An Adaptive Stochastic Model for the Neural Coding Process

ALFRED M. BRUCKSTEIN AND YEHOSHUA Y. ZEEVI

***Abstract*—Neural encoders translate information on the time-varying intensity of stimuli into sequences of membrane depolarization spikes. Their output can be considered the realization of a stochastic point process, the overall encoder behavior being characterized through ensemble-averaged responses to identical stimuli and environmental conditions. A new mathematical model for the coding process is presented and analyzed. The model is an integrate and fire-at-threshold scheme, the stochastic features of its response resulting from random fluctuations in the firing threshold. As a consequence of feedback self-inhibition and threshold control, which is assumed to account for adaptive neural responses, the model output is a self-exciting point process. An approximate description of the averaged encoder response is obtained by considering an ensemble of identical coding units as a whole, instead of concentrating on output sample-path evolution. This approach overcomes the difficulty inherent in the analysis of global behavior of self-exciting point processes. A conceptual decoding scheme, implementing a coding unit in a feedback configuration, is also introduced and discussed.**

> The main role of models is not so much to explain and to predict, though these are the main functions of science, as to polarize thinking and pose questions. Above all, they are fun to invent and to play with, and have a peculiar life of their own. The "survival of the fittest" applies to models even more than to living creatures, they should not, however, be allowed to multiply indiscriminately without real necessity or purpose.
>
> *Mark Kac* [36]

I. INTRODUCTION

RESEARCH ON sensory coding processes and neural communication naturally involves models and techniques from mathematical theory developed for the analysis of man-made communication and information-processing systems. Physiologists experimentally determine input/output relations for various sensory (neural) transducers, and also seek information on details of the encoding process in terms of ionic flow mechanisms and dynamics of excitation at the level of the cell membrane [1]–[3]. Through a series of experimental and theoretical investigations, Hodgkin and Huxley derived an excellent model for excitable membrane dynamics explaining the initiation and propagation of neural depolarization spikes [1]. Their elaborate theory is, however, unsuitable for the analysis of more complex structures involving large numbers of coding units and interactive processes, which call for a probabilistic approach rather than a membrane-level description. Under the probabilistic approach, the neural spike sequences are regarded as realizations of stochastic point processes, and encoder responses are characterized in terms of ensemble averages [4]–[6].

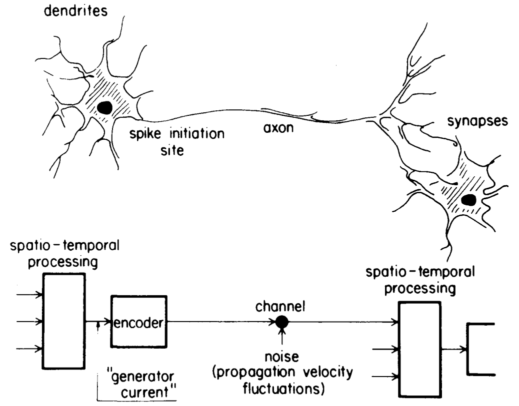

Fig. 1. Neuron as a communication system.

The nerve cells or neurons, building blocks of the whole nervous system, can be considered as basic data-processing modules performing the dual task of encoding and transmitting information (Fig 1). Stimuli affecting the coding units are translated into sequences of "all-or-none" depolarization pulses, called action potentials, which are propagated along the axonal channel. This electrical activity can be recorded and analyzed.

Experimental findings indicate that action-potential pulses are triggered at a certain threshold level of membrane depolarization, and up to the firing moment a cumulative stimulus-dependent buildup of subthreshold voltage is recorded. The rate of spike occurrence is thus modulated by stimulus intensity. At the same time, encoders also exhibit adaptive characteristics in the form of sharp transient responses to step-like changes in stimulus or environmental conditions. At very high stimulus intensity the encoder response saturates to a firing-rate level determined by the absolute refractory period (the time span after an action potential during which the neuronal membrane is not retriggerable).

Simplified mathematical models describing the stimulus-to-spiking-activity transfer are useful since they provide valuable insights into the behavior and performance of biological communication systems [7]–[16]. Widely used in

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The authors are with the Department of Electrical Engineering, Technion—Israel Institute of Technology, Haifa 32000, Israel.

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this context are models of the "fire-at-threshold" class, which are fairly close to physiological descriptions of the coding process yet relatively simple and mathematically tractable. These models define a deterministic or stochastic cumulative processing of "generator currents" (the ionic current flow determined by primary stimuli) with resulting changes in membrane depolarization; an action-potential spike is initiated at a certain threshold level of membrane polarization. Following a spike, after a refractory period, the cumulative processing of input current restarts, and repetitive firing activity is thus generated.

The above definition of the fire-at-threshold encoder model is a simplified representation of basic microscopic phenomena associated with the neural coding process. This paper introduces and analyzes a model of this type, with stochastic adaptive threshold behavior and self-inhibitory feedback, providing a good fit to some experimentally-recorded neural responses [15], [16]. Whereas the randomness in neural response is due to both input noise and fluctuations in the opening and closing of the various ionic channels, it is convenient to lump all these effects and represent them by a stochastic threshold behavior. This functional representation does not necessarily correlate with its biophysical causes.

