Biol. Cybernetics 27, 113–124 (1977)

Biological Cybernetics

A Volterra Representation for Some Neuron Models

T. Poggio[1] and V. Torre[2]

[1] Max-Planck-Institut für biologische Kybernetik, Tübingen, FRG
[2] Università di Genova, Istituto di Fisica, Genova, Italia

Abstract. A Volterra-like polynomial representation is derived and its convergence discussed for two neuronal models in which subthreshold inputs are integrated either without loss (integrate and fire) or with a decay which follows an exponential time course (leaky integrator). This polynomial representation provides a kind of "nonlinear transfer function" for the nonlinear encoding process. Standard formulae are used to derive explicitely the output for various inputs as in linear system theory. Moreover, the nonlinear transfer function associated with cascades or networks of neurons can be also obtained. Finally, extensions and implications of these results are discussed.

1. Introduction

A significant number of nerve cells code a continuous electrotonic input in the form of trains of all-or-none nerve impulses, called spikes. This transformation from a continuous signal to a discrete one—and back from a discrete signal to a continuous one—represents a general principle in the information processing of nervous systems. The generation and time course of the nerve impulses can be quantitatively described by Hodgkin-Huxley type equations (Hodgkin and Huxley, 1952; Frankenhouser and Hodgkin, 1957; McAllister et al., 1975). However, the time of occurence of the spikes and not their shape is the important information carrier in the nervous system (Stein, 1970). From this point of view the temporal pattern of nerve impulses can be modelled using much simpler equations than Hodgkin-Huxley ones.

Two models (the integrate-and-fire and the leaky integrator) have been used extensively for theoretical studies by many authors (for a review see Stein et al., 1972, and Knight, 1972a). The equations associated with the two models also occur in the mathematical literature dealing with stochastic processes in connection with first passage problems. This mathematical analogy has been exploited to develop various stochastic models of neuron activity (Gerstein and Mandelbrot, 1964; Johannesma, 1968). Moreover, the forgetful or leaky integrator, of which the integrate-and-fire is a limiting case, represents a reasonable idealization of the Hodgkin-Huxley equations (Knight, 1973). Several experimental data from *Limulus* (Knight, 1972b), the muscle spindle (Poppele and Chen, 1972; Coenen and Chaplain, 1973) and the stretch receptor of the crayfish (Borsellino et al., 1965) can be described in terms of these two models.

The two models, which represent pulse frequency modulation systems, are nonlinear and their input-output relationship cannot be given in a closed analytical form. For small inputs the two models can be linearized and a linear transfer function then gives a good representation of the encoding process (Borsellino et al., 1965; Knight, 1972a). The transferfunction approach has the advantage of providing

a) an explicit input-output relation, valid for a large class of inputs, deterministic as well as stochastic,

b) the possibility of putting systems together in a standard way, i.e. the possibility of using the "neuron block" in the description of the dynamics of a nervous network.

In this paper we extend the use of transfer function to the nonlinear range, using a Volterra series representation of the two models. The Volterra series method provides a kind of "nonlinear transfer function" for the encoding process, valid outside the linear range. This approach has the advantages of the linear transfer function, i.e. (a) standard formulae characterize the output for various inputs, and (b) it is possible to use directly the nonlinear transfer function to represent the dynamics of cascades or, in general, networks of neurons[1].

[1] A short preliminary report has already appeared (Poggio and Torre, 1975)

The next section deals with the derivation and mathematical properties of the two models. In Section 3 we discuss the derivation of the Volterra-like series representation and the problem of its convergence, and in Section 4 the relationship between the spike rate of a single neuron and the so called population rate. A treatment of stochastic properties is briefly outlined in Section 5. Finally we discuss some experimental data in relation with our Volterra representation; a few applications and extensions of the results of this paper are also suggested.

2. Neuron Models

The Hodgkin-Huxley equations for the axon, as Knight (1973) has shown, can be reasonably simplified when the threshold is not reached. Before the sodium activation m achieves a critical value m_c (the sodium activation threshold) and the full Hodgkin-Huxley dynamics take over, causing a nerve impulse to fire and restoring m to a value near zero, the simple equation

$$\frac{dm}{dt} = -\gamma m + s(t) \tag{1}$$

can be used, where $s(t)$ is proportional to the applied stimulus (input current) and $1/\gamma$ is the time constant of the sodium activation kynetics. Equation (1) can be used to determine the single unit's interspike interval (or instantaneous firing period) $T(t)$ in the following way:

$$m_c = \int_{t-T(t)}^{t} dt' e^{-\gamma(t-t')} s(t') . \tag{2}$$

Equation (2) represents the forgetful integrate-and-fire neuron model (Knight, 1972a) or leaky integrator (Stein et al., 1972). When $\gamma=0$ (2) describes the integrate-and-fire model.

