta T} \right]. \end{aligned}$$

Thus

$$D(T) \cong D_x(X = x(T)) \cdot \lambda(T). \quad (10)$$

From (2) we also have the following:

$$\lambda(T) \cdot I(T) \cong I_x(x(T)).$$

Therefore

$$\begin{aligned} F(T) &= E[\|I(T)\|^{-1} | T \in I(T)] \\ &\cong E[\lambda(T) \|I_x(x(T))\|^{-1} | x(T) \in I_x(x(T))] \end{aligned}$$

yielding

$$F(T) \cong F_x(X = x(T)) \cdot \lambda(T). \quad (11)$$

For the third estimator we have:

$$\begin{aligned} S(T) &= E^{-1}[\|I(T)\| | T \in I(T)] \\ &\cong E^{-1}[\lambda^{-1}(T) \|I_x(x(T))\| | x(T) \in I_x(x(T))] \end{aligned}$$

and finally

$$S(T) \cong S_x(X = x(T)) \cdot \lambda(T). \quad (12)$$

Therefore, regardless of the definition of the estimator for the activity level, we have that the level of activity at the output is related to the threshold statistics, in fact to the "level of activity" of the  $\{x_k\}$  process, in the following way:

$$R(T) \cong R_x(X = x(T)) \cdot \lambda(T) \quad (13)$$

or:

$$R(T) \cong R_x^*(T) \cdot \lambda(T).$$

This also underlines the consistency of the above defined different estimators.

Several assumptions may be made regarding the threshold statistics:

(1) If the threshold random variable  $A$  has fixed, time invariant statistic -  $p_A(a)$ , one obviously obtains a renewal point process  $\{x_k\}$  with uniform activity  $R_x^*(T) = G_0$ , therefore we shall have (Gestri, 1971; Sokolove, 1972):

$$R(t) \cong G_0 \cdot \lambda(t). \quad (14)$$

(2) If the random variable  $A$ , that determines the threshold has time varying statistics, its distribution at  $T$  being  $p_A(a, T)$ , we obtain a time-varying "activity" of  $\{x_k\}$ ,  $R_x^*(T)$ , and thus a variable input-to-output-activity gain  $G_0(T) = R_x^*(T)$ . Accordingly we have (Bruckstein and Zeevi, 1979a, b)

$$R(t) \cong G_0(t) \cdot \lambda(t). \quad (15)$$

### 3. The Adaptive Encoder

It was shown that the spike generating model described above - an integrate to threshold scheme -

results in pulse frequency modulation, the current-to-frequency gain being a function of the threshold statistics.

Considering the continuous rate function  $R(t)$ , rather than particular sequences of spikes as the encoder's output, and relating it directly to the input  $\lambda(t)$ , without an attempt to explain the details of the actual coding process, approximate models are obtained. These are simpler to handle mathematically, yet provide valuable information on the overall behavior. In this context, the model resulting from the assumption that the threshold random variable,  $A$ , has time invariant statistics leads to a linear current-to-frequency converter of constant gain  $G_0$  (Fig. 5a).

Modifications of this simple constant gain current-to-frequency converter model were proposed and studied in an attempt to reproduce the observed adaptive behavior of neural encoders:

(1) A model with an inhibitory feedback current reducing the excitatory input by an amount  $\lambda_i(t)$  continuously dependent upon the output rate, and on its recent history, was shown to yield simple exponential transients of adaptation to step changes in the input current  $\lambda(t)$  (Fig. 5b). A detailed analysis of the resulting simple feedback system and comparison of its behavior to experimental results for the crayfish stretch receptor is found in (Sokolove, 1972). Other researchers studied PFM systems with cumulative feedback as models for coding in the visual system (Dodge, 1969; Michaelis and Chaplain, 1973).

(2) Adaptation can also result from output-dependent temporal changes in the statistics of the threshold leading to a variable, output-controlled, current-to-frequency gain  $G_v(t)$ . It is possible that a high rate of output firing activity over a certain period of time results in an increase of the expected value of the threshold therefore increasing (probabilistically) the subsequent interspike intervals. The net result is a feedback control of the gain thereby reducing the output activity. This "automatic gain control"-like system (Fig. 5c) is also characterized by exponential adaptation to step inputs, as will become clear later, and the transients exhibit input-dependent time constants (Banta, 1964; Bruckstein and Zeevi, 1979a, b).

Let us now define a model that incorporates both self-inhibitory current feedback and adaptive threshold control effects. In this model, a variable gain  $G_v(t)$  applied to the effective excitatory input  $\lambda^*(t)$  yields the output rate  $R(t)$ :

$$R(t) = G_v(t) \cdot \lambda^*(t). \quad (16)$$

The effective excitatory input  $\lambda^*(t)$  is taken as the difference between the input  $\lambda(t)$  and the inhibitory

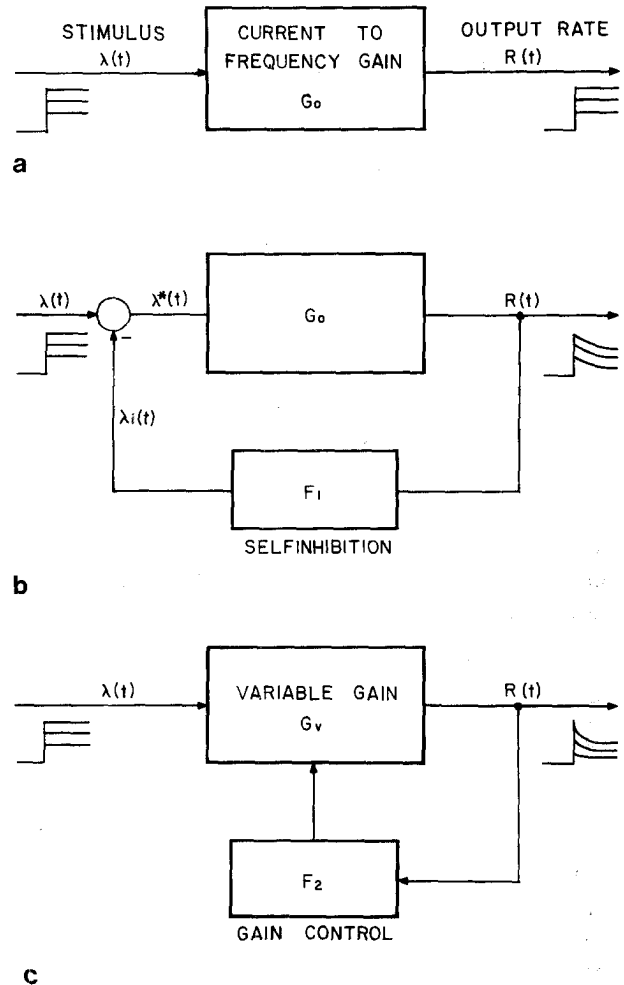


Fig. 5a-c. Encoder as a current to frequency converter: a non-adaptive, constant gain, b adaptive, constant gain with self-inhibition, c adaptive, gain control