II. CHARACTERIZATION OF NEURAL RESPONSE

Since action potentials are membrane depolarization pulses of essentially identical time-courses, the information on time variations of stimulus intensity resides in the sequence of their occurrence times. Let us denote by $S_{\mathrm{OT}} = \{T_1, T_2, T_3, \cdots\}$ the set of neural event occurrence times during some observation period starting at the arbitrary moment $T_0 = 0$. The encoder output, the time-course of membrane potential at some point along the axonal channel, can then be expressed as

$$f_q(t) = \sum_{T_k \in S_{\mathrm{OT}}} q(t - T_k) = q(t) * \sum_{T_k \in S_{\mathrm{OT}}} \delta(t - T_k) \quad (1)$$

where $q(t)$ describes the shape of a typical action potential spike, $\delta(t)$ is the Dirac delta function, and the asterisk is the convolution operator.

The information in the waveform $f_q(t)$ is obviously retained in

$$f(t) = \sum_{T_k \in S_{\mathrm{OT}}} \delta(t - T_k). \quad (2)$$

The set of occurrence times S_{OT} will be considered a realization of the output stochastic point process. We further assume that the relevant information, from the biological viewpoint, resides in the "level of activity" of the output stochastic point process. There are various ways to define the level of activity of the output process. Corresponding to any realization $\{T_k\}_{k \in N}$ of the output point process we can define the associated counting process $N(t)$

$$N(t) = \int_0^t f(\xi)\, d\xi = \text{number of events in } (0, t) \quad (3)$$

and the instantaneous frequency process $F(t)$

$$F(t) = (T_n - T_{n-1})^{-1} \quad (4)$$

where n is defined implicitly by $T_{n-1} < t \leqslant T_n$ (over the ensemble of responses it is obviously a chance variable).

In practice, many experiments are performed to obtain output sequences of a coding unit in response to identical stimuli and environmental conditions, the actual equivalent of considering the output of an ensemble of identical stochastic encoders. The output sequences are then processed off-line, and both $N(t)$ and $F(t)$ are readily obtained.

The level or rate of activity at the moment t, $R(t)$, can be alternatively defined as either the occurrence density of the output process,

$$R_N(t) = \frac{d}{d\xi} E[N(\xi)]\,|_{\xi = t} \quad (5)$$

or the average instantaneous frequency

$$R_F(t) = E[F(t)] \quad (6)$$

where the operator E denotes ensemble averaging.

The analysis of the neural output thus involves a set of responses of a coding unit to identical stimuli. It is important to point out that the above definitions for the level of activity are not expected to provide the same numerical results, and their consistency will be further discussed.

Stationary and Transient Responses

The encoder output is generally a nonstationary (nonuniform) random point process; the rate of activity as well as the stochastic structure of the process vary in time, following changes in stimuli or environmental conditions. It is due to such variations in time in the output process that information can be communicated to other centers of the nervous system.

Slow changes in stimuli lead to responses with modulated spike occurrence rates, whereas jumps elicit sharp transients in the neural activity. Steady states are of less importance in sensory systems, and adaptive neural responses indicate emphasis on stimulus gradients, already at the level of the coding process. A sudden stepwise or other steep change in stimulus leads to a well-defined transient of increase or decrease in the activity level, followed by an essentially two-time-constant decay towards a steady state [17]–[19].

Usually, analysis of the output random point process is carried out sequentially over sliding time intervals of length, say, Δt [5]–[8]. When dealing with steady-state responses, the firing sequences can be analyzed over long observation periods. Based on these data, interspike interval histograms are obtained in order to evaluate the stochastic structure of the output process and its variability. The normalized histograms provide, in this case, an estimate of the global interspike interval probability distribution. When rapid transients are under investigation, the periods of analysis must be reduced below the expected time constants of the changes in the rate of activity, a procedure that prevents the smoothing of important details. (This smoothing is obviously implicit in histogram techniques.) The large sample size of inter-events required for statistical analysis is obtained in this case by increasing the ensemble of transients obtained experimentally under identical controlled stimuli. Slowly modulated responses are analyzed over time windows shorter than the highest expected rates of change in input or output.

Over the period of analysis—the sliding time window of a suitably chosen length Δt—the neural response representation is considered as part of the realization of a stationary stochastic point process. This assumption of so-called *local stationarity* is needed for theoretical convenience.

The Response Regularity

Consider a period of analysis $(t - \Delta t/2, t + \Delta t/2)$. We define the output coefficient of variation $V_{\{t,\Delta t\}}$ as the ratio of the standard deviation and the mean of interspike intervals occurring in this period, namely,

$$V_{\{t,\Delta t\}} = \frac{\sigma_{I\{t,\Delta t\}}}{\mu_{I\{t,\Delta t\}}} \tag{7}$$

where the statistics are inferred from the corresponding global histograms [20]–[23] and $I\{t, \Delta t\}$ represents the set of interspike intervals occurring over the ensemble of responses during the period of analysis. Denoting the length of the interspike interval by i we can write

$$\mu_{I\{t,\Delta t\}} = E\left[i \mid i \in I\{t, \Delta t\}\right] \tag{8}$$

and

$$\sigma^2_{I\{t,\Delta t\}} = E\left[i^2 \mid i \in I\{t, \Delta t\}\right] - \mu^2_{\{t,\Delta t\}}. \tag{9}$$

Some experimental results indicate that the coefficient of variation is constant during steady-state or slowly modulated responses [20], [22], [23]. This constancy implies that the response becomes more regular, synchronized, as the mean rate of activity increases, indicating an interval-distribution scaling effect (σ follows μ). However, during sharp transients in the activity level, the coefficient of variation fluctuates, eventually returning to the constant steady-state value. The sudden increase in the level of activity in response to a positive step in stimulus usually occurs along with a transient decrease of $V_{(t,\Delta t)}$, an over-synchronization effect [22].

