

STOCHASTIC PFM MODELS FOR
THE ANALYSIS OF NEURAL CODING PROCESSES

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ABSTRACT

This report presents models and techniques for the description and analysis of neural encoders' behaviour. The neural coding units translate the input analog information - time varying intensity of stimuli - into sequences of membrane depolarization pulses-"all-or-none" events. The encoder output is therefore considered a realization of a random point process the overall behaviour being characterized through averaging of an ensemble of responses to identical stimulus/environment conditions. The encoder models described are based on the integrate-to-threshold scheme, the stochastic features of the response being a result of randomly fluctuating firing threshold. As a consequence of "long-term memory" assumed in the models to account for adaptation phenomena, the output of the defined stochastic models are generally selfexciting point processes. A conceptual decoding procedure is also defined and discussed.

1. Introduction

Analysis of sensory communication processes and neural coding systems naturally involves models and techniques from the mathematical theory of communication and information processing.

Physiologists experimentally obtain the overall input-output behaviour of various sensory (neural) coding systems and also attempt to gain "inside information" on the details of the encoding process in terms of properties of ionic flows and thermodynamics of the excitable neuronal membrane [1], [2]. As a result of a series of, by now classical, experimental and theoretical investigations Hodgkin and Huxley provided an excellent model describing the "excitable membrane" dynamics and the initiation of the neural depolarization pulses. Their down-to-details theory [1], [2] seems however to be unsuitable for the systemic approach, the large number of units, processes and interactions involved in more complex structures require a probabilistic, overall rather than detailed, description. From the communication theoretic point of view the neurons - building blocks of the whole nervous system - can be considered as basic data processing units performing the coding and transmission of information. The various stimuli are translated into all-or-none spiking activity of the membrane the "action potential" depolarization pulses being well suited for transmission along the axonal channels. It is this activity on the nerve fibers that is recorded and analyzed in order to investigate the coding process. Simplified models describing the stimulus-to-spiking-activity transfer are most useful since they can provide, through the possibility of mathematical treatment, valuable insights to the behaviour and performance of biological communication systems [3]. Most widely used in this context are models that belong to the class of fire-at-threshold schemes; they are both relatively simple mathematically and to some extent close to the physiology of the coding process. [4]-[7]. These models define a (deterministic or stochastic) cumulative processing on generator

current inputs (the ionic flow depending on primary stimuli) to yield changes in membrane depolarization - a spike being initiated when a certain threshold voltage is reached. Following a spike and possibly after a certain refractory period the process restarts thus repetitive firing activity is obtained. The above quite general definition of the fire-at-threshold model accounts for some basic microscopic phenomena at the membrane level, as to the actual stage of our understanding. In this report we shall concentrate on models of this class, in particular on stochastic integrate-to-threshold schemes and on their relation to the "real world" of physiological-experimental results.

2. The Output Point Process

Since action potentials are membrane depolarization pulses of essentially identical time-course the information transmitted by neurons resides in the sequence of their occurrence times. Denote by

$$\{t_k\} = \{0=t_0 < t_1 < t_2 \dots\} \quad (1)$$

the set of occurrence times during some observation period starting at the arbitrary moment $t_0 = 0$. Now the encoder output, the time-course of membrane potential at some point along the axonal channel, can be expressed as :

$$f_p(t) = \sum_{k \in \{t_k\}} p(t-t_k) = p(t) * \sum_{k \in \{t_k\}} \delta(t-t_k) \quad (2)$$

where $*p(t)$ describes the shape of a typical action potential spike and $*\delta(t)$ is the Dirac function

The relevant information in $f_p(t)$ is obviously retained in :

$$f(t) \triangleq \sum_{t_k \in \{t_k\}} \delta(t-t_k) \quad (3)$$

In this study the set of occurrences $\{t_k\}$ will be considered a realization of a random point process called the "output process". We shall assume that the relevant information (from the biological point of view) in the output stochastic point process resides in the "level of activity" it defines at all times, T ($T > 0$). Let's therefore proceed by defining the level of activity of a point process at the moment T .

2.1* The Level of Activity

On the realization $\{t_k\}$ of the output process we define the following functions :

1) the associated counting process $N(T)$ (Fig. 1a)

$$N(T) \triangleq \langle \text{no of occurrences in } (0, T) \rangle$$

formally : $N(T) = \int_0^T f(t) dt \quad (4)$

- 2) the instantaneous frequency process $F(T)$ (Fig. 1b)

$$F(T) \triangleq (t_n - t_{n-1})^{-1}$$

where the definition of n is : $\{n | t_{n-1} < T < t_n\}$ (5)

and over the ensemble of responses n is obviously a chance variable.

- 3) the interspike interval process $S(T)$ (Fig. 1c)

$$S(T) \triangleq t_n - t_{n-1}$$
 (6)

with n defined as above.

Note : From $(f(t), t < T)$, $N(T)$ can be computed, but this is not so for $F(T)$ and $S(T)$ since their definition involves the "future occurrence times" $t_n > T$. In practice, many experiments are performed to obtain output sequences $\{t_k\}^i$, $i = 1, 2, \dots, M$ of a coding unit in response to identical stimuli, the actual equivalent of checking the output of an ensemble of identical stochastic neural encoders. Then the sequences are processed off-line and therefore $F(T)$ and $S(T)$ can be easily obtained, their "predictive nature" practically causing no problems.

It is clear that each of the associated processes $N(T)$, $F(T)$ and $S(T)$ are equivalent to the output point process from the information content point of view.

Now, the "level of activity" or rate of activity at T , $R(T)$ can be alternatively defined as :

- 1) the density of the output point process :

$$R_D(T) \triangleq \left. \frac{d}{dt} E[N(t)] \right|_{t=T} \quad (7)$$

- 2) the average instantaneous frequency :

$$R_F(T) \triangleq E[F(T)] \quad (8)$$

3) the inverse of the average interval :

$$R_S(T) \stackrel{\Delta}{=} E^{-1}[S(T)] \quad (9)$$

Notes * The operator E here stands for ensemble averaging, as usual, (and $E^{-1}(\cdot) \stackrel{\Delta}{=} 1/E(\cdot)$), therefore, practically, the analysis involves averaging over an ensemble of, say, M responses of a coding unit to identical stimuli.

* The above definitions for $R(T)$ - (7), (8) and (9) are not in general expected to provide the same numerical results. We shall, in the sequel, further discuss their consistency.