It is convenient to write $s(t)$ as

$$s(t) = x_0 + x(t) \tag{3}$$

with $x_0 > 0$ and $\overline{x(t)} = 0$; a positive average input provides a carrier firing rate. The average interspike interval is, [for $x(t) \equiv 0$, $\gamma = 0$]

$$T_0 = m_c / x_0 . \tag{4}$$

T_0 corresponds to a constant carrier rate which is determined by the average of the input and the value of the threshold. Equation (2) defines a nonlinear functional with input $x(t)$ and output $T(t)$ (x_0 as well as m_c are taken as parameters of the functional):

$$T(t) = F\{x(t)\} . \tag{5}$$

In the case $\gamma = 0$ (perfect integrator) we define

$$T(t) = B\{x(t)\} . \tag{6}$$

The "instantaneous interspike interval" $T(t)$ can be used as a measure of nervous activity. Independent of the specific form of the neuron model, an equivalent measure is the "instantaneous firing rate", defined as

$$f(t) = \frac{1}{T(t)} , \tag{7}$$

often used in electrophysiology (Shapley, 1971). A quite different measure is the "population rate" $r(t)$, also called "impulse density", defined as the fraction of nervous firing activity per unit time in a population of identical, non-interacting neurons. Knight (1972a) argued that the relation between $r(t)$ and $T(t)$ is

$$N = \int_{t-T(t)}^{t} r(t')dt' , \tag{8}$$

where N is the number of the identical neurons considered in the population. The "impulse density" does not necessarily refer to a population of neurons: it represents also the instantaneous density of spikes of a single neuron. Usually the impulse density is measured from a single neuron, averaging its response over several cycles of the (periodic) input. This seems analogous to measuring the number of neurons instantaneously active (i.e. active in a bin of Δt s) in a population of non-interacting, identical neurons. It is convenient to write $r(t)$ as

$$r(t) = p_0 + p(t) \tag{9}$$

where $p_0 > 0$ is the average number of firing neurons and $r(t)$, with $\overline{p(t)} = 0$, is the modulation of the "impulse density". Equation (8) defines a nonlinear functional

$$p(t) = P\{T(t)\} . \tag{10}$$

From (1), (6), and (8), Knight argues that

$$P = B^{-1} \quad \text{with the parameter} \quad T_0 = \frac{N}{r_0} , \tag{11}$$

since the role of input and output are interchanged in the equations defining the functionals P and B. If B^{-1} exists, it would be easy to derive from a Volterra representation of the integrate-and-fire model (the functional B) using standard formulae (Brilliant, 1958 and Appendix 2), the Volterra representation of P. Since, however, the mapping $r \to T$ is not bijective, its inverse, in general, does not exist. Therefore, the formal representation for B^{-1} has, in general, no sense. This point will be discussed in Section 4.

3. The Volterra Representation

In this section we will derive a Volterra series representation of the functionals F and B. Here we will consider only inputs which can be represented by a finite sum of harmonics, i.e.

$$x(t)=\sum_{1}^{n}{}_i A_i e^{j\omega_i t}, \qquad A_i\in\mathbb{C}. \tag{12}$$

Since the functionals F and B have a finite memory, one can consider input functions of the form of (12), defined on a finite interval $[a,b]$ (which are dense in $L^2[a,b]$). Since the space of infinitely differentiable functions which vanish at the boundary of this finite interval is dense in $L^2[a,b]$ and F and B are smooth, a Volterra-like series expansion exists for both functionals [for a discussion of the validity of Volterra series expansion, see Palm and Poggio (1977)].

Let be

$$T(t)=T_0+\sum_{1}^{\infty}{}_n\frac{1}{n!}\int_{-\infty}^{+\infty}\dots\int_{-\infty}^{+\infty}g_n(t_1,\dots,t_n)\cdot\prod_{1}^{n}{}_i x(t-t_i)dt \tag{13}$$

the Volterra series expansion of the functional F, where $T_0=\frac{1}{\gamma}\log\left(1-\frac{m_c\gamma}{x_0}\right)$ and $g_n(t_1,\dots,t_n)$ are the kernels characterizing the functional F. The functional representation (13) is specified when the kernels g_n or their Fourier transforms $G_n(\omega_1,\dots,\omega_n)$ are given. To find the G_n we will use the harmonic input method of Bedrosian and Rice (1971). This method relies on the fact that, when (13) holds, and

$$x(t)=\sum_{1}^{n}{}_i e^{j\omega_i t}, \tag{14}$$

ω_i incommesurable, the G_n are given by: $G_n(\omega_1,\dots,\omega_n)$ = coefficient of $e^{j(\omega_1+\dots+\omega_n)t}$ in expansion (13).

Now, let (14) be the input to the functional F: (2) becomes

$$m_c=\int_{t-T(t)}^{t}dt'e^{-\gamma(t-t')}\left(x_0+\sum_{1}^{n}{}_i e^{i\omega_i t}\right).$$

Setting $T_1=T-T_0$, we obtain

$$0=\int_{t-T_1-T_0}^{t-T_0}x_0 e^{-\gamma(t-t')}dt'+\int_{t-T}^{t}\sum_{1}^{n}{}_i e^{j\omega_i t'}e^{-\gamma(t-t')}dt'$$

and therefore

$$0=\frac{x_0}{\gamma}e^{-\gamma T_0}(1-e^{-\gamma T_1})+\sum_{1}{}_i\frac{(1-e^{-(j\omega_i+\gamma)T})}{j\omega_i+\gamma}e^{j\omega_i t}.$$

In the case of $\gamma T_1 \ll 1$, that is when $1-e^{-\gamma T_1}\sim\gamma T_1$, one has

$$T_0=T+\sum_{1}^{n}{}_i C_i(1-e^{-(j\omega_i+\gamma)T}) \tag{15}$$

where $C_i=\frac{e^{j\omega_i t}}{x_0 e^{-\gamma T_0}(j\omega_i+\gamma)}$.