It should be pointed out that the constancy of the coefficient of variation is by no means a universal characteristic of neural encoders. Several experimental results indicate, for example, power-law relationships between the mean interval and the standard deviation. This would imply that V is some function of μ [24]. Other reported results show no consistent variability behavior among the coding units analyzed [25].

Global Interval Distributions and Instantaneous Rates

The level of activity at the moment t can be evaluated using the procedures defined above, but an estimate is also obtainable from the global interspike interval distribution for a time window about t. We shall next investigate the relation between the probability distribution density of interspike intervals $p_{I\{t,\Delta t\}}(i)$ as estimated through histograms, and the rate of activity at t as defined by (5) and (6).

Consider for simplicity that over the period $(t - \Delta t/2, t + \Delta t/2)$ the output can be modeled as a renewal process, i.e., the length of successive interspike intervals being realizations of independent identically distributed (i.i.d.) positive random variables with a distribution density given by $p_{I\{t,\Delta t\}}(i)$. Assuming that over the time window of interest we have realizations of a renewal process in a stationary regime, we obtain as immediate consequences of the theory of renewal processes that for $\xi \in (t - \Delta t/2, t + \Delta t/2)$:

$$E[N(\xi)] = E[N(t - \Delta t/2)] + \mu^{-1}_{I\{t,\Delta t\}}(\xi - t + \Delta t/2). \tag{10}$$

Also, the distribution of intervals including the time t, $I(t)$, is given by

$$p_{I(t)}(i) = \mu^{-1}_{I\{t,\Delta t\}} i p_{I\{t,\Delta t\}}(i). \tag{11}$$

The shift towards longer intervals in (11) is due to the fact that longer intervals have, over the ensemble of realizations, a higher probability of "covering" the chosen moment t [26]. From the above we have that

$$\begin{aligned} R_N(t) &= \frac{d}{d\xi} E[N(\xi)]\big|_{xi=t} = \mu^{-1}_{I\{t,\Delta t\}} \\ R_F(t) &= E[1/I(t)] = \mu^{-1}_{I\{t,\Delta t\}}. \end{aligned} \tag{12}$$

These results also indicate that, according to both estimators defined in Section II, the level of activity is inversely proportional to the mean length of interspike intervals.

The renewal assumption made in the above analysis implies no dependence between consecutive intervals. Such a dependence, if present, can easily be detected through interval histograms conditioned on preceding intervals, or through serial correlation analysis. Experimental results do in fact indicate such dependence in some neural coding processes [20]. Therefore a first or higher order Markovian description of the output sample-path evolution may be needed for a better fit to the recorded data [15], [27]. Yet the above analysis remains the most appropriate for the description of ensemble responses, due to the inherent difficulty in the analysis of global behavior for self-exciting point processes with realization-dependent sample path evolution.

III. A MODEL FOR THE NEURAL CODING PROCESS

Models for the neural coding process proposed thus far either concentrate on the excitable membrane dynamics (and are therefore concerned with the details of ionic flows at a microstructural level) or seek simplified schemes directly concerned with the stimulus-to-spiking-activity transfer. Some input–output models are, however, based on rough mathematical descriptions of the basic microscopic processes at the membrane level. We concentrate on a particular model of the latter class which, although mainly concerned with input–output behavior, also provides useful insight into, if not explanations for, some inner mechanisms of the coding process [9]–[13]. Moreover, some of the assumed functional interconnections have physiological interpretations in terms of self-inhibitory and cumulative refractoriness phenomena.

The General Fire-at-Threshold Scheme

We consider the primary stimuli to be translated, through some spatiotemporal preprocessing, into changes in ionic current flows. The intensity of these "generator currents" controls in turn the process leading to spike initiation by the excitable membrane. If $\lambda(t)$ is the time-varying current intensity, the model has to specify either the set of spike initiation moments S_{OT}, defining $f_P(t)$, or the overall characteristics of the output point process, in terms of $\lambda(t)$.

Let $u_t > 0$ denote the membrane polarization related to the resting level $u_0 = 0$. For $t \in (T_k, T_{k+1}]$ we can write

$$u_{T_k^+} = 0; \qquad u_t = \Psi\{\lambda(\xi), T_k < \xi \leqslant t; f(\eta), \eta \leqslant t\}. \tag{13}$$

Here u_t is an increasing process over the interspike interval that depends on the input $\lambda(t)$ through the causal operator $\Psi\{\cdot\}$. Note that the behavior of the membrane voltage may be output-dependent.

The occurrence times of the output point process $\{T_1, T_2, T_3, \cdots\}$, T_0 being the arbitrary time origin, are defined as the instants when u_t first upcrosses a certain threshold function A_t. Therefore over an interspike interval we have

$$u_t < A_t; \qquad u_{T_{k+1}} = A_{T_{k+1}}. \tag{14}$$

A more specific model is obtained through some further assumptions on the operator Ψ and on the threshold process A_t (Fig. 3).

Assumption 1: The membrane integrates an effective ionic current of intensity $\lambda^*(t)$ that depends on the input generator current and also on the output realization up to t. Thus we have

$$u_t = \int_{T_k}^{t} \lambda^*(\xi)\, d\xi, \qquad \text{for } t \in (T_k, T_{k+1}). \tag{15}$$

The effective input is in turn given by the difference between the input current and an output-dependent self-inhibition factor λ_i [18], [34], [35].

$$\lambda^*(t) = \left(\lambda(t) + \lambda_i\{f(\eta), \eta < t\}\right)^+ \tag{16}$$

where $(\cdot)^+$ denotes a rectifier operation ensuring a nonnegative input to the integrator, thus a nondecreasing u_t.

