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The Volterra-Wiener approach in neuronal modeling

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***Abstract*— Systems identification is being used increasingly in quantitative neurophysiology, including the auditory, visual and somatosensory systems. In this context, the Volterra-Wiener approach, which is an important branch of nonlinear systems identification, has met with considerable success in neuronal systems modeling, as these systems often exhibit complex nonlinear behavior. The Volterra-Wiener approach provides a comprehensive data-driven framework that does not place any a priori assumptions on the system structure. Therefore, it can approximate highly complex nonlinear mappings provided that experimental protocols are carefully designed in order to meet the requirements of the corresponding estimation procedure. In the present paper, we present a brief overview of Volterra-Wiener models and methodologies for their estimation as they relate to modeling neuronal systems. We also examine a specific example from a mechanoreceptor system.**

Index Terms: Systems neuroscience, nonlinear models, systems identification

I. INTRODUCTION

Quantitative neurophysiology, particularly sensory neurophysiology, has relied on the use of systems identification techniques in order to examine and predict the function of neurons in an accurate, quantitative manner [1]. The aim of systems identification is to estimate mathematical descriptions of a system (models) that are typically causal and dynamic, whereby the output depends on present and past input values, from experimental input/output observations. The identification of nonlinear systems, which corresponds to the class of systems that do not obey the principle of superposition, is of particular interest for physiological systems and neuronal systems in particular, as these systems often exhibit nonlinear characteristics. For instance, the neural encoding of stimuli into action potentials is a strongly nonlinear phenomenon, whereas interaction between neuronal stimuli in the form of facilitation or inhibition is typical of systems that do not obey the principle of superposition. As a simple example that illustrates this last case, consider the case of Fig. (1) where we show typical examples of the response of a linear and a nonlinear system to a pair of impulsive stimuli. In the case of a linear system, the principle of superposition holds, whereas in the second case the response to the second stimulus is influenced by the preceding stimulus and is either increased (facilitation) or decreased (inhibition) compared to when the stimuli are presented individually.

Applications of nonlinear systems identification to neuronal systems have included the visual, auditory and somatosensory systems (for reviews see [1], [2], [3], [4], for recent applications see [5], [6], [7], [8]), as well as memory

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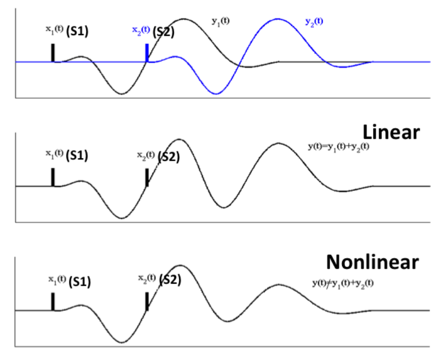

Fig. 1. Schematic representation of the output of a linear and a nonlinear system to two successive impulsive-like stimuli. When applied separately, the two stimuli $x_1(t)$ and $x_2(t)$ elicit the output waveforms $y_1(t)$ and $y_2(t)$ respectively (top panel). When the two stimuli are applied simultaneously, the total output of a linear system is simply the addition between $y_1(t)$ and $y_2(t)$ (middle panel). On the other hand, the output of a nonlinear system is not equal to $y_1(t) + y_2(t)$ (bottom panel).

function [9]. The Volterra-Wiener approach is a general framework that represents the dynamic characteristics of a nonlinear system in the form of a hierarchy of kernel functions without any a priori assumptions about its structure (i.e., it views the system as a "black-box"). Therefore, it provides a comprehensive quantitative description of its function in a general context, as Volterra/Wiener models may approximate any causal dynamic system with finite memory. As a result, this approach has been used in systems neuroscience and with more efficient estimation methods being developed, computational power increasing and experimental procedures being refined, it presents an attractive alternative for studying neural systems. Here, we present an overview of Volterra-Wiener models as they relate to neuronal systems, as well as recent results from an insect mechanoreceptor [6].