2.2* 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 may change in time following changes in stimuli and surrounding conditions. It is exactly due to variations in time in the output process that the relevant information can be communicated to higher levels of the nervous system. Steady states are of little and sometimes even of no importance to the biological systems therefore transients reporting changes in stimuli or environment are enhanced, preemphasized, in the coding process. Adaptation phenomena illustrate well the preemphasis given to transients since a sudden stepwise or other steep change in stimulus elicits a well-defined transient of increase/decrease in the level of activity followed by a decay toward a steady state [2], [9].

In the analysis of sequences of spikes (in fact of ensembles of responses) we shall concentrate on steady-state and step-response transients as well as on the case of slowly changing stimuli causing, not sharpening of response, but rather its modulation. Generally the analysis of the random point process is done over a sliding window in time, with length ΔT (the interval or period of analysis) [10] [11].

* When dealing with steady state responses the firing sequences can be analyzed over long periods and in order to evaluate the stochastic structure of the output process and its variability interspike interval histograms are obtained. The normalized histograms clearly provide an estimate of the interspike interval probability distribution.

* If rapid transients are under investigation the periods of analysis have to be reduced below the time constants of the observed changes, a procedure that prevents the smoothing of important details in the temporal structure of the response through the averagings implied by histogram techniques. The large number of interspike intervals for statistics is obtained by increasing the analyzed ensemble of transients to identical stimuli.

* Slowly modulated responses are analyzed over periods shorter than the highest rates of change in the input/output.

In all cases however, over the period of analysis, -the sliding window in time of suitably chosen length ΔT - the response will be considered as part of a realization of a stationary stochastic sequence of spikes : this is, in fact, an assumption of local stationarity.

2.3* Response Regularity

Consider a period of analysis starting at T , $(T, T + \Delta T)$. We shall define the "coefficient of variation" $V_{\{T, \Delta T\}}$ as the ratio of the standard deviation and the mean of interspike intervals in $(T, T + \Delta T)$, the statistics being inferred from the corresponding histogram [10], [11]. Hence,

$$V_{\{T, \Delta T\}} = \sigma_{I\{T, \Delta T\}} / \mu_{I\{T, \Delta T\}} \quad (10)$$

where

* $I\{T, \Delta T\}$ is the ensemble of interspike intervals in $(T, T + \Delta T)$ and, if i is the length of interspike interval I

$$* \mu_{I\{T,\Delta T\}} = E[i | I \in I\{T,\Delta T\}] \quad (11)$$

$$* \sigma_{I\{T,\Delta T\}}^2 = E[i^2 | I \in I\{T,\Delta T\}] - \mu_{I\{T,\Delta T\}}^2 \quad (12)$$

Several experimental results on $V_{I\{T,\Delta T\}}$ are now available [10], [11]: the coefficient of variation seems to be constant in steady state responses at different levels of activity and also during slow, modulated, changes in output level. However during fast transients it may temporarily change returning eventually to the former constant value. The constancy of $V_{I\{T,\Delta T\}}$ implies that the response becomes more regular, synchronized, as the mean level of activity increases ($\mu_{I\{T,\Delta T\}}$ decreases together with $\sigma_{I\{T,\Delta T\}}$). At the beginning of fast transients (as for example in step responses) temporary changes in $V_{I\{T,\Delta T\}}$ occur and the sharp increase in the level of activity in a response to a positive step in stimulus occurs together with a transient over-synchronization (decrease of $V_{I\{T,\Delta T\}}$). [11].

2.4* The Interspike Interval Distribution and the Defined Instantaneous Rate

The level of activity at the moment T can be evaluated using the procedure defined in 2.1 but obviously we also have an estimate of it from the average interspike interval $\mu_{I\{T,\Delta T\}}$. We shall next investigate the relation between $p_{I\{T,\Delta T\}}(i)$ - the probability distribution density of interspike interval length over $\{T,\Delta T\}$ - (as estimated through histograms) and the defined rate of activity at T . Consider for simplicity that over $(T, T+\Delta T)$ the output point process is a renewal process, i.e. the length of successive interspike intervals are independent identically distributed (iid) positive random variables with distribution $p_{I\{T,\Delta T\}}(i)$. As immediate results from the theory of renewal processes we obtain, considering that over $(T, T+\Delta T)$ we look at part of a process started long ago (i.e. already in stationary regime, or $t_0 = -\infty$) we can write:

$$E[N(t)] = \mu_{I\{T,\Delta T\}}^{-1} \cdot t \quad (13)$$

The distribution of intervals covering T, I_T is given by:

$$P_{I_T}(i) = \mu_{I\{T,\Delta T\}}^{-1} \cdot i p_{I\{T,\Delta T\}}^{(i)} \quad (14)$$

since longer intervals have a higher probability to cover T (see Feller [14]).

We therefore have from (13) and (14):

$$* \left. \frac{d}{dt} E[N(t)] \right|_{t=T} = \mu_{I\{T,\Delta T\}}^{-1}$$

$$* E[F(T)] = E[1/i_T | I_T = T] = \mu_{I\{T,\Delta T\}}^{-1}$$

$$* E[S(T)] = \mu_{I\{T,\Delta T\}}^{-1} \cdot \frac{1}{1 + V_{I\{T,\Delta T\}}^2}$$

Thus is clear that according to all estimators of 2.1:

$$R(T) \sim \mu_{I\{T,\Delta T\}}^{-1} \quad (15)$$

as indeed would be expected [8].

Note : The assumption of a renewal process over $(T, T+\Delta T)$ implies no dependence between consecutive intervals. Such a dependence can be easily detected through histograms of intervals conditioned on previous interspike interval length or alternatively through serial correlation analysis. Experimental results indicate that there is some direct statistical dependence between sequences of successive intervals. See for example [8], [12]^[16] for a Markovian description of the output process.

The next chapter presents and analyses some simple stochastic models for the coding process; also assumptions concerning the output process will be further discussed in the framework of the defined models.

3. Models for the Coding Process

A wealth of models for the neural coding process were proposed and analyzed. We shall concentrate on a particular fire-at-threshold model that accounts for some very basic microscopic phenomena and could be considered a rough mathematical description of physiological processes. Some physiologists will certainly (and rightly) regard these models as interconnections of functional blocks with no intimate relation to the actual, very complex series of processes that lead to pulse series responses to incoming stimuli. Indeed, these models are mainly concerned with input-output behaviour though they attempt to provide insight into, if not explanations for the inner mechanisms of the coding process [8], [10].