Assumption 2: The threshold remains constant during interspike intervals assuming a new random value at each occurrence time, thus

$$A_t = a_k, \qquad \text{for } t \in (T_k, T_{k+1}]. \tag{17}$$

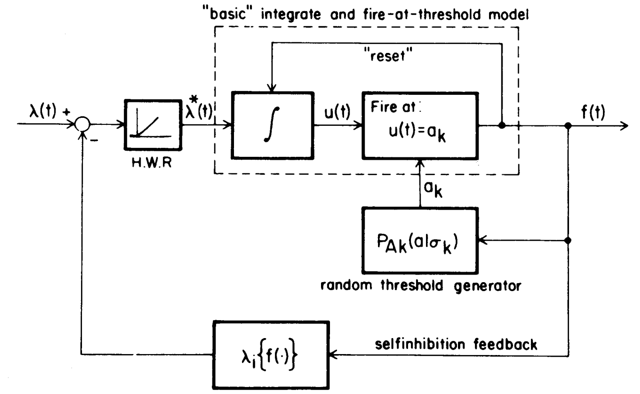

Fig. 2. Adaptive integrate and fire-at-threshold model.

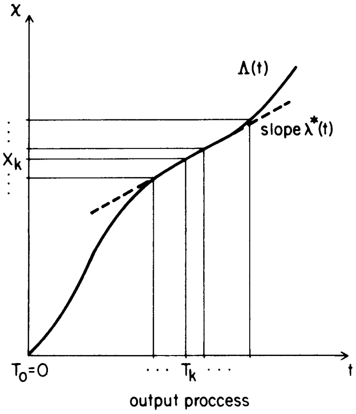

Fig. 3. Representation of the coding process.

Here the a_k are realizations of random variables A_k, the threshold behavior being described by a stochastic process with piecewise constant realizations [10], [14]. The random values a_k are successively drawn according to probability distributions dictated by the past realization of the output point process, given by

$$P_{A_k}(a|\sigma_k), \qquad k = 1, 2, 3, \cdots \tag{18}$$

where σ_k formally represents the information content in the output and threshold processes, up to the time T_k.

Since both the effective input and threshold statistics are influenced by the past evolution of the coding process, the encoder output is a self-exciting point process [28]. Note that, as shown in Fig. 2, two output feedback effects are assumed in this coding scheme: the self-inhibition determining the effective input, and the influence of the output activity on the firing-initiation threshold, modeling cumulative refractoriness [15], [16].

The above coding model yieldis the following implicit formula for the kth occurrence time of the output process:

$$\int_0^{T_k} \lambda^*(\xi)\, d\xi = X_k, \qquad \text{where } X_k = \sum_{r=0}^{k-1} a_r. \tag{19}$$

Here the T_k are the moments at which the nondecreasing function $A_t = \int_0^t \lambda^*(\xi)\, d\xi$ upcrosses the levels X_k (Fig. 3). In other words, the encoder output is the image, in the time domain, of another point process with interval statistics determined by the threshold random variables A_k [10], [11].

Note that the encoder model assumes that integration of effective input restarts immediately after firing and thus neglects the absolute refractory period. The result is a slight increase in the output rate for most of the physiological range of activity rates. The absolute refractory period may also be regarded as an integral part of the neural depolarization event.

The Self-Exciting Output Point Process

Since the output of the neural encoder model is a stochastic point process with past-dependent sample-path evolution, results are mainly obtainable on the local instantaneous-rate process (defined as the conditional probability, given the past history of the process, of an occurrence at the time t).

Consider the output of the encoder up to the time $t, \{f(\eta)|\eta \leqslant t\}$, and define the event M_n as the set of output occurrence times $\{T_1, T_2, \cdots, T_n\}$ with $n = N(t)$. Assuming that the set M_n and the input $\lambda(t)$ deterministically define the effective input $\lambda^*(t)$ for the interval (T_n, T_{n+1}), we have that the process u_t is measurable on the past, hence the realization of A_n and the next occurrence time uniquely specify each other. The deterministic operator that yields the effective input from the stimulus intensity, and the past output activity thus makes the threshold process A_t and the encoder output informationally equivalent.

According to the described encoding procedure, given $M_n, u_t = \int_{T_n}^{t} \lambda^*(\xi) d\xi$ should be compared to the realization a_n of a random variable with distribution density $p_{A_n}(a|M_n)$. The next occurrence time, T_{n+1}, is the first time at which $u_t = a_n$. Following [28] we can define the "survival probability" of T_{n+1} beyond t, given the past output sample-path evolution, as

$$\Pi_{T_{n+1}}(t) = \Pr\{T_{n+1} > t|M_n\}. \tag{20}$$

As an immediate result we can write

$$\Pi_{T_{n+1}}(t) = \Pr\left\{\int_{T_n}^{t} \lambda^*(\xi) d\xi < a_n|M_n\right\} = 1 - P_{A_n}((u_t)|M_n) \tag{21}$$

where P_A is the cumulative distribution function associated to p_A.