In order to carry out the identification of the Volterra kernels, (15) must be solved in terms of $T(t)$. The Lagrange formula for the reversion of a power series can be applied here (Lagrange, 1770; Copson, 1975; Comtet, 1974): if $y=y_0+wF(y)$ determines y as a series in w with constant term y_0, then the solution to $y=y_0-F(y)$ is

$$y=y_0+\sum_{1}^{\infty}{}_n\frac{(-1)^n}{n!}\frac{d^{n-1}}{dz^{n-1}}\{F^n(z)\}_{z=y_0}.$$

Therefore, we have

$$T(t)=T_0+\sum_{1}^{\infty}{}_m\frac{(-1)^m}{m!}\frac{d^{m-1}}{dx^{m-1}}\cdot\left\{\sum_{1}^{n}(1-e^{-(j\omega_i+\gamma)z})C_i\right\}^m_{z=T_0}. \tag{16}$$

From (16) the Fourier transform of the kernels can be identified from the coefficients of the term $e^{(\omega_1+\dots+\omega_n)t}$ as

$$F_1(\omega)=-\frac{e^{\gamma T_0}}{x_0}\frac{1-e^{-(j\omega+\gamma)T_0}}{j\omega+\gamma} \tag{17}$$

$$F_2(\omega_1,\omega_2)=\frac{e^{2\gamma T_0}}{x_0^2}\operatorname{sym}\left\{\frac{e^{-(j\omega_1+\gamma)T_0}(1-e^{-(j\omega_2+\gamma)T_0})}{j\omega_2+\gamma}\right\} \tag{18}$$

and for the higher order as

$$F_n(\omega_i,\dots,\omega_n)=\frac{(-1)^n e^{n\gamma T_0}}{x_0^n\prod_{1}^{n}{}_i(j\omega_i+\gamma)}\frac{d^{n-1}}{dz^{n-1}}\cdot\left\{\prod_{1}^{n}{}_i(1-e^{-(j\omega_i+\gamma)z})\right\}_{z=T_0}. \tag{19}$$

Substitution of (17)–(19) in (13) gives

$$T(t)=T_0+\sum_{1}^{\infty}{}_n\frac{1}{n!}\frac{1}{(2\pi)^n}\cdot\int_{-\infty}^{+\infty}\dots\int_{-\infty}^{+\infty}d\omega_1\dots d\omega_n F_n(\omega_1,\dots,\omega_n)\cdot e^{j(\omega_1+\dots+\omega_n)t}\prod_{1}^{n}X(\omega_r)d\omega_r \tag{20}$$

where $X(\omega)$ is the Fourier transform of the input $x(t)$. Equation (17) is the linear transfer function derived by Knight (1972a) and by Stein et al. (1972) when the system is linearized. F_2 is the second order kernel. When the input has a large modulation, it is necessary to consider all higher kernels to obtain a good representation of the functional F. The kernels for the functional B, that is for the perfect integrator, are easily obtained from (17)–(18), setting γ equal to zero. The instantaneous frequency $f(t)=\frac{1}{T(t)}$ can be obtained from (20) and the Volterra-like expansion of the

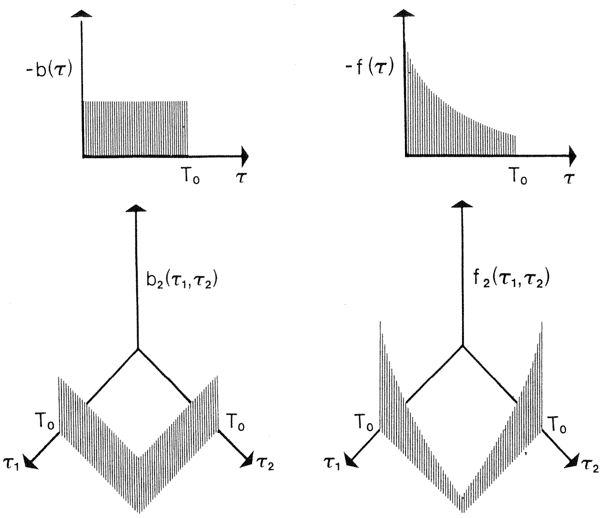

Fig. 1. First and second order kernels in the time domain for the integrate-and-fire (left) and the forgetful integrate-and-fire (right) encoder models

"division" system 1/0, according to the formulae of Appendix 2.

Equation (20) describes the functional F in the frequency domain; it would be interesting to obtain an analogous representation in the time domain and possibly an explicit form for the output $T(t)$. Here we will derive a time domain representation for the perfect integrator ($\gamma=0$) and an explicit form for $T(t)$. When $\gamma \neq 0$ it is still possible to obtain the same results, but they are more complicated.

When $\gamma=0$ the Fourier transforms of the kernels of B are

$$B_n = \frac{(-1)^n}{x_0^n \prod_{1}^{n} {}_i j\omega_i} \frac{d^{n-1}}{dz^{n-1}} \left\{ \prod_{1}^{n} {}_i a_i \right\}_{z=T_0} \tag{21}$$

where $a_i = 1 - e^{-j\omega_i z}$, $T_0 = \frac{m_c}{x_0}$.

From the binomial formula one obtains

$$B_n = \frac{(-1)^n}{x_0^n} \sum_{0=i_1}^{n-1} \sum_{0=i_2}^{i_1} \dots \sum_{0=i_{n-1}}^{i_{n-2}} \cdot \binom{n-1}{i_1} \binom{i_1}{i_2} \dots \binom{i_{n-2}}{i_{n-1}} \cdot \frac{a_1^{(n-1-i_1)}}{j\omega_1} \frac{a_2^{(i_1-i_2)}}{j\omega_2} \dots \frac{a_n^{(i_n-1)}}{j\omega_n}$$

where $a_i^{(k)} = \frac{d^k}{dz^k} a_i |_{z=T_0}$.