3.1 The General Fire-at-Threshold Model

We shall consider that the primary stimulus is translated into changes in ionic currents and it is the intensity of these "generator currents" through the neural membrane that controls the process leading to spike initiation. Mathematically, if $\lambda(t)$ is the time varying intensity of the current, the model has to define in terms of $\lambda(t)$ the set of spike initiation moments $\{t_k\}$, or the characteristics of the output point process.

Let $u(t) > 0$ be the (positive) change in membrane polarization related to the resting level $u_0 = 0$. We write for $t_k < t < t_{k+1}$:

$$\begin{cases} u(t) = T\{\lambda(\xi), t_k < \xi < t\} \\ u(t_k^+) = 0 \end{cases} \quad (16)$$

and consider $u(t)$ over $[t_k, t_{k+1})$ to be an increasing process depending on the input $\lambda(t)$ through the operator $T\{\cdot\}$.

The occurrence times of the output point process $\{t_k\} = \{t_0, t_1, \dots, t_k, \dots\}$ will be defined as the moments when $u(t)$ reaches a certain threshold level $A_t > 0$, $t_0 = 0$ being defined as the arbitrary time origin. Therefore over $[t_k, t_{k+1})$ one has :

$$\begin{cases} u(t) < A_t \\ u(t_{k+1}) = A_{t_{k+1}} \end{cases} \quad (17)$$

Let us now proceed by defining a more specific model by some further assumptions on the operator $T\{\cdot\}$ and on the threshold process A_t . (Fig. 2).

Consider that :

$$1) \quad u(t) = T\{\lambda(\xi), t_{k-1} < \xi < t\} = \int_{t_{k-1}}^t \lambda^*(\xi) d\xi \quad (18)$$

where $\lambda^*(t)$ the "effective input" is or depends on $\lambda(t)$ and possibly on the output up to t_{k-1} .

$$2) \quad A_t = A_{t_k^+} = a_k \quad \text{for } t \in [t_k, t_{k+1}] \quad (19)$$

where a_k 's are random values.

Thus A_t is a stochastic process with realizations constant over the interspike intervals [6].

The r.v $A_{t_k^+}$ have probability distributions conditional on the whole past of the process up to t_k^+ given generally by :

$$p_{A_0}(a) , \quad p_{A_{t_k^+}}(a | \sigma_{t_k^+}) , \quad k \in \mathbb{N} \quad (20)$$

where σ_s represents the information content in the past of the output and threshold processes up to s . Since generally $\lambda^*(t)$ is output dependent and A_t is also influenced by the past history of the encoder the output point process will be a "selfexciting point process".

3.2* The Selfexciting Output Process

Consider the output of the encoder up to the moment T ,

$$f(t) = \sum_{t_k < T} \delta(t-t_k) \text{ and define as } M_n \text{ the event}$$

$$M_n = \{\text{first } n \text{ occurrences of the output process at } t_1, t_2, \dots, t_n\}$$

Assuming that the event M_n and the input $\lambda(t)$ uniquely and deterministically define $\lambda^*(t)$ for $t \in [t_n, t_{n+1})$ we have that $(u(T), T > t_n)$ is also determined and therefore the realization of $A_{t_n^+}$ and t_{n+1} (the next occurrence) completely determine each other. The deterministic operator that yields $\lambda^*(t)$ from the input $\lambda(t)$ and the events M_n makes therefore the threshold process A_t and the output $f(t)$ informationally equivalent.

From the described encoding procedure, given M_n and $t_n \leq T$, one has to compare at T the value

$$u(T) = \int_{t_n}^T \lambda^*(\xi) d\xi \text{ to } a_n, \text{ a realization of a r.v. } (A_{t_n^+}) \text{ with}$$

distribution density :

$$p_{A_n}(a | \sigma_{t_n^+}) \sim p_{A_n}(a | M_n)$$

and t_{n+1} is the first moment at which $u(t_{n+1}) = a_n$.

Following Snyder [13] we define the probability of survival of t_{n+1} over T given M_n as :

$$P_{t_{n+1} | M_n}(T) = \text{Prob}\{t_{n+1} > T | M_n\} \quad (21)$$

and therefore :

$$P_{t_{n+1} | M_n}(T) = \text{Prob}\left\{ \int_{t_{n+1}}^T \lambda^*(\xi) d\xi < a_n | M_n \right\} = 1 - P_{A_n}(u(T) | M_n) \quad (22)$$

and here P_{A_n} is the distribution of $A_{t_n^+}$.

From $P_{t_{n+1}} | M_n(T)$ one can obtain the instantaneous rate $\tilde{\rho}_T(M_n)$

defined as :

$$\tilde{\rho}_T(M_n) = \lim_{\Delta t \rightarrow 0} \frac{\text{Prob}\{\text{one occurrence in } (T, T+\Delta t) | M_n\}}{\Delta t} \quad (23)$$

We can write [13] :

$$\tilde{\rho}_T(M_n) = \left. \frac{\partial \ln P}{\partial t} \right|_{t=T} = \frac{P_{A_n}(u(T) | M_n)}{1 - P_{A_n}(u(T) | M_n)} \cdot \lambda^*(T) \quad (24)$$

Thus for $t_n < T < t_{n+1}$ we have $\tilde{\rho}_T(M_n)$ given by (24) and knowing the encoding procedure that determines $P_{A_n}(a | M_n)$ and $\lambda^*(T | \lambda(t), M_n)$ we obtain, sequentially, the instantaneous probability of firing for all output realizations.

The stochastic process :

$$\rho(t) = \tilde{\rho}_t(M_n) \quad (\text{with } n \text{ defined from } t_n < t < t_{n+1}) \quad (25)$$

can be called the "instantaneous rate" process and its realizations are determined uniquely given the realizations of the output [13].

In order to find the overall response it is needed to find the behaviour of the ensemble rate or the unconditional expected value of $\rho(t)$, $E(\rho(t))$ when the input realization $\lambda(t)$ is given (a deterministic, usually slowly changing function). However the above description is suited for obtaining the local conditional behaviour from the basic encoding laws and it seems impossible to derive analytically the ensemble response. Some further results on some special cases of (24) can be obtained. For examples of the case of controlled exponential threshold distribution, for the renewal type processes and for Markovian Processes see references [8], [16].

One approach to obtain the ensemble behaviour could be through extensive computer simulations and subsequent averaging of results over many independent runs. Next, a different approach will be presented which, based on different assumptions, proves useful in obtaining further results and insights.