From $\Pi_{T_{n+1}}(t)$ one can readily obtain the probability of T_{n+1} occurring in an infinitesimal interval about t, or the instantaneous rate function $\rho(t)$, defined as

$$\rho(t) = \lim_{\delta \to 0} \frac{\Pr\{T_{n+1} \in (t, t+\delta)|M_n\}}{\delta}. \tag{22}$$

The result is the following [28]:

$$\rho(t) = \left.\frac{\partial \ln \Pi_{T_{n+1}}(\xi)}{\partial \xi}\right|_{\xi=1} = \frac{p_{A_n}(u_t|M_n)}{1 - P_{A_n}(u_t|M_n)} \lambda^*(t). \tag{23}$$

This formula shows that the instantaneous rate of the output process can be computed as the product of the effective input and a similarly defined instantaneous rate of the threshold-defined point process at $\Lambda_t = X_n + u_t$ (on the x-axis of Fig. 3) [10], [11], [14]. Since the encoding procedure determines the threshold probability distribution and the effective input, we can compute causally the instantaneous probability of firing at t, associated to the output $f(t)$. This defines a stochastic process called the instantaneous rate process, and in order to find the overall encoder response to a given input, one has to find the ensemble rate of firing, i.e., the unconditional expected value of $\rho(t)$, which is not always analytically feasible. Some further results can be obtained, in the case of an exponentially-distributed threshold where the output becomes a Poisson process. Also, general renewal-type threshold behavior and some Markov dependences yield analytically tractable models [11], [15], [27].

The straightforward approach to obtain the ensemble response is through extensive computer simulations and subsequent averaging of the results, either directly on the resulting instantaneous frequency and counting processes or on the computed local rate process. An alternative approach, based on different assumptions on the feedback processes in the encoder, leads to an approximate description of the ensemble-averaged behavior and provides further useful insights and results.

Modeling the Ensemble Behavior

In this section we assume that, for an interval of length Δt, about t, the threshold random variables are independent and identically distributed with density $p_{A(t)}(a)$ that depends on the history of the output *ensemble rate* up to t. We further assume that $\lambda^*(t)$, the effective input, is also output rate-dependent but with very slow dynamics so that it can safely be considered constant over a period of length Δt. Generally, we write

$$p_{A(t)} = H_A\{R(\eta); \eta < t\} \tag{24}$$

$$\lambda^*(t) = H_{\lambda^*}\{R(\eta), \lambda(\eta); \eta < t\} \tag{25}$$

where H_A and H_{λ^*} are operators describing the control of the threshold and of the effective input. Following the first assumption of Section III, we write in a more specific way

$$H_{\lambda^*}\{R, \lambda\} = (\lambda - \lambda_i\{R\})^+. \tag{26}$$

According to the encoding procedure, the following simple scaling relation between input, threshold realizations, and interspike intervals holds over the interval of interest

$$\lambda^*(t) i = a. \tag{27}$$

The interspike interval i is the realization of a random variable $I\{t, \Delta t\}$, and the threshold value a is the realization of a positive threshold random variable $A(t)$. By virtue of (27), the distribution of the interspike intervals over $(t - \Delta t/2, t + \Delta t/2)$ can be written in terms of the threshold distribution. Since the thresholds are assumed to be independent identically distributed, so are the successive interspike intervals, and their distribution is

$$p_{\{I(t, \Delta T)\}}(i) = p_{A(t)}(i\lambda^*(t))\lambda^*(t). \tag{28}$$

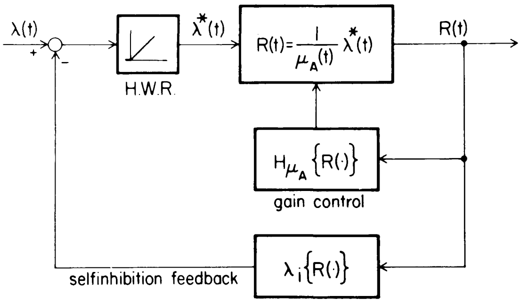

Fig. 4. Model for the ensemble dynamic response.

Accordingly, we have the following results relating the expected values and standard deviations of the threshold and interval random variables:

$$\mu_{I\{t,\Delta t\}} = (\lambda^*(t))^{-1}\mu_{A(t)} \tag{29}$$

$$\sigma_{I\{t,\Delta t\}} = (\lambda^*(t))^{-1}\sigma_{A(t)}. \tag{30}$$

This analysis, together with the results of Section II, yields for the output rate at t

$$R(t) = \frac{1}{\mu_{A(t)}}\lambda^*(t). \tag{31}$$

Therefore, in order to find the dependence between the input $\lambda(t)$ and the output rate of activity, one should consider the following dynamic system:

$$\begin{aligned} R(t) &= G_v\lambda^*(t) \\ G_v &= \frac{1}{\mu_{A(t)}} = \frac{1}{H_{\mu_A}\{R(\eta);\eta < t\}} \\ \lambda^*(t) &= (\lambda(t) - \lambda_i\{R(\eta);\eta < t\})^+ \end{aligned} \tag{32}$$

where H_{μ_A} describes the output influence on the average value of the threshold, i.e.,

$$H_{\mu_A}\{R(\eta);\eta < t\} = E[A(t)] \tag{33}$$

with respect to the measure $H_A\{R(\eta);\eta < t\}$.