Antitransforming ($\mathscr{I}^{-1}$ denotes the inverse Fourier transform)

$$\mathscr{I}^{-1}\left(\frac{a_i}{j\omega_i}\right) = \mathscr{I}^{-1}\left(\frac{1-e^{-j\omega_i T_0}}{j\omega_i}\right) = u_{T_0/2}\left(t - \frac{T_0}{2}\right) \tag{22}$$

where $u_a(t)=1$ if $0 \leqq t \leqq 2a$ and $u_a(t)=0$ if $t<0$ and $t>2a$ and

$$\mathscr{I}^{-1}\left(\frac{a_i^{(k)}}{j\omega_i}\right) = \mathscr{I}^{-1}((-a)^n (j\omega_i)^n (-e^{-j\omega_i T_0})) = (-1)^{n-1} \delta^{(n-1)}(t-T_0) \tag{23}$$

where $\delta^{(i)}$ is the i-th derivative of the delta distribution. From Equations (13), (21)–(23) we can derive an explicit form for $T(t)$

$$\begin{aligned} T(t) = {} & T_0 - \frac{1}{x_0} y_1 + \frac{1}{x_0^2}(y_1 x(t-T_0)) \\ & + \frac{1}{x_0^3 3!}(3! y_1 x^2(t-T_0) - 3y_1^2 x^{(1)}(t-T_0)) \\ & + \frac{1}{x_0^4 4!}(y_1^3 x^{(2)}(t-T_0) 4 + 4! y_1 x^3(t-T_0) \\ & - 36 y_1^2 x(t-T_0) x^{(1)}(t-T_0)) + \dots \end{aligned} \tag{24}$$

where

$$y_1 = \int_0^{T_0} dt' x(t-t')$$

and y_1^l indicates the l-th power of y_1, whereas $x^{(l)}$ indicates the l-th derivatives of x.

The higher order terms can be easily computed from (13), (22), and (23). From (22) and (23), the first two kernels in the time domain are

$$b_1(t) = -\frac{1}{x_0} u_{T_0/2}(t - T_0/2)$$

$$b_2(t', t'') = \text{sym}\left\{ \frac{1}{x_0^2} u_{T_0/2}(t') \delta(t'' - T_0) \right\}$$

which are shown in Figure 1.

In the case of the leaky-integrator, (21) has to be substituted by (19), and in a similar way an explicit form for $T(t)$ can be derived (see Fig. 1).

The smoothness of the functional F and the properties of the input functions $x(t)$ are sufficient to ensure the existence of a Volterra series expansion. Interestingly, the series is not a Volterra series in the strict original sense (of Vito Volterra), since the kernels [(21)] are, in general, distributions, but it is a Volterra-like series (Palm and Poggio, 1977), i.e. the integral representation of the Taylor development of a Fréchet-differentiable functional (Hille and Phillips, 1957), since the kernels are derivatives of some functions (Palm and Poggio, 1977, Theorem 1). Observe that, accordingly, the first order kernel does *not* contain distributions, the second order one contains a delta, the third order kernel contains the *first* derivative of the delta distribution and so on. Let us now examine the region of convergence of the series expansion (13).

The Equation (16) can be viewed as a power series expansion in T_0 of equation

$$T_0 = T + f(T), \tag{25}$$

where

$$f(T) = \sum_1^n {}_i C_i(1 - e^{-(j\omega_i + \gamma)T}) \quad \text{and}$$

$$C_i = \frac{A_i e^{j\omega_i t}}{x_0 e^{-\gamma T_0}(j\omega_i + \gamma)}.$$

The problem of finding the region of convergence of our Volterra series expansion is related to the problem of finding the region of convergence of the power series in T_0, that is the solution of (25). This problem can be easily studied in the complex plane.

Let consider the equation

$$T_0 = h(T) = T + f(T) \tag{26}$$

where T, $T_0 \in \mathbb{C}$. From the theory of functions of complex variables (Goursat, 1918; Copson, 1935), the necessary and sufficient condition that (26), with $h(T)$ analytic, has to fulfil to have a unique solution $T = F(T_0)$ analytic in a neighbourhood of 0, is that $h'(0) \neq 0$.

From (25) and (26)

$$h'(T) = 1 + f'(T) = 1 + \sum_1^n {}_i \frac{A_i e^{j\omega_i t}}{x_0 e^{-\gamma T_0}}$$

$$= 1 + \frac{x(t)}{x_0 e^{-\gamma T_0}} \tag{27}$$

Since (by hypothesis) $x_0 > 0$ and $\overline{x(t)} = 0$, $h'(0) \neq 0$ and (27) implies for every t

$$x_0 e^{-\gamma T_0} + x(t) > 0. \tag{28}$$

In the case of the perfect-integrator, (28) implies $s(t) > 0$, for every t. Therefore, because in the neighbourhood around 0, $T = F(T_0)$ converges absolutely and uniformly, in the same neighbourhood the series (16) also converge and is there analytic. Thus, the Volterra series expansion exists and converges when condition (28) is satisfied.

Now let us find a lower bound on the radius of convergence of series (16). The radius of convergence of series (16) is at least (see Copson, 1935, p. 123)

$$|T_0| < \frac{R^2 a^2}{6M} \tag{29}$$

where $a = \inf_t |h'(0)|$, M the maximum of $|h(T)|$ in the region of the complex plane $T \leqq R$.