3.3 Modeling the Ensemble Behaviour

In this section we shall assume that for a period of length ΔT starting at T , $(T, T+\Delta T)$, the threshold r.v.'s are i.i.d with distribution density $P_{A(T)}(a)$ that depends on the history of the output ensemble rate $R(T)$ up to T . We also assume that $\lambda^*(t)$ is output rate dependent but very slowly changing so that it can be safely considered constant over a period of length ΔT .

Lets write generally that [8] :

$$P_{A(T)}(a) = H_A\{R(t), t < T\} \quad (26)$$

$$\lambda^*(T) = H_\lambda\{R(t), \lambda(t), t < T\} \quad (27)$$

where H_A and H_λ are some operators (filters) on the respective variables describing the control of the threshold statistics and of the effective input.

Form the encoding procedure one obviously has over $(T, T+\Delta T)$:

$$\lambda^*(T) \cdot i = a \quad (28)$$

where * i is the interspike interval, realization of a r.v. $I\{T, \Delta T\}$

* a is the threshold value, realization of a r.v. $A(T)$

From (28) and the distribution of $A(T)$ one readily obtains the distribution of the interspike intervals over $(T, T+\Delta T)$. Since the threshold r.v are i.i.d so are the successive interspike intervals and their distributin is [14] .

$$P_{I\{T, \Delta T\}}(i) = P_{A(T)}(i\lambda^*(T))\lambda^*(T) \quad (29)$$

Therefore we immediately have that

$$\mu_{I\{T,\Delta T\}} = (\lambda^*(T))^{-1} \cdot \mu_{A(T)} \quad (30)$$

and

$$\sigma_{I\{T,\Delta T\}} = (\lambda^*(T))^{-1} \cdot \sigma_{A(T)} \quad (31)$$

where μ and σ are the mean and the standard deviation of the respective r.v's.

The above analysis, together with results of Chapter 2, leads to the conclusion that the rate $R(T)$ will be given by

$$R(T) = (\text{Constant}) \cdot \lambda^*(T) \cdot 1/\mu_{A(T)} \quad (32)$$

where the value of the constant depends on the particular way of evaluating $R(T)$ as described in 2.1 and 2.4.

The coefficient of variation of the response over $(T, T+\Delta T)$ will be :

$$V_{\{T,\Delta T\}} = \frac{\sigma_{I\{T,\Delta T\}}}{\mu_{I\{T,\Delta T\}}} = \frac{\sigma_{A(T)}}{\mu_{A(T)}} \quad (33)$$

with no direct dependence on $\lambda^*(T)$, a very useful result. Subsequently we shall briefly discuss the behaviour of the dynamic system :

$$\begin{cases} R(T) = \text{Const} \mu_{A(T)} \cdot \lambda^*(T) \\ \mu_{A(T)} = H_{\mu_A} \{R(t), t < T\} \\ \lambda^*(T) = H_{\lambda^*} \{R(t), \lambda(t), t < T\} \end{cases} \quad (34)$$

with some simple assumptions on operators H_{μ_A} and H_{λ^*} (H_{μ_A} describes part of the action H_A , namely the output influence on the first order statistic of $A(T)$).

Fig. 3 represents a block diagram of the system described by the above equations; it is a quite general and abstract scheme though it emphasizes the fact that two output dependent factors control the behaviour of output rate: the threshold dynamics and the input dependent effective value of the operator current.

From the scheme in Fig. 3 it is quite clear which mechanisms can be responsible for transients of adaptation that preemphasize step responses. A step increase in the input $\lambda(t)$ will suddenly increase $\lambda^*(t)$ then the output rate will effect the threshold distribution so that an increase in μ_A will result, and also the effective generator current will decrease. What was presented is in fact a scheme combining automatic gain control (through μ_A) with so-called selfinhibitory feedback reducing the effective input [8], [9].

There is experimental evidence to prove the effect of selfinhibition [2], and it was found that it is responsible for relatively slow transients in $R(t)$. However most experimental physiologists report a two phase adaptation transient to step displacements in input [9], [11] : this could be explained by assuming that the threshold control operator H_{μ_A} is much faster (time constant: τ_{μ_A}) than the selfinhibition effect (H_{λ} with $\tau_{\lambda} \gg \tau_{\mu_A}$). In [9] a simple system is assumed on the basis of Fig. 3 showing how further experimental facts concerning the response time constants in two phase adaptation in $R(t)$ can easily be accounted for in this model.

Considering the variability in the response, we first observe that $V_{\{T, \Delta T\}}$ does not depend directly on the selfinhibition process (involving changes in $\lambda^*(t)$). The dynamics of $\sigma_{A(T)}$ will be written as

$$\tilde{\sigma}_{A(T)} = H_{\sigma_A} \{R(t), t < T\} \quad (35)$$

and we have

$$\mu_{A(T)} = H_{\mu_A} \{R(t), t < T\} .$$

Therefore the behaviour of $V_{\{T, \Delta T\}}$ depends on H_A the output dependent changes in $p_{A(T)}$ (a) (threshold statistics). Experiments show that the variability in firing is constant for slowly modulated responses and changes in $V_{\{T, \Delta T\}}$ accompany mostly sudden, drastic changes in $R(t)$ (the fast phases of step responses). We can account

for this behaviour by assuming that H_σ and H_μ have similar dynamics with different main time constants, if for example H_μ responds to $R(t)$ faster than H_σ one obtains, following a jump in $R(T)$, a temporary imbalance in the ratio σ_Δ/μ_Δ explaining the transient over synchronization (decrease in V) in step responses. When $R(t)$ changes slowly (so that both the dynamics of σ and μ can follow the time course of $R(\tau)$) we shall have σ/μ approximately constant as desired, to match the "real-world" behaviour.

After considering the above theory as a description of the ensemble behaviour we can assume, as a first approximation, that the output of each encoder is a realization of a nonuniform Poisson process with rate function $R(t)$, the ensemble response to a certain input $\lambda(t)$ (or equivalently that the pooled response is a Poisson process with rate proportional to $R(t)$ -[13]).

4. Decoding Mechanisms

In this section we shall propose and analyze a decoding scheme, in fact a demodulator for the case of information transmitted through the variable rate of a point process [8]. The demodulator is interesting mainly from the mathematical point of view, since almost nothing can be said about how the higher levels of the nervous system's organizational hierarchy "decode" or "understand" the incoming information. In fact we may safely assume that there is no need for the neural system to recover the modulating signals $\lambda(t)$ at the receiving end - the all-or-none signals can be directly processed to generate biological responses to stimuli (in form of spike trains sent as orders to motor units or coded information to other processing centers).