The dynamic system (32) describes the ensemble behavior of the encoder, directly providing the output rate of activity. Considering Fig. 4, it becomes clear which mechanisms are responsible for transients of adaptation that preemphasize sudden changes in the input level. A step increase in the input $\lambda(t)$ immediately increases the effective input $\lambda^*(t)$. The resulting increase in the output rate of firing in turn affects the threshold distribution, causing an increase in its mean value μ_A, and also the effective generator current λ^* which subsequently decreases. The two factors, however, have different effects on the output: the scheme under consideration is a system combining an "automatic gain-control" through the threshold dynamics with a negative self-inhibition feedback [15], [16]. We note that there is ample experimental evidence of having an effect of self-inhibitory output feedback [18], [19]. In stretch receptors it is mediated by an electrogenic ion pump that transports across the membrane the surplus of ions cumulating within the nerve cell due to repetitive firing. However, experimental physiologists report a two-phase adaptation transient in response to step stimuli [18], [19], [22], with both the rapid- and the slow-phase adaptation transient time-constants being input-dependent. As the input step amplitude increases, an increase in the latter is observed while the initial rapid decay in firing rate becomes steeper and more pronounced. This results in a gradual transition from an approximately exponential to biexponential adaptation responses.

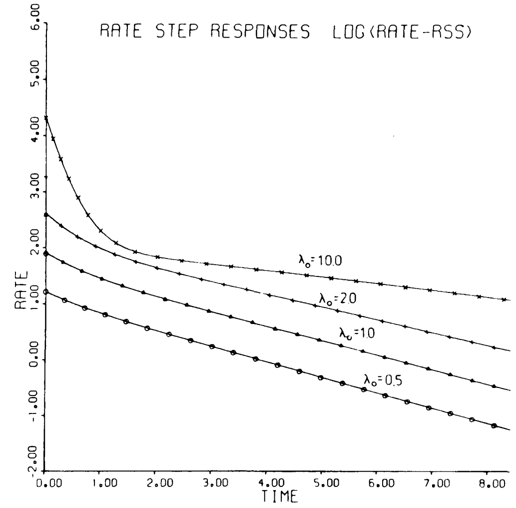

Fig. 5. Log-plots of step-response transients in ensemble output rate. (Note the transition from exponential to biexponential behavior with increase of input amplitude λ_0.)

The above behavior can be accounted for by hypothesizing that the threshold control operator has much faster dynamics than the self-inhibitory feedback. Further considerations lead to a very simple dynamic system combining a fast automatic-gain-control with a much slower negative feedback, which is readily seen to yield the correct qualitative features of adaptive transients. A sudden change in the input leads to a rapid transient due to gain-control, with a time-constant that decreases with higher input amplitude, then the self-inhibition feedback comes into action, already about an adjusted gain that increases the slow transient's time constant (Fig. 5). This dynamic system also accounts for the characteristics of modulated and bursty neural responses [15], [16].

As to the issue of response regularity, the coefficient of variation of the output over $(t - \Delta t/2, t + \Delta t/2)$ is given by

$$V_{\{t,\Delta t\}} = \frac{\sigma_{I\{t,\Delta t\}}}{\mu_{I\{t,\Delta t\}}} = \frac{\sigma_{A(t)}}{\mu_{A(t)}}. \tag{34}$$

From this result we conclude that $V_{\{t,\Delta t\}}$ does not depend directly on the self-inhibition process, being determined by threshold statistics alone. From the output-dependent action of H_A we defined the operator H_{μ_A} that provides the threshold average value and can similarly define the operator providing its standard deviation as

$$\sigma_{A(t)} = H_{\sigma_A}\{R(\eta);\eta < t\}. \tag{35}$$

The behavior of the coefficient of variation is therefore determined by the output-dependent threshold statistics through the operators H_{μ_A} and H_{σ_A}. As discussed before, the variability in firing is found in some studies to be constant during slowly-modulated activity, and notable changes in $V_{\{t,\Delta t\}}$ accompany drastic changes in the output activity as, for example, in the fast phases of step responses [22], [23]. We can account for this behavior by assuming that H_{σ_A} and H_{μ_A} have similar dynamics with slightly different time constants. If $\mu_{A(t)}$ responds to changes in $R(t)$ faster than $\sigma_{A(t)}$, a jump in the output activity level is followed by a temporary imbalance in their ratio, accounting for transient over-synchronization observed at the initial phase of step responses. When $R(t)$ changes slowly, so that both the dynamics of H_{σ_A} and H_{μ_A} can follow its variations, we have that the coefficient of variation is constant.

As we pointed out before, a universal result concerning the behavior of the coefficient of variation does not exist. The above analysis only stresses the point that, if the adaptive integrate-to-threshold encoder is used to model the neural response, the threshold behavior can be inferred from the output point process. We should also mention that models assuming leaky integration predict a dependence of V on the mean rate of firing [29].

In summary, the above theory yields an adequate description of the ensemble behavior and also provides a good approximate representation of the individual unit response (under the assumptions of the previous section). We also note that the pooled response of many identical coding units can be considered a modulated Poisson process with rate proportional to the predicted $R(t)$, with dynamics predicted by (22).

IV. A DECODER MODEL

This section introduces a decoding scheme, in fact a demodulator information transmitted through the variable rate of a point process [5]. The demodulator is interesting mainly from a theoretical point of view, since very little is yet known about the way the incoming information, coded in patterns of spikes, is interpreted by the higher levels of the nervous system. Postsynaptic neuronal membranes perform some sort of low-pass filtering on the sequences of depolarization pulses. The higher level neurons process integratively a large number of inputs, and we may safely assume that there is no need to recover the analog modulating signals for further processing. The sequences of spikes are, most likely, processed directly to generate responses on efferent pathways or on links to other processing centers. The decoding scheme is therefore mainly of interest in comparing the defined adaptive pulse frequency modulation performance to other pulse modulation techniques and evaluating the amount of information recoverable from the pulse patterns.