current  $\lambda_i(t)$ :

$$\lambda^*(t) = (\lambda(t) - \lambda_i(t))^+ \triangleq \begin{cases} \lambda(t) - \lambda_i(t), & \lambda_i(t) < \lambda(t) \\ 0, & \lambda_i(t) > \lambda(t), \end{cases} \quad (17)$$

where we shall assume that a high self-inhibitory current cuts off the integration process at the membrane level. For the inhibitory current we introduce:

$$\lambda_i(t) = F_1[R(t), \tau_i], \quad (18a)$$

where  $F_1$  is a general filtering operator describing the dynamics of the self-inhibitory current,  $\tau_i$  being its main time constant. We shall assume here simple first order LPF dynamics for  $\lambda_i(t)$ :

$$\tau_i \dot{\lambda}_i(t) + \lambda_i(t) = MR(t). \quad (18b)$$

The variable gain  $G_v(t)$ , resulting from threshold control, will be considered as:

$$G_v(t) = F_2[R(t), \tau_g], \quad (19a)$$

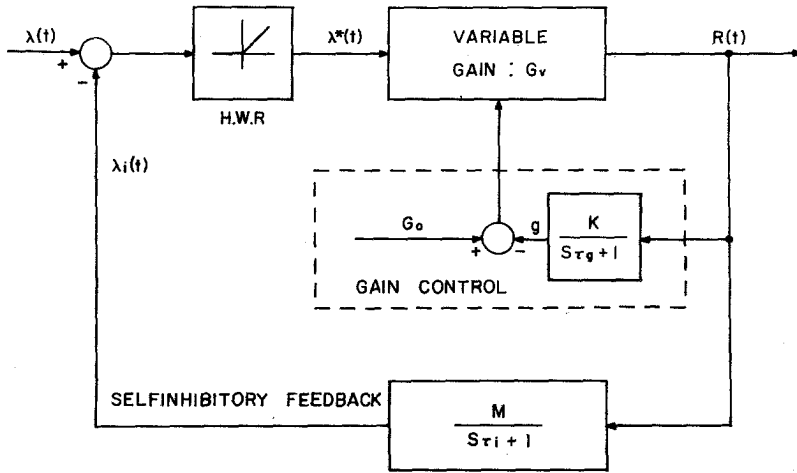


Fig. 6. The combined model with self-inhibition and adaptive gain control

where  $F_2$  is a general operator describing the variable gain dynamics of dominant time constant  $\tau_g$ . The variable gain can for simplicity be taken as:

$$G_v(t) \triangleq G_0 - g(t),$$

where  $g(t)$  has the following output-dependent behavior:

$$\tau_g \dot{g}(t) + g(t) = KR(t). \quad (19b)$$

Note that there is no need to set  $G_v(t) = 0$  for  $g(t) > G_0$  in order to prevent a negative gain since, as will become clear later, if  $g(t)$  is initially less than  $G_0$  it cannot exceed  $G_0$  for any positive input  $\lambda^*(t)$ . The resulting model is given in Fig. 6 (Bruckstein and Zeevi, 1979b).

The above presented scheme approximates the behavior, in terms of the expected output firing activity, of an adaptive, random integrate-and-fire-at-threshold model. It is in fact a deterministic nonlinear dynamic system, the state variables of which could, for example, be  $g(t)$  and  $\lambda_i(t)$ , the set of equations representing it are:

$$\begin{cases} \dot{\lambda}_i = \frac{1}{\tau_i} (MR(t) - \lambda_i) \\ \dot{g} = \frac{1}{\tau_g} (KR(t) - g) \end{cases} \quad (20)$$

and the output rate according to (16) is:

$$R(t) = (G_0 - g(t)) \cdot (\lambda(t) - \lambda_i(t))^+. \quad (21)$$

For a step input  $\lambda(t) = \lambda_0 u(t)$ , Eqs. (20) describe a classical autonomous dynamic system. In the sequel we shall use phase plane analysis to gain some information on the behavior of this model in response to step stimuli. Computer simulations are useful in evaluating phase plane trajectories and step responses as well as responses to ramp and sine stimuli.

#### 4. Analysis of the Encoder Model

##### 4.1. Phase Plane Analysis

Given that a step input is applied to the system (20),  $\lambda(t) = \lambda_0 u(t)$ , and the initial state being  $(\lambda_{i0}, g_0)$ , we have  $\lambda(t) \equiv \lambda_0$ , for all  $t > 0$ , and since Eqs. (20) are of the general form:

$$\begin{cases} \dot{\lambda}_i = M_A(\lambda_i, g) \\ \dot{g} = M_B(\lambda_i, g) \end{cases} \quad (22)$$

an autonomous nonlinear dynamic system is obtained. This nonlinear system is analysed in a straightforward way, through the classical methods of phase plane analysis. The phase plane plot  $(\lambda_i - vs - g)$  for the above system is sketched in Fig. 7. As pointed out before, we have  $g(t) < G_0$  provided  $g_0 < G_0$ . If  $\lambda_{i0} > \lambda_0$ , the system is described by two independent exponential decays with time constants  $\tau_i$  and  $\tau_g$  until  $\lambda^*(t) = (\lambda_0 - \lambda_i(t))^+$  becomes positive. Accordingly we shall concentrate on the region  $S \triangleq \{(\lambda_i, g) | 0 < \lambda_i < \lambda_0, 0 < g < G_0\}$  of the phase plane. At any moment the behavior of the system is determined from the state  $(\lambda_i, g)$  and the resulting magnitudes of  $\dot{\lambda}_i$ , and  $\dot{g}$ , and therefore the phase plane trajectories followed by the system from a given initial state can readily be plotted. These trajectories are usually estimated from the phase plane isoclines of the system, defined as the loci of points where  $d\lambda_i/dg$  is a constant  $\alpha$ . We can write the equation determining the isoclines from (20):

$$\frac{d\lambda_i}{dg} = \frac{\dot{\lambda}_i}{\dot{g}} = \frac{\tau_g}{\tau_i} \cdot \frac{\lambda_i - MR(t)}{g - KR(t)} = \alpha \quad (23)$$

and denoting  $\frac{\tau_i \alpha}{\tau_g} = p$  we get from (23) and (21)

$$\begin{aligned} \lambda_i &= pg \quad \text{for } R(t) = 0 \text{ (i.e. for } \lambda_i > \lambda_0) \\ \lambda_i &= \frac{g[p - \lambda_0(M - pK)] + \lambda_0 G_0(M - pK)}{g(pK - M) + 1 + G_0(M - pK)} \quad \text{for } \lambda_i < \lambda_0. \end{aligned} \quad (24)$$