A relation between M and R is easily found. For simplicity let consider the case of the perfect integrator ($\gamma = 0$). In this case

$$h(T) = T - \sum_1^n {}_i \frac{A_i e^{j\omega_i t}}{j\omega_i x_0}\left(-j\omega_i T + \frac{(-j\omega_i T)^2}{2!} - \ldots\right)$$

which can be written as

$$h(T) = T + \frac{x(t)}{x_0} T - \frac{x^{(1)}(t)}{x_0}\frac{T^2}{2!} + \frac{x^{(2)}(t)}{x_0}\frac{T^3}{3!} + \ldots.$$

Since $x(t)$ is band-limited [compare (12)] and $\bar{\omega} = \omega_n$ is its cutoff frequency we obtain, with $S = \sup_t |x(t)|$, for n sufficiently large, $|x^{(n)}(t)| \leqq \bar{\omega}^n S$. Therefore,

$$|h(T)| < \left| T + k + \frac{S}{x_0 \bar{\omega}}\left(\bar{\omega} T + \frac{(\bar{\omega} T)^2}{2!} + \ldots\right)\right|$$

$$\leqq R + \frac{S(e^{\bar{\omega} R} - 1)}{x_0 \bar{\omega}} + k,$$

where k is a positive constant and

$$M \leqq R + \frac{S(e^{\bar{\omega}}R - 1)}{x_0 \bar{\omega}} + k.$$

The radius of convergence of series (16) is at least

$$|T_0| < \frac{R^2 a^2}{\left(R + \frac{S}{x_0 \bar{\omega}}(e^{\bar{\omega} R} - 1) + k\right)}. \tag{30}$$

When

$\frac{S}{x_0 \bar{\omega}}(e^{\bar{\omega} R} - 1) \to O(R)$, i.e. of the order R or smaller, (30) becomes

$$|T_0| < \frac{R^2 a^2}{(R + O(T) + k)}. \tag{30'}$$

Since $a^2 > 0$ and R can be arbitrary large, (30′) implies two interesting consequences:

— for inputs with low frequencies ($\bar{\omega} \to 0$), there is convergence for every T_0 and every modulation S/x_0,

— for inputs with low modulation ($S/x_0 \to 0$), there is convergence for every T_0 and every frequency.

An upper bound on the radius of convergence of series (16) is the distance from the origin 0 to the nearest zero of $h'(0)$, which in general exists and is finite. Similar results can be obtained for the leaky integrator, although in a more complex way[2].

It may be of interest to compare the exact solution of Equation (2) with the first terms of series (24). We will consider Equation (13) for the perfect integrator ($\gamma = 0$) up to the first six kernels. Let consider inputs of the following type:

$$s(t) = x_0 + A \sin \omega t.$$

---

[2] The Volterra representation can be extended to cases in which the input becomes negative, through a modification of the basic model. In the case of the integrate-and-fire model, negative values of the inputs are considered as having zero value, which amounts to putting a halfwave rectifier in front of the encoder. The Volterra representation can be easily obtained from the kernels of a rectifier and the formulae of Appendix 2

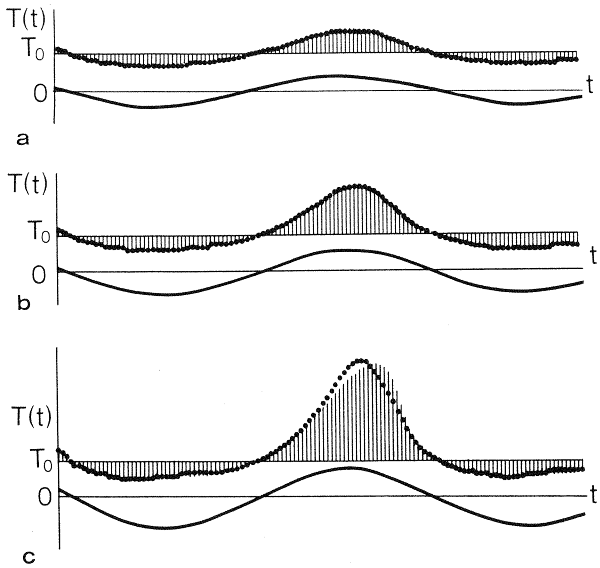

Fig. 2a—c. Instantaneous firing period $T(t)$ as a function of time, obtained from a digital simulation of the integrate-and-fire model (vertical bars) and from the Volterra series representation (24) up to the sixth-order kernel (full dots). The continuous curve is the contribution of the linear kernel. In all three cases $m_c = 1$, $x_0 = 1.5$, implying $T_0 = 0.66$ s. In **a** the input $x(t)$ is a sine-wave with amplitude $A = 0.6$ and frequency $\omega = 0.6$; the modulation is 40%. In **b** the amplitude is increased to $A = 0.9$ corresponding to a modulation of 60%. The Volterra approximation is significantly different from the linear model. In **c** the amplitude is $A = 1.2$ corresponding to a modulation of 80%

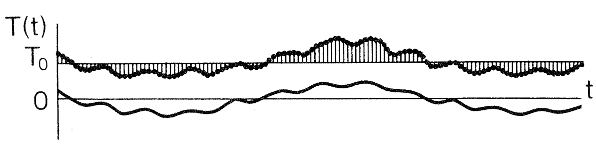

Fig. 3. The input $x(t)$ consists of two sinusoidal waves with amplitude $A_1 = 0.6$, $A_2 = 0.3$ and frequencies $\omega_1 = 0.6$, $\omega_5 = 5$. All other parameters are as in Figure 2. The maximum modulation amounts to 60%