The Demodulation Scheme

The main idea in the demodulating scheme is the use of a "neural" encoder unit in a feedback configuration, essentially the phase or frequency-lock loop technique (Fig. 6). An estimate of the modulating signal $\hat{\lambda}(t)$, the decoder output, drives a local encoder whose response $\hat{f}(t)$ is compared to the received sequences of spikes. The estimate of the encoder input is continuously updated on the basis of an error signal generated through comparisons of $f(t)$ with $\hat{f}(t)$. The update procedure consists of a comparison of the rates of firing of the remote and local encoders. Referring to Fig. 6, we can write

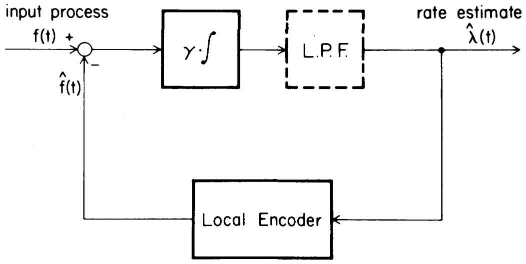

Fig. 6. Decoding scheme.

$$\hat{\lambda}(t) = \gamma\int_0^t \left(f(\xi) - \hat{f}(\xi)\right)d\xi = \gamma\left(N(t) - \hat{N}(t)\right). \quad (36)$$

Thus the decoder output is the difference of two counting processes, one associated with the encoder output and the other with the local encoder response. Now, given that the local coding procedure and the primary coding processes are known, we wish to evaluate how good an estimate of the input $\hat{\lambda}(t)$ is. Note that, as a difference of counting processes, the decoder output will assume values which are multiples of γ. Furthermore, no negative values will be attained. One could also consider a decoding scheme with a long memory filter instead of the integrator; however, since in this case the analysis becomes substantially more complicated, we shall concentrate of the model presented previously.

Let us assume that the local encoder is nonadaptive and yields an output process for which

$$\Pr\{\hat{N}(t+\delta) - \hat{N}(t) = 1 | \hat{\lambda}(t)\} = \hat{\lambda}(t)\delta + o(\delta). \quad (37)$$

The thresholds are thus taken an independent identically distributed random variables (see (23)).

The input to the decoder is considered a realization of a Poisson process with time-varying density or rate of occurrence $r(t)$, carrying information on the primary stimulus intensity $\lambda(t)$. The primary encoder is considered an adaptive one, thus we have in general $r(t) \neq \lambda(t)$. The output rate could be, for example, the ensemble firing rate as obtained in the previous section. The decoder output becomes, accordingly, a particular type of Markov process: a linear nonhomogeneous birth and death process [26]. Indeed an "excitatory" input pulse, from $f(t)$, increases the output by γ, whereas a "self-inhibitory" pulse form $\hat{f}(t)$ decreases $\hat{\lambda}(t)$ by the same amount. The decoder output performs a random walk on the levels $k\gamma$, hopefully converging to and tracking the input intensity.

Turning to the analysis of this decoding method, we now define (following [26])

$$P_n(t) = \Pr\{\hat{\lambda}(t) = n\gamma\}, \qquad n = 0,1,2,\cdots, \quad (38)$$

and seek the evolution of the defined output level distribution $\{P_n(t)\}_{n\in N}$, as a function of the stimulus applied to the encoder. From the transition probabilities of the Markov process we have

$$\begin{aligned} P_n(t+\delta) &= P_{n-1}(t)r(t)\delta + P_{n+1}(t)(n+1)\gamma\delta \\ &\quad + P_n(t)[1-(r(t)+n\gamma)\delta] \\ P_0(t+\delta) &= P_0(t)[1-r(t)\delta] + P_1(t)\gamma\delta \end{aligned} \tag{39}$$

which immediately yield the following differential equations for the evolution of the output distribution:

$$\begin{aligned} \frac{d}{dt}P_n(t) &= -P_n(t)(r(t)+n\gamma) + P_{n-1}(t)r(t) \\ &\quad + P_{n+1}(t)(n+1)\gamma \\ \frac{d}{dt}P_0 &= -P_0(t)r(t) + P_1(t)\gamma. \end{aligned} \tag{40}$$

These equations provide a complete description of the behavior of the decoder output. We next introduce a distribution generating functional

$$Q(s,t) = \sum_{n=0}^{\infty} P_n(t)s^n \tag{41}$$

and, using (40), obtain the following partial differential equation for it:

$$\frac{\partial}{\partial t}Q(s,t) = (s-1)\left[r(t)Q(s,t) - \gamma\frac{\partial}{\partial s}Q(s,t)\right]. \tag{42}$$

This equation can be solved for some cases of $r(t)$. However we are interested mainly in the evolution of the first- and second-order statistics of the decoder output.