Thus the isoclines are either linear for  $\lambda_i > \lambda_0$ , or hyperbolic functions  $\lambda_i(g)$ , with asymptotes at  $g_{as} = G_0 + \frac{1}{M - pK}$ , where  $g(pK - M) + 1 + G(M - pK) = 0$  (vertical) and  $\lambda_i = \lambda_0 + \frac{p}{pK - M}$  as  $g \rightarrow \pm \infty$  (horizontal). Two of them, the nullclines, are of particular importance.

$$1. \alpha = 0 \Rightarrow \frac{d\lambda_i}{dt} = 0 - \text{the zero-slope isocline}$$

$$2. \alpha = \infty \Rightarrow \frac{dg}{dt} = 0 - \text{the infinite-slope isocline}$$

and are drawn in the phase plane plot of Fig. 7.

The intersection of  $\dot{\lambda}_i = 0$  and  $\dot{g}_i = 0$  yields a singular point -  $P$  in the state space: it is a stable equilibrium point (as readily seen from the behavior of  $\dot{\lambda}_i$  and  $\dot{g}_i$  in the neighboring region) and represents the steady state eventually reached by the system (as  $t \rightarrow \infty$ ) in response to a step input. The steady state point coordinates ( $\lambda_{iss}, g_{ss}$ ) can easily be computed from the system Eqs. (20) by setting  $\dot{\lambda}_i = \dot{g}_i = 0$ , and we have:

$$\begin{aligned} \lambda_{iss} &= MR_{ss} \\ g_{ss} &= KR_{ss} \end{aligned} \quad (25)$$

yielding for  $R_{ss}$  the equation

$$R_{ss} = (G_0 - KR_{ss})(\lambda_0 - MR_{ss}). \quad (26)$$

Note that an immediate result is that  $\lambda_{iss} = (M/K)g_{ss}$ , i.e. the stable points for all  $\lambda_0$  lie on the line  $\lambda_i = (M/K)g$  (Figs. 7 and 9).

#### 4.2. Theoretical Results on Step Responses

The simple current-to-frequency transducer of constant gain  $G_0$  obviously provides for the output a non-adaptive modulated response  $R(t) = G_0\lambda(t)$  (Fig. 5a).

The inhibitory current feedback model with constant forward gain  $G_0$  (the case  $K=0$  in the scheme of Fig. 6) is governed by the following differential equation [for  $\lambda_i(t)$ ]:

$$\tau_i \dot{\lambda}_i(t) + \lambda_i(t) = \begin{cases} MG_0(\lambda(t) - \lambda_i(t)), & \lambda_i(t) < \lambda(t) \\ 0, & \lambda_i(t) > \lambda(t) \end{cases}$$

or using the step function  $u(\cdot)$ :

$$\dot{\lambda}_i + \frac{1}{\tau_i}(1 + MG_0 \cdot u(\lambda - \lambda_i))\lambda_i = \frac{1}{\tau_i}MG_0\lambda u(\lambda - \lambda_i)$$

with the well known solution for  $\lambda_i < \lambda$ :

$$\lambda_i(t) = \exp(-t/\tau_{s1}) \left\{ C + \int^t \left[ \exp(\xi/\tau_{s1}) \frac{MG_0}{\tau_i} \lambda(\xi) d\xi \right] \right\}.$$

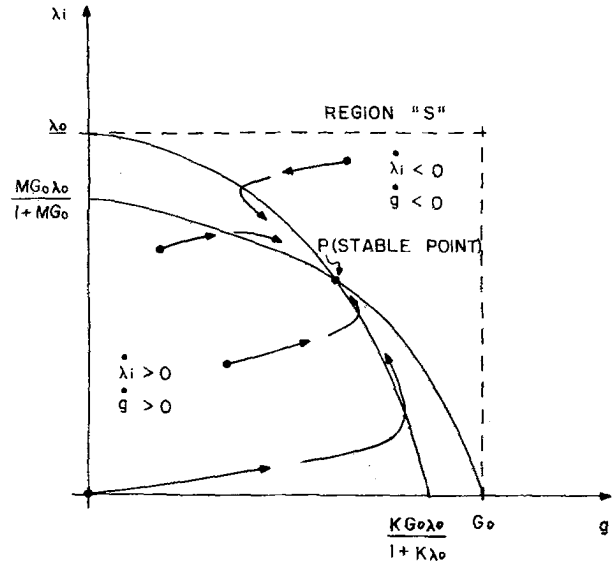


Fig. 7. Phase plane image of encoder model for step stimuli, indicating the steady state point  $P$

$C$  being a constant determined according to initial conditions. Thus

$$R(t) = G_0(\lambda(t) - \lambda_i(t))^+. \quad (27a)$$

Setting  $\lambda(t) = \lambda_0 u(t)$  (step response) we readily obtain:

$$R(t) = G_0\lambda_0(1 + MG_0)^{-1} [1 + M_0 G_0 e^{-t/\tau_{s1}}], \quad (27b)$$

an exponential decay in output activity proceeding from  $G_0\lambda_0$  to  $G_0\lambda_0(1 + MG_0)^{-1}$  with time constant:

$$\tau_{s1} = \tau_i(1 + MG_0)^{-1}. \quad (27c)$$

Sokolove (1972) compared this behavior with the experimentally recorded accommodation transients in the crayfish stretch receptor and concluded that for step currents of low intensity ( $\lambda_0 \cong 1 \div 5$  nA) good fitting to data can be obtained by adjusting the parameters  $M$ ,  $G_0$ , and  $\tau_i$ . However, the slow adaptation time constants were found to increase slightly with increasing  $\lambda_0$  (even for the low input range) and at higher input steps, in addition to the slow transient towards a steady state a rapid initial decay was also observed. It was clear that such a behavior could not be accounted for in an essentially linear model.