4.1 The General Decoding Model

The main idea in the decoding scheme is to use a "neural" encoder unit in a feedback configuration - essentially the phase lock (frequency-lock) demodulation technique. An estimate of the modulating signal $\hat{\lambda}(t)$, the decoder output, drives the local encoder whose output $\hat{f}(t)$ is compared to the incoming series of spikes $f(t)$. The local estimate $\hat{\lambda}(t)$ is updated continuously based upon an error signal generated through comparison of $f(t)$ to $\hat{f}(t)$. Referring to Fig. 4 we write that :

$$\begin{aligned}\hat{\lambda}(t) &= \Delta \cdot \int_0^t (f(\xi) - \hat{f}(\xi)) d\xi = \\ &= \Delta \cdot (N(t) - \hat{N}(t))\end{aligned}\tag{36}$$

where $N(t)$ is the counting process associated to the input therefore depending on $\lambda(t)$ and $\hat{N}(t)$ is the local counting process controlled by $\hat{\lambda}(t)$. The purpose is now to find, assuming that the local encoder and the primary neural coding scheme are known, how good an estimate of $\lambda(t)$ is the obtained $\hat{\lambda}(t)$.

We note that since the decoder output is a difference of two counting processes it will only assume values which are multiples of Δ ($k\Delta, k \in \mathbb{N}$). No negative values will be reached since the general neural encoder will obviously produce no output pulses for an input $\hat{\lambda}(t) = 0$. One could also consider the case of a long memory filter instead of the simple integrator in the demodulator, this case being more complicated; we will concentrate on the simple model as presented above.

Now let's assume for simplicity that the local encoder yields an output process so that

$$\text{Prob \{No. of occurrences = 1, (T, T+dt)\} | \hat{\lambda}(T) \} = \hat{\lambda}(T)dt + o(dt) \quad (37)$$

thus for example its thresholds are independent identically exponentially distributed r.v.'s (24). Further we consider that the input to the decoder is a realization of a Poisson process with time varying density $\rho(t)$ carrying the information about the primary stimulus intensity $\lambda(t)$. The primary encoder is not assumed to be a simple nonadaptive one as the coding unit in the decoder feedback therefore generally $\rho(t) \neq \lambda(t)$. For example we can assume that $\rho(t) = R(t)$ the rate obtained for the ensemble behaviour as described in 3.4.

The decoder output can now be regarded as a particular Markovian process - a linear non-homogeneous birth and death process [14]. Indeed an excitatory input pulse (from $f(t)$) will increase the output by Δ whereas a selfinhibitory one (from $\hat{f}(t)$) will result in a decrease by the same amount. The output therefore performs a random-walk on the levels $k\Delta$. Following Feller [14] let's define :

$$P_n(t) = P_x\{\hat{\lambda}(t) = n\} \quad (38)$$

and concentrate on the behaviour of the distribution $\{P_n(t)\}_{n \in \mathbb{N}}$.

We have, obviously, the following relations from the transition probabilities of the Markov chain:

$$P_n(t+dt) = P_{n-1}(t)\rho(t)dt + P_{n+1}(t)(n+1)\Delta dt + P_n(t)(1-\rho(t)-n\Delta)dt$$

and (39)

$$P_0(t+dt) = P_0(t)(1-\rho(t))dt + P_1(t)\Delta dt$$

yielding the following differential equations :

$$\begin{cases} P_n'(t) = -P_n(t)(\rho(t) + n\Delta) + P_{n-1}(t)\rho(t) + P_{n+1}(t)(n+1)\Delta \\ P_0'(t) = -P_0(t)\rho(t) + P_1(t)\Delta \end{cases} \quad (40)$$

4.2 First and Second Order Statistics of the Response

The equations (40) yield a complete description of the stochastic behaviour of the output. We can define the distribution generating functional

$$P(s,t) = \sum_{n=0}^{\infty} P_n(t) \cdot s^n \quad (41)$$

and using (40) obtain a partial differential equation for it.

The result is :

$$\frac{\partial}{\partial t} P(s,t) = (s-1)[\rho(t)P(s,t) - \Delta \frac{\partial}{\partial s} P(s,t)] \quad (42)$$

and can be solved for some cases of $\rho(t)$.

We shall be interested in the behaviour of the first and second order statistics. Lets therefore define.

$$M_1(t) \triangleq \sum_{n=0}^{\infty} n P_n(t) \quad (43)$$

$$M_2(t) \triangleq \sum_{n=0}^{\infty} n^2 P_n(t)$$

The initial equations provide, through some algebraic manipulation :

$$M_1'(t) + \Delta M_1(t) = \rho(t) \quad (44)$$

$$M_2'(t) + 2\Delta M_2(t) = \rho(t) + M_1(t)(2\rho(t) + \Delta)$$

Now since $E(\hat{\lambda}(t)) = \mu_{\hat{\lambda}}(t) = \Delta \cdot M_1(t)$ and $E[\hat{\lambda}^2(t)] = \sigma_{\hat{\lambda}}^2(t) + \mu_{\hat{\lambda}}^2(t) = \Delta^2 M_2(t)$ we easily derive the behaviour of $\mu_{\hat{\lambda}}$ and $\sigma_{\hat{\lambda}}$ in time. We finally obtain (after some algebra):

$$\begin{cases} \mu_{\hat{\lambda}}'(t) + \Delta \mu_{\hat{\lambda}}(t) = \Delta \rho(t) \\ (\sigma_{\hat{\lambda}}^2(t))' + 2\Delta(\sigma_{\hat{\lambda}}^2(t)) = \Delta^2(\rho(t) + \mu_{\hat{\lambda}}(t)) \end{cases} \quad (45)$$

and for the steady state, when $\rho(t) = \rho_0$ constant the result is :

$$\begin{cases} \mu_{\hat{\lambda}}(t) = \rho_0 & , t \gg 0 \\ \sigma_{\hat{\lambda}}^2(t) = \Delta \rho_0 & , t \gg 0 \end{cases}$$

yielding a signal-to-noise ratio of

$$S/N = \rho_0^2 / \Delta \rho_0 = \rho_0 / \Delta \quad (50)$$

Thus we shall need small Δ for high S/N and large Δ for good tracking of rapid changes in $\rho(t)$. However rapid changes in $\rho(t)$ occur at step response transients, when the stimulus is $\lambda(t) = \lambda_1 + \lambda_2 u(t)$, and in this case no tracking is required; in fact the rapid transients of $\rho(t)$ will cause a quicker, step like response in $\hat{\lambda}(t)$ to steps of $\lambda(t)$ - and this is a good feature of the decoder. For slowly changing $\lambda(t)$, $\hat{\lambda}(t)$ will follow $\rho(t) \approx \lambda(t)$ and this will be possible even for small Δ .