Evolution of First- and Second-Order Statistics

Let us define the moments of the decoder output-level distribution as

$$M_1 = \sum_{n=0}^{\infty} nP_n(t), \qquad M_2 = \sum_{n=0}^{\infty} n^2P_n(t). \tag{43}$$

For the evolution in time of the above-defined moments, (40) yield, through some algebraic manipulation, the following differential equations:

$$\begin{aligned} &\frac{d}{dt}M_1(t) + \gamma M_1(t) = r(t) \\ &\frac{d}{dt}M_2(t) + 2\gamma M_2 = r(t) + M_1(t)[2r(t)+\gamma]. \end{aligned} \tag{44}$$

Now, since the output mean is $\gamma M_1(t)$ and its variance is given by $\gamma^2[M_2(t) - M_1^2(t)]$, we easily obtain the corresponding relations for the decoder output estimating the signal $\lambda(t)$

$$\begin{aligned} &\frac{d}{dt}\mu_{\hat\lambda}(t) + \gamma\mu_{\hat\lambda}(t) = \gamma r(t) \\ &\frac{d}{dt}[\sigma_{\hat\lambda}^2(t)] + 2\gamma[\sigma_{\hat\lambda}^2] = \gamma^2[r(t) + \mu_{\hat\lambda}(t)]. \end{aligned} \tag{45}$$

These equations describe the evolution of the output statistics of interest, and for the steady-state case, when $r(t) = r_0$, they provide $\mu_{\hat\lambda}(t) \to r_0$, $\sigma_{\hat\lambda}^2 \to \gamma r_0$, yielding a signal-to-noise ratio (mean squared over variance) of r_0/γ. Thus small values for γ result in high accuracy at steady-state demodulation but also in poor tracking of changes in $r(t)$, while large values yield better tracking at the expense of higher steady-state error. Note that the decoder does not recover $\lambda(t)$ but rather the resulting level of activity of the encoding signal. This, however, is not a problem since for slowly changing stimuli, and of course for constant inputs, the adaptive encoder produces a good replica of their time-course (multiplied by a known nonlinear static gain factor). Rapid changes in the output rate occur, for example, as step-responses, and in this case the decoder output is not required to track the fast transients in $r(t)$. The adaptive responses, following steps in the stimulus intensity, will cause a more rapid step-like transient in $\hat\lambda$, a desirable feature of the decoder.

We note that the result concerning the dynamics of the decoder output statistics resembles the behavior of a simple low-pass-filter demodulator. If a linear system with weighting sequence $h(t)$ is used to filter the sequences of spikes, we have from the well-known generalized Campbell laws [28]

$$\begin{aligned} \mu_{\mathrm{LPF}}(t) &= \int_{-\infty}^{t} r(\tau)h(t-\tau)\,d\tau \\ \sigma_{\mathrm{LPF}}^2 &= \int_{-\infty}^{t} r(\tau)h^2(t-\tau)\,d\tau. \end{aligned} \tag{46}$$

Accordingly, if $h(t) = \gamma e^{-\gamma t}1(t)$, where $1(t)$ is the unit-step function, we realize that the two demodulation methods yield the same behavior for the mean of their output. However, for the birth–death process the second-order statistics depend also on the behavior of the mean. It is interesting to note that the low-pass-filter decoder yields a better signal-to-noise ratio at steady state ($= 2r_0/\gamma$); while a moving-window counter decoder, with $h(t) = 1$ for $t \in (0, 1/\gamma)$, yields the same steady-state signal-to-noise ratio as the birth–death process. The higher steady-state signal-to-noise ratio for the nonlinear decoder is due to the fact that its output assumes values only at the discrete levels $n\gamma$ and therefore there is no smoothing. It is expected that the performance of a decoding scheme with a local encoder would improve considerably through the use of a smoothing filter in the feedback loop.

Several other estimation and parameter identification techniques for the decoding of information from the output of an adaptive neural encoder model were considered in [30].

V. DISCUSSION AND CONCLUSION

Considering the neural encoder from a communication-theoretic viewpoint, it was found that fire-at-threshold schemes permit adequate mathematical descriptions for its basic function, namely translation of analog stimulus-strength information into sequences of neural depolarization spikes. At first sight, the neural encoder may seem to resemble certain engineering pulse-frequency-modulation schemes [9], [14], but a closer look reveals major differences. The biological coding process is highly asynchronous with pronounced adaptive characteristics, which maintain the overall activity of the system at a moderate level and at the same time permit an extremely wide dynamic range of functioning with high sensitivity.

In order to reproduce the experimental results on adaptive behavior, plausible structural feedback effects in the integrate-to-threshold scheme were assumed. Of these, the self-inhibition effect is well-supported experimentally, and several models dealt with it in a different framework [18], [31], [34], [35]. It should be noted, however, that self-inhibition alone results in an essentially linear input to firing rate "signal-transfer." As such it cannot generate input-dependent self-adjustment of time constants as exhibited experimentally [18] and reproduced by our model. This is a fundamental property of our nonlinear feedback scheme with automatic gain-control, which differs from all previously proposed neural encoding models. The adaptive threshold control, responsible for the AGC effect, is indeed a satisfactory functional assumption yielding input–output behavior closely reproducing experimental results. It is consistent with our understanding of electrically excitable membrane biophysics and is further supported by recent findings [23].

A study of the functioning of the neural coding units, and the relevant mathematical models that describe their behavior, may yield some engineering insight. The adaptive pulse-frequency modulation of the type described may find useful applications, for example in optical communication systems. Conversely, while the decoder proposed and analyzed in the last section of the paper is an engineering scheme, with probably little relevance to the modeling of processes occurring in the nervous system, we note that, if needed, it might easily be implemented by the nervous system using available local encoders with inhibitory and excitatory synapses. The main purpose of considering a decoder was, however, to obtain an estimate of the amount of information carried by individual sequences of spikes.

Once the functioning of individual coding units is more or less understood and properly modeled, the way is open for analysis of various higher level sensory arrays and their responses, like, for example, the retina and the image processing performed by it, or the motor, multiunit, and multipath communication systems, in which reliability is ensured through redundancy, in spite of the relatively poor performance of individual channels [32], [33].

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