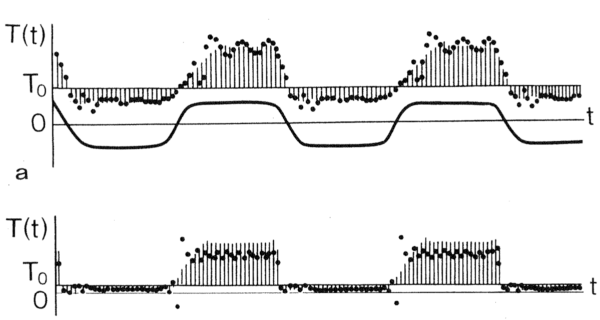

Fig. 4a and b. The input is an approximate square wave, synthetized through the first four Fourier components of an ideal square wave. In **a** the amplitude of the fundamental harmonic is $A = 1.018$ (modulation 67%), its frequency is $\omega = 1$. The other parameters are as in Figure 2. When the modulation is increased to about 100% ($A = 1.57$) and the threshold is decreased to $m_c = 0.26$ (thus T_0 decreases from 0.66 s to 0.17 s) the fit worsens considerably but the Volterra series does not dramatically diverge (**b**)

A/x_0 is the amplitude of modulation of the signal. Figure 2 shows the effect of increasing the modulation of the input. With a modulation of 40% the Volterra series representation fits perfectly the instantaneous firing period, computed from a digital simulation of the integrate-and-fire model. The response is essentially linear. Strong nonlinear distortions appear for $A/x_0 = 60\%$ but the fit (with the first 6 kernels) is still very good. With $A/x_0 = 80\%$ it would be necessary to include kernels of higher order to give a perfect fit. Figure 3 shows a case in which the input consists of two sinusoids with a maximum modulation of 60%. Figure 4 shows the same comparison for an input consisting of an approximated square wave, containing the first four Fourier components of an ideal square wave.

For a modulation of the fundamental harmonic of 67% the Volterra approximation is still satisfactory (Fig. 4a). When the modulation increases to 104% the fit is poor but the series appears to converge almost everywhere (Fig. 4b). Observe that in this case the threshold m_c was decreased from $m_c = 1$ (Fig. 4a) to $m_c = 0.26$: as a consequence the average interspike interval T_0 decreases $\left(T_0 = \frac{m_c}{x_0}\right)$ and the convergence radius [see (30)] increases.

The derivation of the formulae obtained in this section can be extended to more sophisticated models. Appendix 1 outlines the derivation of a Volterra representation, that takes into account a decaying threshold, an absolute refractory period and the case γT_1 not small.

4. Population or Density Rate

In Section 3 we derived the kernels B_n of the perfect integrator and the kernels F_n of the leaky integrator. In this section we will deal with the problem of the transduction from "single unit rate" $T(t)$ to the population rate $r(t)$, for the two types of neuron models. The relation between the firing rate of the population $r(t)$ and the single unit's rate is, according to Knight (1972):

$$N = \int_{t-T(t)}^{t} dt'(p_0 + p(t')) \tag{31}$$

where p_0 is the steady population rate.

As we mentioned earlier, the mapping $p(t) \to T(t)$ with $T_0 + T_1(t) = T(t)$ is not bijective and therefore the inverse mapping $T_1(t) \to p(t)$ does not exist in general. Equation (31) does not determine $p(t)$ uniquely for a given $T(t)$. For instance, in the simple case $T(t) = T_0$ ($T_1 \equiv 0$), (31) *provides the solution*

$$r(t) = p_0 + f(t), \tag{32}$$

where $p_0 = \frac{N}{T_0}$ and $f(t)$ can be *any* function which integrates to zero over the period T_0. As the mapping $T_1 \to p_1$ is not uniquely determined by (31), the inverse of the linear kernel of the mapping $p_1 \to T_1$ does not exist bounded everyhwere. The Fourier transform

$$P_1(\omega) = B_1^{-1} = \frac{p_0 \omega}{1 - e^{-j\omega N/p_0}} \tag{33}$$

becomes infinite for ω such that

$$\frac{\omega N}{p_0} = 2\pi n \qquad n = 0, 1, 2, \ldots . \tag{34}$$

The usual theorems (Halme et al., 1971) that ensure the invertibility of a polynomial mapping (and therefore the applicability of the formulae of Appendix 2) require that the inverse of the linear kernel exists. Thus, these theorems cannot be applied to the mapping $p_1 \to T_1$ if domain and range W are "normal" spaces. One could try to restrict V and W suitably, excluding in the range W the zero outputs of the linear mapping $p_1 \to T_1$ induced by B_1, since then the inverse p_1 would exist bounded. This is, however, a very strong restriction on V depending on the order of the polynomial mapping. If the mapping is linear, exclusion of the zero frequency vectors of the mapping (and small neighbourhoods) implies the same exclusion on V. If the mapping is quadratic, V must be restricted to the space of those input vectors with Fourier transform $X(\omega)$ such that $X(\omega) \equiv 0$ for $\omega \geqq \frac{\pi}{T_0}$. If the order of the polynomial mapping, approximating B, is n, the conditon $X(\omega) \equiv 0$ must hold for $(\omega) \geqq \frac{\pi}{nT_0}$. Thus, the complete Volterra representation of the mapping $r_1 \to T_1$, being an infinite series, cannot be inverted for a non empty input space V. This is also clear since the Brilliant formulae yield a Volterra series with poles at all rational values of $\frac{\omega T_0}{\pi}$, if the input is $\sin \omega t$. Composition of the integrate-and-fire law with the mapping defined by the kernels P_n formally obtained with the formulae of Appendix 2, yields (but only for this encoding law) the correct answer:

$$[P*G]_1(\omega) = \frac{r_0}{x_0}, \; [P*G]_n(\omega_1, \ldots, \omega_n) \equiv 0 \quad n \geqq 2 . \tag{35}$$