If the accommodation is attributed to gain control alone, in fact to adaptive threshold changes (setting  $M=0$ , in Fig. 6), we also obtain that a step input causes an exponential decay but here the time constants decrease with increasing  $\lambda_0$ .

The differential equation for the gain control variable  $g$  in this AGC-like system is:

$$\tau_g \dot{g}(t) + g(t) = K(G_0 - g(t)) \cdot \lambda(t)$$

or

$$\dot{g} + \frac{1}{\tau_g}(1 + K\lambda(t))g = \frac{1}{\tau_g}G_0\lambda(t)$$

with the solution

$$g(t) = \exp\left[-\int_0^t \frac{1 + K\lambda(\xi)}{\tau_g} d\xi\right] \cdot \left\{ C + \int_0^t K G_0 \frac{\lambda(\xi)}{\tau_g} \exp\left[\int_0^\xi \frac{1 + K\lambda(\eta)}{\tau_g} d\eta\right] d\xi \right\} \quad (28a)$$

or writing it in a slightly different way:

$$g(t) = C \cdot \exp\left[-\int_0^t \frac{1 + K\lambda(\xi)}{\tau_g} d\xi\right] + G_0 \left\{ 1 - \exp\left[-\int_0^t \frac{1 + K\lambda(\xi)}{\tau_g} d\xi\right] \cdot \left( 1 + \frac{1}{\tau_s} \int_0^t \exp\left[\int_0^\xi \frac{1 + K\lambda(\eta)}{\tau_g} d\eta\right] d\xi \right) \right\}.$$

From here it is clear that  $g(t)$  cannot exceed  $G_0$  for all positive inputs  $\lambda(t)$ , provided  $g(0) < G_0$  (see Sect. 3). Setting  $\lambda(t) = \lambda_0 u(t)$ , the step response is obtained, and finally we get for  $R(t)$ :

$$R(t) = \frac{G_0 \lambda_0}{1 + K \lambda_0} (1 + K \lambda_0 e^{-t/\tau_{s2}}) \quad (28b)$$

with overall time constant

$$\tau_{s2} = \tau_g (1 + K \lambda_0)^{-1}. \quad (28c)$$

Thus in this model an input dependent decay time constant  $\tau_{s2}$  is obtained, and the steady state is  $G_0 \lambda_0 (1 + K \lambda_0)^{-1}$ . Note that (28b) has a form identical to (27b) if one interchanges  $K \lambda_0$  with  $M G_0$ . A glance at the corresponding differential equations shows that this is hardly a strange coincidence.

When both AGC and the self-inhibitory feedback effects are in action, the analysis of the differential equations describing the system becomes quite difficult for convenient manipulation. In these circumstances it is preferable to resort to the phase plane analysis and computer simulation, which yield a fairly comprehensive image of the model behavior. It was clear from the phase plane-sketch of the system that when a step input is applied, the output firing rate reaches a steady state given by Eq. (26), and the solution reads:

$$R_{ss} = \frac{2G_0\lambda_0}{(1 + K\lambda_0 + G_0M) + \sqrt{(1 + K\lambda_0 + G_0M)^2 - 4KM G_0\lambda_0}}. \quad (29)$$

Actually Eq. (26) has two solutions, but one of them can be immediately discarded as corresponding to a point outside the region  $S$ , and therefore to zero output.

The experimental and theoretical investigations (Jack et al., 1975; Sokolove and Cooke, 1971) have firmly established that a self-inhibitory current generated by an electrogenic  $\text{Na}^+$  pump is indeed responsible for the slow transients in adaptation. As discussed before, a rapid initial decay is also observed that could not be attributed to the current-feedback process and as Sokolove (1972) points out "... it may be that sudden, intense depolarizing current directly affect the *spike generation mechanisms* to produce an inhibitory effect which adds to the type of inhibition considered" (self-inhibitory feedback). Many authors have pointed out that cumulated refactoriness (in the form of a higher threshold of firing) is responsible at least in part for adaptive behavior.

In our model, the threshold control reflects this additional effect. This is quite a natural assumption and the threshold variation indeed reflects changes in the spike initiation process. In a series of recent studies on the neural coding in the visual system of the fly, Mastebroek (1974) and Zaagman (1977) considered the implications of modelling the process by a stochastic integrate-to-threshold scheme (Gestri, 1971). Their study leads to the conclusion that dynamic changes in threshold statistics have to be assumed to account for the loss of the so-called "structural invariance" under nonstationary stimulus conditions (Gestri et al., 1980). If the output activity  $R(t)$  is estimated, and the modulated point process, describing the encoder output, is transposed on a new time scale according to the transform  $\int_0^t R(\xi) d\xi$ , the assumption that  $R(t) = G_0 \lambda^*(t)$  (i.e. invariant threshold statistics) provides interspike interval histograms that describe the threshold statistics (a return to the  $x$ -axis in Fig. 4).

The so-"demodulated" point process exhibited however changes in the "interval" statistics under different dynamic stimulus conditions, therefore, the assumption of invariant threshold statistics must be discarded (Gestri et al., 1980). Note that if  $R(t) = G_0(t) \cdot \lambda^*(t)$  we cannot possibly separate, through this method, the effects of the variable gain (i.e. threshold statistics) and of the effective input  $\lambda^*(t)$ . Zaagman (1977), also reported results on the responses of movement-detector encoders of the fly indicating a gain control effect of input dependent reduction in adaptation time constants.

In the following analysis we shall assume that the gain control process is much faster than the self-inhibitory current feedback, thus  $\tau_g \ll \tau_i$ . In order to simplify the analysis we shall consider that the response to a step input  $\lambda(t) = \lambda_0 u(t)$  has two phases:

1. A phase of *initial rapid decay* mainly due to *threshold variations* hence to gain control action; in this



period it is assumed that the slow self-inhibitory current changes are negligible. The rapid decay in output activity proceeds from  $R(0^+) = G_0 \lambda_0$  [initial conditions (0, 0)] with a time constant of

$$\tau_R = \tau_{s2} = \tau_g (1 + K \lambda_0)^{-1}. \quad (30)$$

2. A *slow accommodation period* follows when the influence of the *self-inhibitory current dynamics* is apparent. We shall consider that by then, the variable gain  $G_v(t)$  has already reached, through the rapid gain control process, a value close to its steady state value

$$G_{vss} \cong G_0 - g_{ss}$$

and does not change drastically in this phase. Accordingly the slow adaptation has a time constant approximately given by the dynamics of a linear control system with forward gain  $G_{vss}$ :

$$\tau_s = \tau_{s1} = \tau_i (1 + M G_{vss})^{-1}. \quad (31)$$

Since  $g_{ss}$  is increasing with the step amplitude  $\lambda_0$  it is readily seen that so does the slow phase time constant (since  $G_{vss}$  decreases); this is *exactly* the behavior of the slow transients as reported in experiments (Sokolove and Cooke, 1971; Sokolove, 1972).