We note that the result obtained is similar to the behaviour of the simple Low Pass Filter estimator of $\lambda(t)$. If a LPF with weighting sequence, $h(t)$ is used in demodulating the incoming sequence of pulses we have from the well known generalized Campell laws [15] :

$$\begin{aligned} \mu_{\hat{\lambda}_{\text{LPF}}}(t) &= E(\hat{\lambda}_{\text{LPF}}(t)) = \int_{-\infty}^t \rho(\tau) h(t-\tau) d\tau \\ \sigma_{\hat{\lambda}_{\text{LPF}}}^2(t) &= E(\hat{\lambda}_{\text{LPF}}^2(t)) - \mu_{\hat{\lambda}_{\text{LPF}}}^2(t) = \int_{-\infty}^t \rho(\tau) h^2(t-\tau) d\tau \end{aligned} \quad (51)$$

If now $h(t-\tau) = \Delta \cdot e^{-\Delta t} u(t)$ the similarity to (45) becomes even more obvious for the behaviour of the mean. The second order statistics is however in (45) controlled by $\mu_{\lambda}^{\wedge}(t)$ too. In steady state we have

$$\begin{aligned} \mu_{\lambda_{LPF}}^{\wedge}(t) &= \rho_0 \int_0^{\infty} h(\tau) d\tau = \rho_0 \\ \sigma_{\lambda_{LPF}}^{\wedge 2}(t) &= \rho_0 \int_0^{\infty} \Delta^2 e^{-2\Delta t} d\tau = \rho_0 \frac{\Delta}{2} \end{aligned} \quad (52)$$

Therefore here the signal to noise ratio is $\rho_0^2 / (\rho_0 \Delta / 2) = 2\rho_0 / \Delta$ an improvement of 3 db. over the previous case

If however a moving ^{window} counter-filter is used with weighting sequence :

$$h(t) = \begin{cases} 1 & 0 < t < \frac{1}{\Delta} \\ 0 & \frac{1}{\Delta} < t < \infty \end{cases}$$

we obtain

$$\mu_{\lambda_{LPF}}^{\wedge} = \int_{t-\frac{1}{\Delta}}^t \rho(t) d\tau$$

and

$$\sigma_{\lambda_{LPF}}^{\wedge 2} = \int_{t-\frac{1}{\Delta}}^t \rho(t) d\tau$$

Thus $S/N = \int_{t-\frac{1}{\Delta}}^t \rho(t) d\tau$ and for steady state $\frac{S}{N} = \frac{\rho_0}{\Delta}$ as in the previous case.

It is expected that if a smoothing Low Pass Filter will be used in the decoder of Fig. 4 better S/N will be attained.

5. Conclusions

In this report we presented and analyzed problems of neural coding and some related topics. The neural system is a very complex one and through the mathematical models and theoretical descriptions we can only try to gain some insight into the inner mechanisms governing the experimentally recorded overall behaviour. The description we gave here to the neural spike trains was a probabilistic one: they were regarded as realizations of stochastic point processes and we only evaluated the overall behaviour of an ensemble of identical (stochastic) encoders.

Adaptation to stimuli in an ensemble of coding units was analyzed assuming simple models that incorporate some possible structural relations and feedback effects. Some of the assumptions (for example the selfinhibition in the adaptive encoder) were experimentally proven to be true, others remain as functional assumptions yielding input-output behaviour close to the reported experimental results. For the variable threshold assumption, some recent indirect experimental evidence seems to strongly support it [10].

The decoder analyzed in Section 4 is a conceptual one, however the neural system could easily implement something like it using neural units with selfinhibitory and excitatory synaptic connections.

The mathematical description of the neural system behaviour continues to raise interesting and challenging theoretical problems. Our hope is that the continuing interaction between experimental physiologists, mathematicians and engineers will bring a real progress in our understanding of these aspects of nature.

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THE OUTPUT PROCESS:

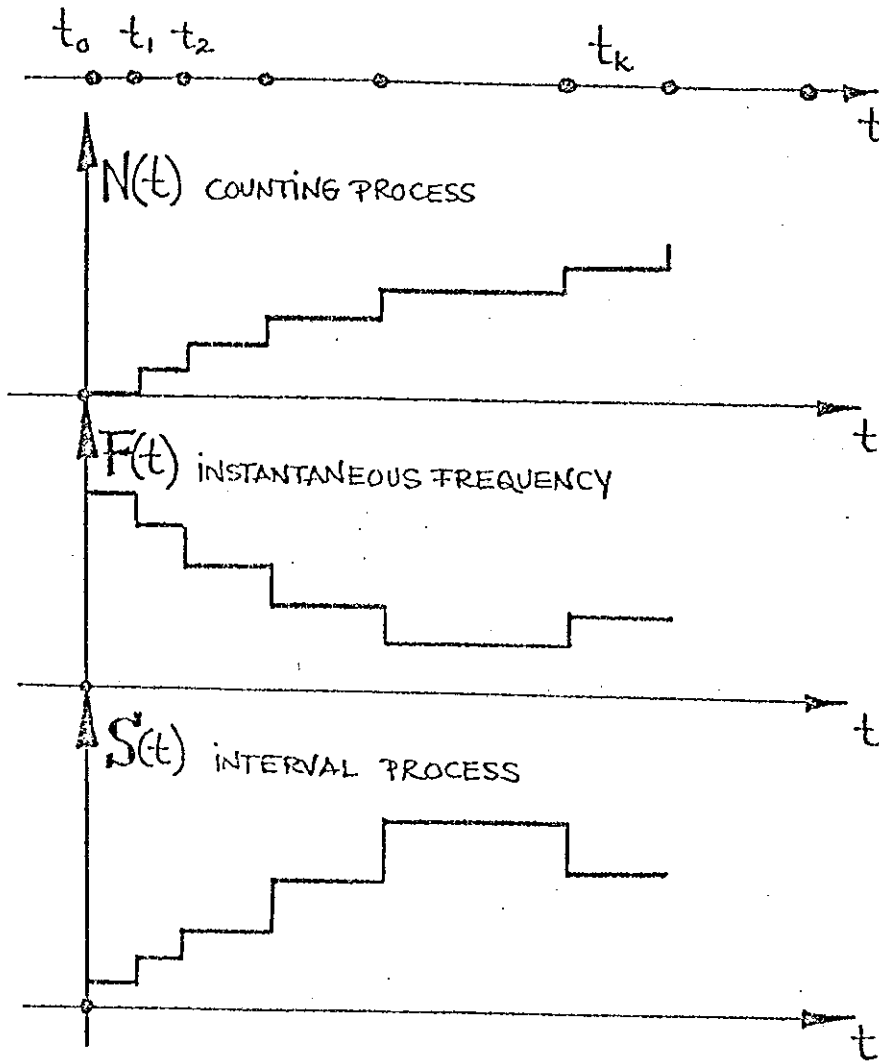


FIG 1 THE OUTPUT PROCESS & ASSOCIATED PROCESSES

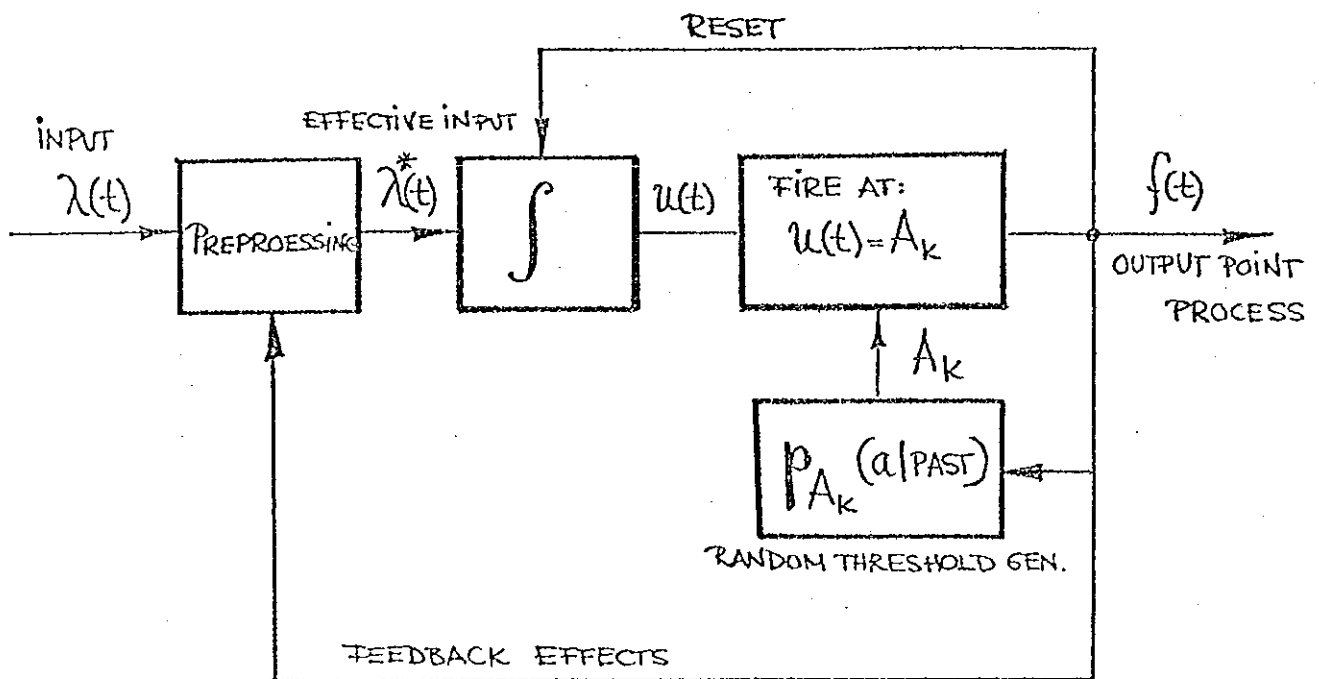


FIG 2 THE INTEGRATE-AND-FIRE-AT-THRESHOLD MODEL

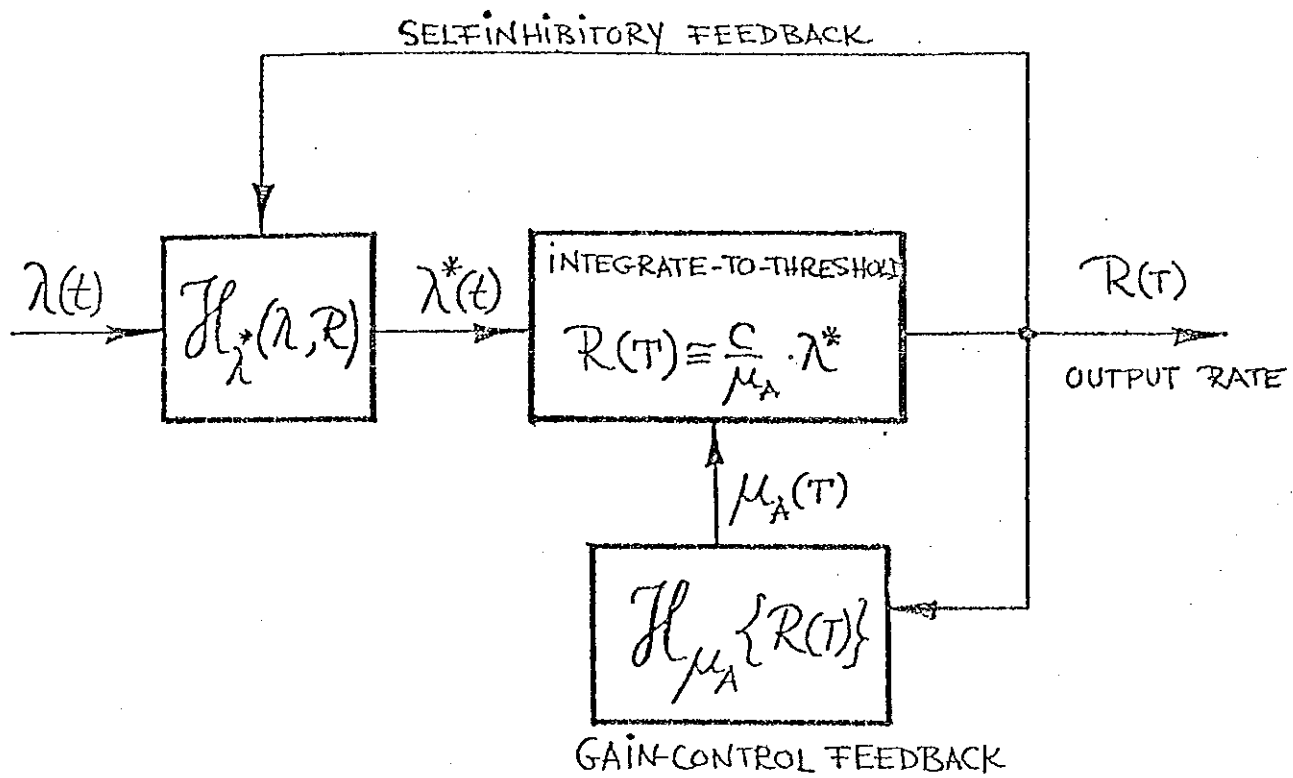