The population rate, defined as the number of active neurons at each instant in a population of N integrate-and-fire neurons (with homogeneous distributions of their "integrated potential"), is a perfect copy of the stimulus. This result can be obtained with independent arguments and is not based on definition (31) (see Knight, 1972a). Knight maintains that the resonant poles of the linear kernel $P_1(\omega)$ disappear if intrinsic variability of the encoding process is taken into account. Simple arguments of this type, however, seem insufficient. Let us assume that T_0, which parametrizes the mapping $p_1 \to T_1$, is distributed according to the probability distribution $Q(T_0)$, because, for instance, m_c is a random variable. The ensemble average of the Volterra representation of the mapping can be easily derived as

$$\langle B_1 \rangle = \frac{1 - \langle e^{-j\omega T_0} \rangle}{p_0 \omega}$$

$$\langle B_2 \rangle = \frac{1}{p_0^2} \operatorname{sym} \left\{ \frac{\langle e^{-j\omega_1 T_0} \rangle - \langle e^{-j(\omega_1 + \omega_2) T_0} \rangle}{j\omega_2} \right\} \ldots , \tag{36}$$

where

$$\langle e^{-j\omega T_0} \rangle = \int_{-\infty}^{+\infty} Q(T_0) e^{-j\omega_0} dT_0 .$$

This "average" polynomial representation is now bijective and can be inverted. Since $|\langle e^{-j\omega T_0} \rangle| < 1$, $\langle P_1 \rangle = \langle B_1 \rangle^{-1}$ exists and the inverse theorem applies. Since, however, the inverse of the average of a mapping can be different from the average of the inverse mapping, the physical meaning of the mapping associated to $\langle P_n \rangle$ is not clear.

5. Stochastic Inputs

In principle, a Volterra representation like (20) represents a canonical method for dealing with a large variety of stochastic inputs, whereas probabilistic approaches to stochastic models of neurons [for instance, Gernstein and Mandelbrot (1964); Johannesma (1969); Capocelli and Ricciardi (1971)] give solutions only for specific inputs, and extensions to slightly different inputs usually represent completely new and difficult problems. In practice, however, the Volterra formulae are infinite series in which the labor of computing the nth term increases rapidly as n increases. Even with the relatively simple kernels of the integrate-and-fire, the computation of terms of order higher than the second or the third, although straightforward, becomes very time consuming. Algebraic manipulation programs of the type already existing [possibly exploiting reduction techniques of the Laplace type, see Crum and Heinen (1974)] could overcome this difficulty. Bedrosian and Rice (1971) have provided various useful "Volterra" formulae for stochastic inputs. Additional ones can be often derived in a straightforward way. Appendix 3 outlines a few examples.

6. Discussion

This paper is intended to serve two main purposes. Firstly, the Volterra representation of the forgetful integrate-and-fire neuron model provides the nonlinear transfer function for the neuronal encoding process. Experimental data, in which nonlinearities are not negligible, can be treated in terms of our approach, and

References

Ascoli,C., Barbi,M., Frediani,C., Ghelardini,G., Petracchi,D.: Rectification and spike synchronization in the Limulus lateral eye. Kybernetik **14**, 153 (1974)

Barlow,R.B., Lange,G.D.: A nonlinearity in the inhibitory interactions in the lateral eye of *Limulus*. J. gen. Physiol. **63**, 579 (1974)

Bedrosian,E., Rice,S.O.: The output properties of Volterra systems driven by harmonic and gaussian inputs. Proc. IEEE **59**, 1688 (1971)

Borsellino,A., Poppele,R.E., Terzuolo,C.A.: Transfer functions of the slowly adapting stretch receptor organ of Crustacea. Cold Spring Harbour Symp. Quant. Biol. **30**, 581 (1965)

Brilliant,M.B.: Theory of the analysis of nonlinear systems. Res. Lab. El. M.I.T. Rep. 345 (1958)

Büttner,C., Büttner,U., Grüsser,O.J.: Interaction of excitation and direct inhibition in the receptive field center of retinal neurons. Pflügers Arch. **322**, 1 (1971)

Capocelli,R.M., Ricciardi,L.M.: Diffusion approximation and first passage time problem for a model neuron. Kybernetik **8**, 241 (1971)

Chaplain,R.A.: Small-signal analysis of the encoder mechanism in the lobster stretch receptor and the frog and cat muscle spindle. Biol. Cybernetics **17**, 1 (1975)

Coenen,R., Chaplain,R.A.: Systems analysis of biological receptors. The transfer characteristics of the frog muscle spindle. Kybernetik **13**, 183 (1974)

Comtet,L.: Advanced combinatories. Dortrecht: Reidel,D. 1974

Copson,E.T.: An introduction to the theory of functions of a complex variable. Oxford: Clarendon Press 1935

Crum,L.A., Heinen,J.A.: Simultaneous reduction and expansion of multidimensional Laplace transform kernels. SIAM J. appl. Math. **26**, 4 (1974)

De Santis,R.M., Porter,W.A.: On the analysis of feedback systems with a polynomic plant. Int. J. Control **21**, 159 (1975)

Frankenhauser,B., Hodgkin,A.: The action of calcium on the Electrical properties of squid axons. J. Physiol. **137**, 218—244 (1957)

Gernstein,G.L., Mandelbrot,B.: Random walk models for the spike activity of a single neuron. Biophys. J. **4**, 41 (1964)

Goursat,E.: Course d'Analyse. Paris: Gauthier-Villars 1918

van de Grind,W.A., Grüsser,O.J., Lunkenheimer,H.U.: Temporal transfer properties of the afferent visual system. Handbook of Sensory Physiol. VII/3A, pp. 431. Berlin-Heidelberg-New York: Springer 1973

Halme,A., Orava,J., Blomberg,H.: Polynomial operators in nonlinear systems theory. Int. J. Systems. Sci. **2**, 25 (1971)