Writing  $\tau_R$  explicitly and comparing its dependence on  $\lambda_0$  to that of  $\tau_s$  (Fig. 8):

$$\tau_R = \frac{\tau_g}{1 + K \lambda_0} \leftrightarrow \tau_s = \frac{\tau_i}{1 + M(G_0 - g_{ss}(\lambda_0))}$$

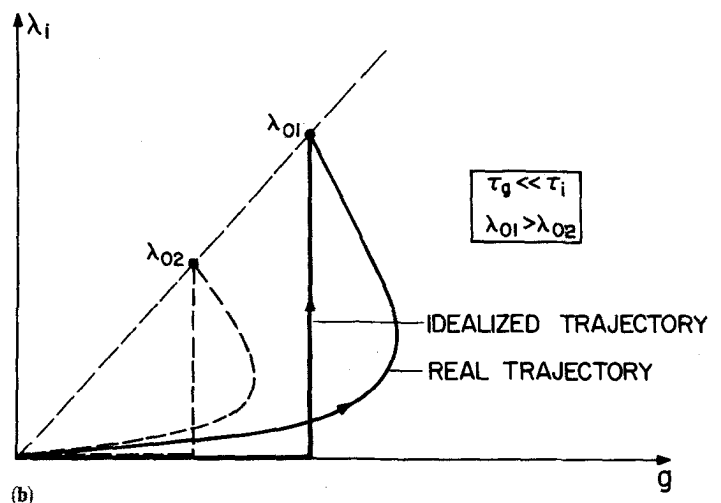
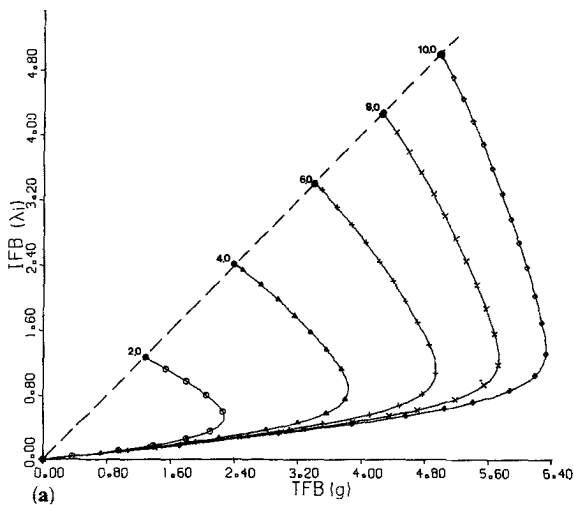


Fig. 9a and b. Phase plane step response trajectories as computed for steps of increasing amplitude (a) and compared to idealized trajectories assumed in approximated analysis (b)

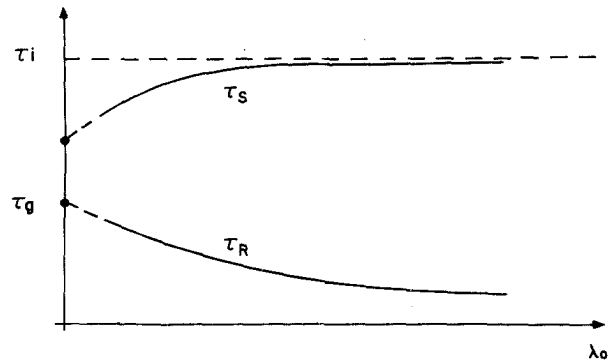


Fig. 8. Schematic representation of rapid,  $\tau_R$ , and slow,  $\tau_s$ , time constants' dependence on input step intensity  $\lambda_0$

one realizes why at low input intensities the biexponential characteristic of the adaptation transients is less pronounced – almost unobservable in Sokolove's experimental results. However, the difference between  $\tau_R$  and  $\tau_s$  increases with  $\lambda_0$  and therefore the two phases of adaptation become more and more evident (see Fig. 8). Also noteworthy is the fact that the initial rapid decay sweeps a smaller range of output firing frequencies when  $\lambda_0$  is small. The range of AGC adaptation is [also for initial state (0, 0)]:

$$\Delta R_{AGC} = R(0)^+ - R_{ss \text{ due to AGC}} \cong G_0 K \frac{\lambda_0^2}{1 + K \lambda_0}.$$

#### 4.3. Computer Simulations

To supplement the above analysis and for further insight into the behavior of the adaptive model, step, ramp and sine responses were simulated using con-

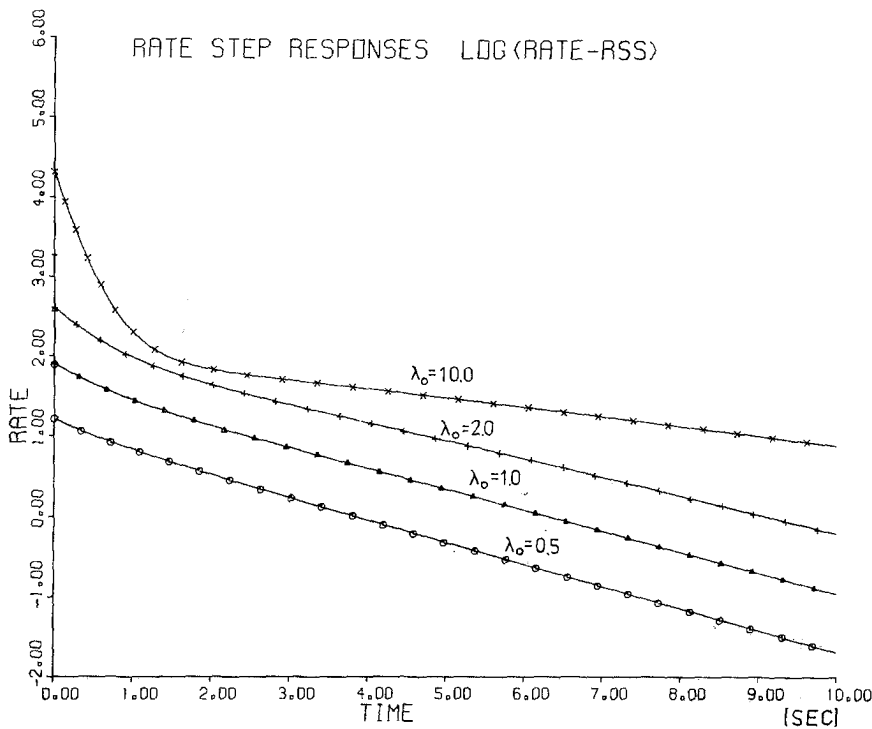


Fig. 10. Log plot of simulated step responses demonstrating transition from single- to two-phase behavior with increase in step amplitude  $\lambda_0$