FIG. 3: A SCHEMATIC DYNAMIC SYSTEM DESCRIBING ENSEMBLE BEHAVIOUR

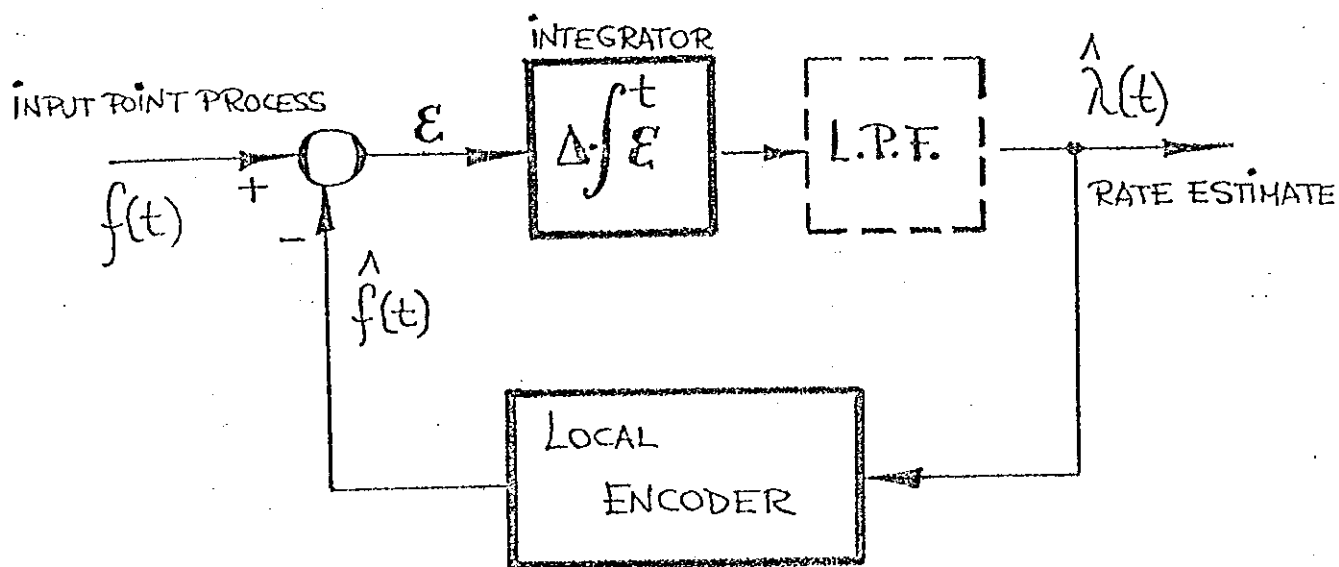


FIG. 4: THE DECODING SCHEME

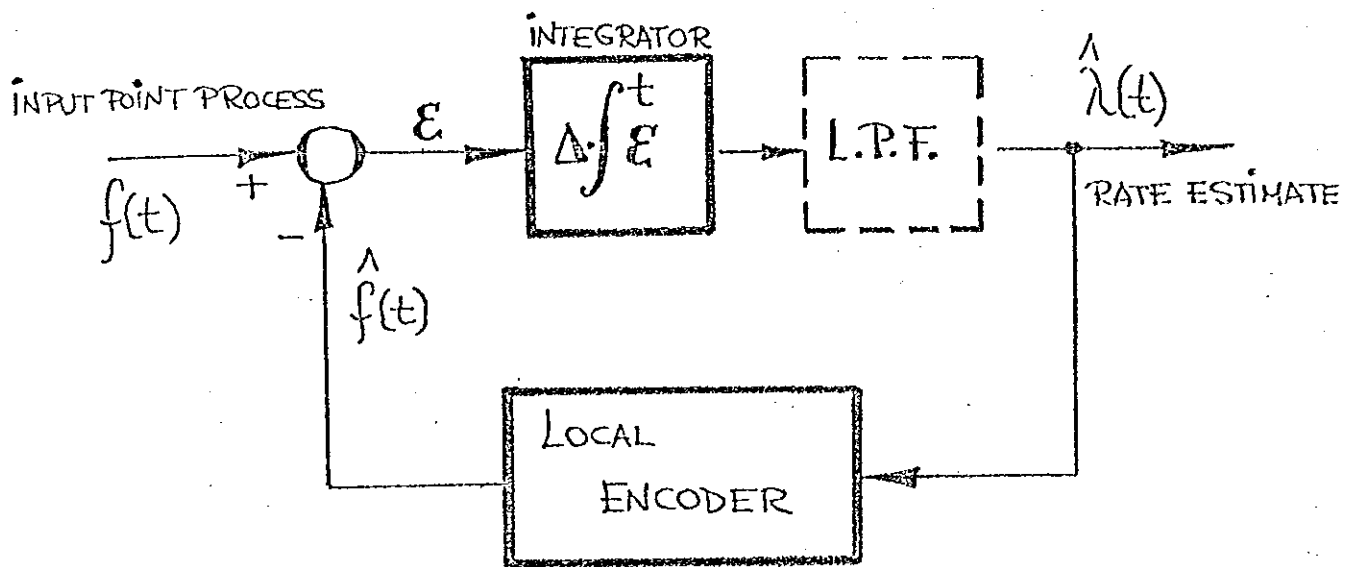


FIG. 4: THE DECODING SCHEME