Hochstein,S., Shapley,R.M.: Linear and nonlinear spatial subunits in *Y* cat retinal ganglion cells. J. Physiol. **262**, 265—284 (1976)

Hodgkin,A.L., Huxley,A.F.: A quantitative description of membrane current and its application to conduction and excitation in nerve. J. Physiol. **117**, 500 (1952)

Holden,A.V.: The response of excitable membrane models to a cyclic input. Biol. Cybernetics **21**, 1 (1976)

Kirkwood,R.A.: The frequency response of a frog muscle spindle under various condition. J. Physiol. **222**, 135 (1972)

Knight,B.W.: Dynamics of encoding in a population of neurons. J. gen. Physiol. **59**, 734 (1972a)

Knight,B.W.: The relationship between the firing rate of a single neuron and the level of activity in a population of neurons. J. gen. Physiol. **59**, 767 (1972b)

Knight,B.W.: Some questions concerning the encoding dynamics of neuron populations. In: Symposial Papers of the International Biophysics Congress, Moscow (1973)

Knight,B.W.: The horseshoe crab eye: a little nervous system that is solvable. In: Lectures on Mathematics in the Life Sciences. 5. Some Mathematical Questions in Biology. J.D.Cowan, ed. Am. Math. Soc. Providence, R.I. (1976)

Johannesma,P.I.M.: Diffusion models for the stochastic activity of neurons. In: Neural Networks, Caianiello,E.R., ed. Berlin-Heidelberg-New York: Springer 1969

Lagrange,J.L.: Nouvelle methode pour résoudre les équations littérales par le moyen des series. Mem. Ac. Berlin XXIV, p. 25 (1770)

McAllister,R.E., Noble,D.S., Tsien,R.W.: Reconstruction of the electrical activity of cardiac Purkinje fibres. J. Physiol. **251**, 1—60 (1975)

McCullogh,W.S., Pitts,W.H.: A logical calculus of ideas immanent in nervous activity. Bull. Math. Biophys. **5**, 115—133 (1943)

Melvill Jones,G., Milsum,J.H.: Characteristics of neural transmission from the semicircular canal to the vestibular nuclei of cats. J. Physiol. **209**, 295 (1970)

Palm,G., Poggio,T.: The Volterra representation and the Wiener expansion: validity and pitfalls. SIAM J. appl. Math. **33**, 2 (1977)

Poggio,T.: Stochastic linearization, central limit theorem and linearity in (nervous) black boxes. I: Atti del II Congresso Nazionale di Cibernetica e Biofisica, S. Marino 3—5 Ottobre 1974, Pisa, 349 (1975)

Poggio,T., Reichardt,W.: Considerations on models of movement detection. Kybernetik **13**, 223 (1973)

Poggio,T., Reichardt,W.: Visual control of orientation behaviour in the fly. Part II. Quart. Rev. Biophys. **9**, 3, 67 (1976)

Poggio,T., Torre,V.: A nonlinear transfer function for some neuron models. In: Proc. of the I. Symp. on Testing and Identification of Nonlinear Systems. McCann,G.D., Marmarelis,P.Z., eds. Pasadena (1975)

Rescigno,A.R., Stein,R.B., Purple,R.L., Poppele,R.E.: A neuronal model for the discharge patterns produced by cyclic inputs. Bull. Math. Biophys. **32**, 337 (1970)

Poppele,R.E., Chen,W.J.: Repetitive firing behaviour of mammalian muscle spindle. J. Neurophysiol. **35**, 357 (1972)

Redman,S.J.: A quantitative approach to integrative function of dendrites. Int. Rev. Physiol., Neurophys. Vol. 10, Porter,R., ed. Baltimore: University Park Press 1976

Schmitt,F.O., Parvati,Dev., Smith,B.H.: Processing of information by brain cells. Science **193**, 114—120 (1976)

Shapley,R.: Fluctuations of the impulse rate in *Limulus* eccentric cells. J. gen. Physiol. **57**, 539 (1971)

Spekreijse,H.: Rectification in the goldfish retina: analysis by sinusoidal and auxiliary stimulation. Vision. Res. **9**, 1461 (1969)

Stein,R.B.: The role of spike trains in transmitting and distorting sensory signals. In: The Neurosciences, Second Study Program, pp. 597. Schnitt,F.O., ed. New York: Rockefeller University Press 1970

Stein,R.B., French,A.S., Holden,A.V.: The frequency response coherence and information capacity of two neuronal models. Biophys. J. **12**, 295 (1972)

Terzuolo,C.A., Knox,C.K.: Static and dynamic behaviour of the slowly adapting stretch receptor organ of Crustacea. In: Handbook of Sensory Physiology Vol. 1, pp. 500. Berlin-Heidelberg-New York: Springer 1971

Victor,J.D., Shapley,R.M., Knight,B.W.: Nonlinear analysis of cat retinal ganglion cells in the frequency domain. Preprint (1977)

Received: 19 May 1977

Dr. T. Poggio
MPI für biolog. Kybernetik
Spemannstr. 38
D-7400 Tübingen
Federal Republic of Germany

Verantwortlich für den Textteil: Prof. Dr. W. Reichardt, Max-Planck-Institut für biologische Kybernetik, Spemannstr. 38, D-7400 Tübingen. Verantwortlich für den Anzeigenteil: L. Siegel, G. Sternberg, Springer-Verlag, Kurfürstendamm 237, D-1000 Berlin 15, Fernsprecher: (030) 8821031, Telex: 01-85411. Springer-Verlag, Berlin · Heidelberg · New York. Druck der Brühlschen Universitätsdruckerei, Lahn-Gießen. Printed in Germany.