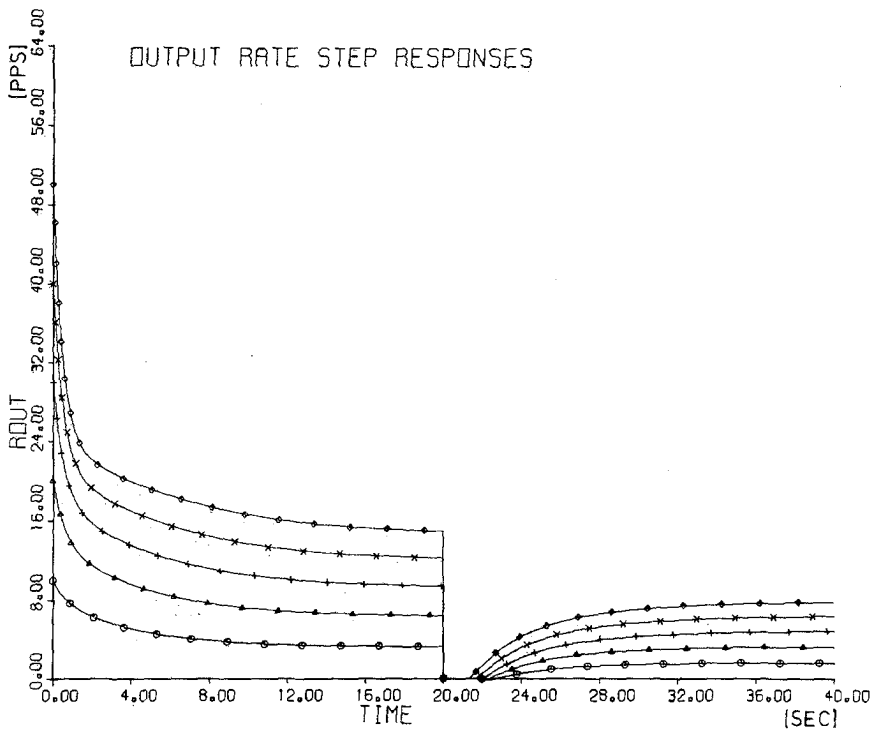


Fig. 11. Simulated "on-off" responses to the following stimuli:  $\lambda(t) = \lambda_0 u(t) - \lambda_0/2 u(t - 20.0)$ ,  $\lambda_0 = 1.0 \div 5.0$ . Note the silencing of encoder at the "off" transition as exhibited in experiments

tinuous system modelling programs (IBM System 370, CSMP User's Guide). The parameters of the system were adjusted to reproduce the static and dynamic behavior of stretch receptor as well documented in Sokolove's study (Sokolove and Cooke, 1971) and accordingly, the choice of parameters was:  $G_0 = 10$  - to account for the approximate curve of  $R(0^+) \cong 10\lambda_0$ ;  $k = 0.2$ ;  $M = 0.2$  - to yield a saturation level of  $R(\infty)$  as

$\lambda_0 \rightarrow \infty$  at 50 pulses/s;  $\tau_i = 10.0$  - for the self-inhibition, and  $\tau_g = 1.0$  for the AGC dynamics.

*Step Responses.* Adaptation transients to input steps of increasing amplitude  $\lambda_0 = 1, 2, \dots, 10$  and phase plane trajectories were obtained.

Comparing the phase plane trajectories of step responses (Fig. 9a) with the idealized trajectories

(Fig. 9b), it can be concluded that the approximation separating the gain control and self-inhibitory dynamics for the purpose of analysis is justified and in fact captures the important trends of encoder behavior during adaptation.

As noted previously, some encoders exhibit a transition from a simple exponential (one phase) transient to two-phase adaptation as input intensity increases. This behavior is reproduced by the model presented herein as illustrated in the log plots of output activity (Fig. 10).

It is also interesting to study “off responses” – due to a step decrease input intensity. Superimposed in Fig. 11 are encoder responses to inputs of the form  $\lambda_0(t) = \lambda_0 u(t) - (\lambda_0/2)u(t - T)$  for different intensities  $\lambda_0$ . Such records of on-off transient are frequently encountered in experimental studies (Jansen et al., 1970; Grinell, 1977; Jack et al., 1975) and most studies report ramp and sinusoidal responses as well. To enable as complete a comparison as possible, we therefore simulated these responses too.

*Ramp Responses.* Figure 12a shows the sequence of responses to different ramps truncated at the same maximum intensity level. As expected, these indicate that the steeper the ramp the more pronounced is the transient overshoot. This accommodation effect is also seen in a sequence of responses to ramps of different slopes truncated at the same time (Fig. 12b). The similarity of the simulated responses to experimental data is in particular apparent in considering the case of the stretch receptor encoder (Grinell, 1977).

*Sine Responses.* At low modulation depth ( $m$ ) and also for low frequencies the sinusoidal responses closely follow the input  $\lambda(t) = \lambda_0 + m\lambda_0 \sin \omega t$  (Fig. 13a and b). However, as modulation depth increases (or as the frequency is increased) the output activity is cut off at the low input phase, exhibiting the so-called “phase lock” effect or bursty response. This behavior of neural encoders is also well documented in experimental studies (Angelini and Petracchi, 1978; Jansen et al., 1970; Grinell, 1977).

To study the exact behavior of an integrate to threshold scheme, a hardware model was also implemented and simulations with this analog computer model also confirmed the validity of the continuous approximation applied in our analysis.

#### 4.4. Variability in Interspike Intervals of Encoder's Output

One important facet of the integrate to threshold encoder output characteristics is the dependence of the

variability of interspike intervals on the mean rate of firing.

Considering first the slow adaptation transient, we shall assume that the threshold random variable has a fixed statistics during this period. Under this assumption the output interspike interval statistics will be affected by the changes in the effective input  $\lambda^*(t)$  only.

Since we have  $a_i \cong \lambda(T) \cdot \Delta t_i$  and it is reasonable to assume that  $\lambda^*(t)$  changes slowly, we obtain (through a simple scaling) (Papoulis, 1965):

$$E[\Delta t_i | \text{over } (T, T + \Delta T)] \\ \cong \frac{1}{\lambda(T)} E[a_i \text{ during } (T, T + \Delta T)]$$

and (32)

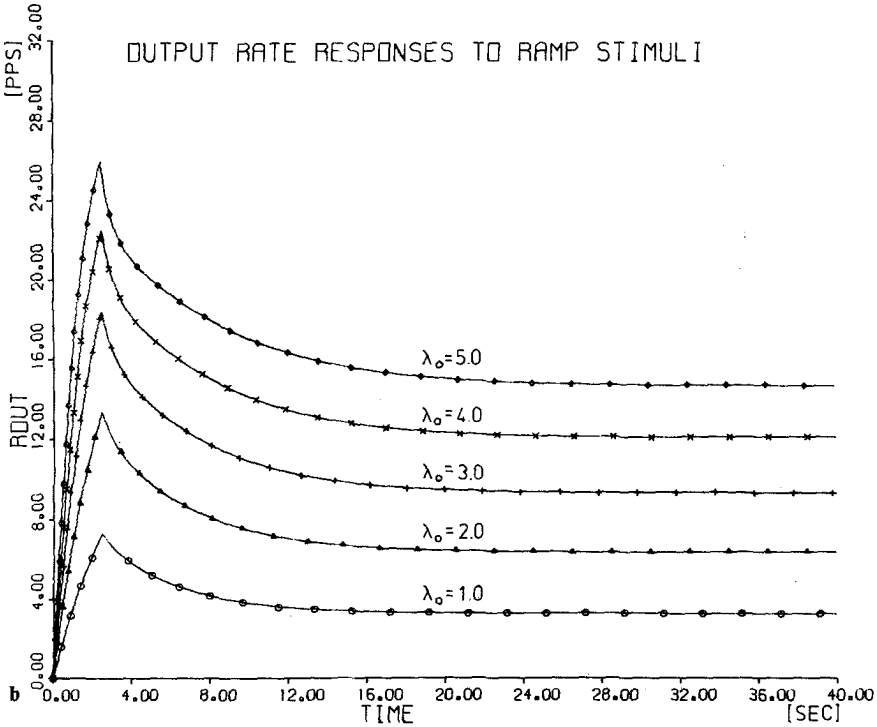
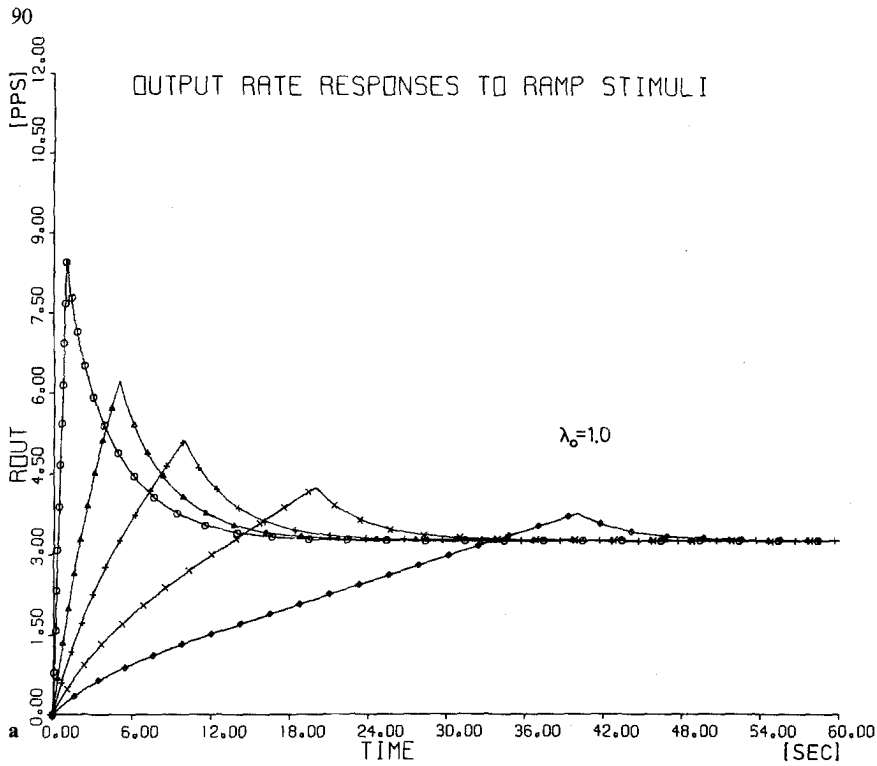
$$E[\Delta t_i^2 | \text{over } (T, T + \Delta T)] \\ \cong \frac{1}{\lambda^2(T)} E[a_i^2 \text{ during } (T, T + \Delta T)].$$

From these equations one readily obtains that the ratio of standard deviation over mean interval is independent of  $\lambda(T)$ . The behavior of the second order statistics during the fast adaptation phase was not studied carefully in experiments.

According to our model, and assuming that the second order statistic of the threshold random variable is not influenced by adaptive variations in its mean, in the rapid-initial phase there should be a sudden increase in regularity (Bromm and Tagmat, 1977). If then the threshold statistics become static during the second phase in such a way that the standard deviation of  $A$  over its mean is a constant independent of  $\lambda_0$  (which implies a later increase in the threshold spread by the end of the rapid phase) we obtain that the ratio of the standard deviation to the mean interspike interval is constant both over a wide range of steady firings and also during slow adaptation transients (Bromm and Tagmat, 1977; Sanderson et al., 1979). The variability in interspike intervals during the initial adaptation phase should be further investigated experimentally to yield deeper understanding of the threshold behavior (under assumption of the above presented model).

## Discussion

Modelling of adaptation phenomena by combining threshold control with self-inhibition reproduces a wide range of experimental results (Jansen et al., 1970; Sokolove and Cooke, 1971; Grinell, 1977; Jack et al., 1975; Bromm and Tagmat, 1977; Sanderson et al., 1979). Considering the mechanism of threshold control, it was already shown qualitatively that similar

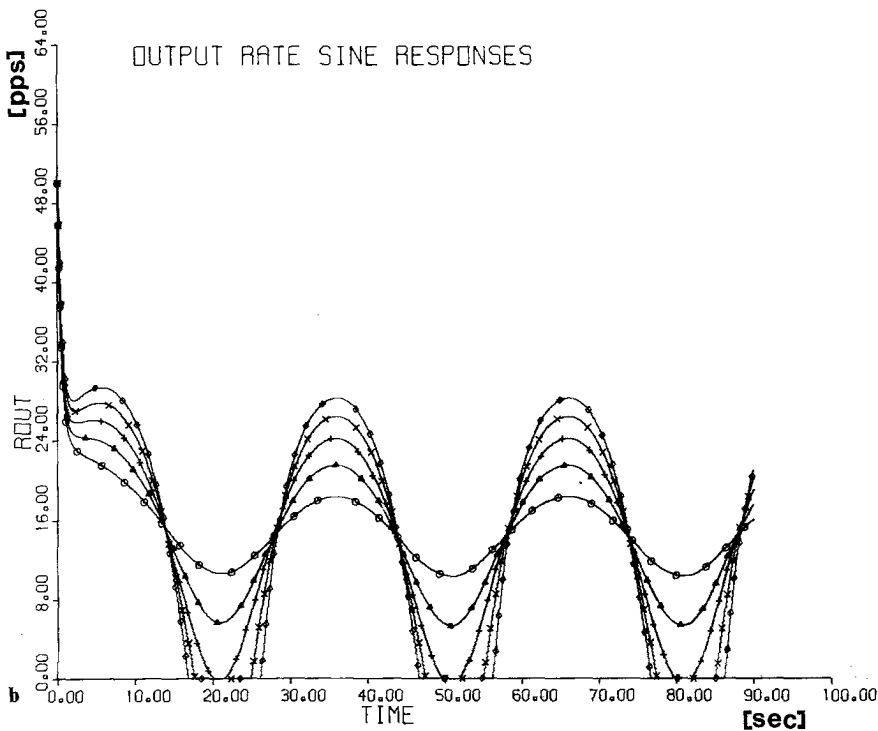
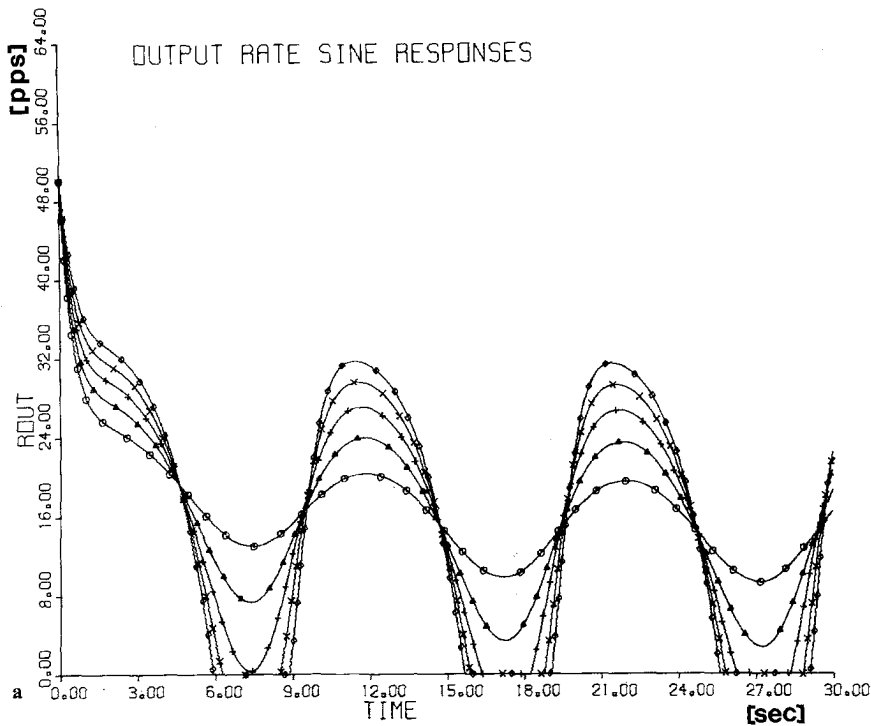


**Fig. 12a and b.** Ramp responses: **a** input reaching the level  $\lambda_0 = 1.0$  at different times, **b** input reaching different levels  $\lambda_0 = 1.0-5.0$  at time  $t = 2.0$

overall behavior could be achieved by either feedforward or feedback schemes (Bruckstein and Zeevi, 1979a). The authors have also hinted at what could be the biophysical basis of such adaptive threshold control. Relating the well documented physiological input-output relationship to the characteristics of the presented model of the spike generating mechanism, one concludes that adaptation in the threshold level, –

for example, through cumulative refractoriness, – must be assumed (Mastebroek, 1974; Zaagman, 1977; Gestri et al., 1980).

The functional components as represented in the neural encoder's model describe what apparently are lumped complex mechanisms physiologically regarded as spike initiator loci. Therefore the question of whether there exists a feedback loop controlling the thresh-



**Fig. 13a and b.** Sine responses: exhibiting "phase-locking" effect at higher modulation indexes **a**  $T=10$  s, **b**  $T=30$  s

old in the strict sense of backward information flow may be difficult or impossible to resolve. It is reasonable however to assume that in order to maximize reliability in outward information flow, in particular during the transients which become of outmost importance in adaptive systems, nature would prefer output dependent control. As for the self-inhibition mecha-

nism, there is evidence indicating various possibilities of physiological implementation, the simplest one being by means of a self-inhibitory synaptic loop as for example encountered in visual systems (Dodge, 1969).

An alternative feedback effect, the outward current flow resulting from the activity of an electrogenic sodium pump activated by the ionic influx due to

output firing (Sokolove, 1972; Sokolove and Cooke, 1971; Michaelis and Chaplain, 1973), is well established experimentally. In both of these examples the functional feedback loop indicates real backward flow of information on the encoder output (and the loops can be physically opened).

The combined model (Fig. 6) incorporates the minimal functional requirements needed to reproduce two-phase adaptation transients (to step inputs) with the correct dependence of both time constants on input amplitude. It also provides a good fit to sine responses reproducing the "phase-locking" effect and to adaptation transients to current ramps of different slopes. In comparison, previously presented models, although more complicated in structure and as such untractable analytically, do not reproduce a wider range of experimental results (Fohlmeister et al., 1977).

It has to be pointed out that in sensory encoding systems adaptation occurs also at the very first stage of stimulus-to-generator current transduction; this in addition to the adaptation in the current-to-impulse frequency conversion as analysed in this work provides the wide dynamic range needed in some sensory systems.

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