II. VOLTERRA-WIENER MODELS

Volterra models may be viewed as a generalization of the convolution sum or as an extension of the multivariate Taylor expansion to vectors of infinite dimension (in this case, continuous time signals). They relate the input and the output of a nonlinear causal system as follows [10]:

$$\begin{aligned} y(t) = & \sum_{q=0}^{Q} \int_0^\infty \dots \int_0^\infty k_q(\tau_1, \dots, \tau_q) \\ & x(t-\tau_1) \dots x(t-\tau_q) d\tau_1 \dots d\tau_q \\ = & k_0 + \int_0^\infty k_1(\tau) x(t-\tau) d\tau + \\ & \int_0^\infty \int_0^\infty k_2(\tau_1, \tau_2) x(t-\tau_1) x(t-\tau_2) d\tau_1 d\tau_2 + \dots \end{aligned} \quad (1)$$

where $x(t)$ is the system input, $y(t)$ is the system output and k_q denotes the q-th order Volterra kernel of the system. The Volterra kernels describe the linear ($q = 1$) and nonlinear ($q > 1$) dynamic effects of the input on the output. Specifically, the linear kernel $k_1(\tau)$ operates on the system input in a similar manner to the impulse response of a linear system, quantifying the effect of past input values on the present output value at t, while the nonlinear kernels quantify the effect of q-th order products between past input values on the output at present. For finite memory systems the integrals in (1) are defined from 0 to M, where M is the system memory. For instance, the operation of the first- and second-order Volterra kernels is visualized in Fig. (2).

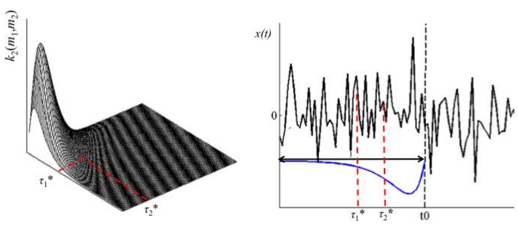

Fig. 2. Operational interpretation of the function of the first- and second-order kernels in a Volterra model. Left panel: A typical second-order kernel. Right panel: the value of k_2 at (m_1^*, m_2^*) quantifies the effect of past input values m_1^*, m_2^* before the "present" time lag t_0 on the value of the output $y(t_0)$. All these effects are integrated to yield the total second-order kernel effect. The linear kernel (blue) operates in a similar manner to a linear system impulse response, i.e. it weighs the effect of past input values on the present output value.

In the context of a neurophysiological experiment, the input $x(t)$ is typically a neuronal stimulus, e.g. a sensory stimulus, and the output $y(t)$ is a measure of the resulting response, such as action potential occurrences, spike counts, membrane potential, local field potential or instantaneous firing rate [1], depending on the type of the neuronal system and the experimental setup. Depending on these, the input and/or output may be graded or binary signals; therefore, the formulation and/or estimation of the Volterra-Wiener should be made accordingly. For example, in [**?**] the Volterra model is formulated in a point-process context such that kernels depend on the timing between binary events (Poisson-Volterra model). An example of the Volterra formulation for a mechanoreceptor system with graded input (displacement) and binary output (action potential events) is given below [6]. In discrete-time, the Volterra model may be written as [10]:

$$y(n) = k_0 + \sum_m k_1(m)x(n-m) + \sum_{m_1}\sum_{m_2} k_2(m_1, m_2)x(n-m_1)x(n-m_2) \quad (2)$$

The Wiener series is an alternative representation for nonlinear systems that is related to the Volterra series representation [11]. Wiener suggested orthogonalization of the Volterra series by a Gram-Schmidt procedure, which orthogonalizes the Volterra functionals of different orders for a Gaussian White noise (GWN) input. The resulting Wiener series take the form:

$$\begin{aligned} y(t) &= \sum_{n=0}^{\infty} G_n[h_n; x(t'), t' \leq t] \\ &= \sum_{q=0}^{\infty}\sum_{m=0}^{[n/2]} \frac{(-1)^n n! P^n}{(n-2m)!m!2^m} \int_0^\infty \dots \int_0^\infty \\ &\quad h_n(\tau_1, \dots, \tau_{n-2m}, \lambda_1, \lambda_1, \dots, \lambda_m, \lambda_m) \\ &\quad x(t-\tau_1)\dots x(t-\tau_{n-2m})d\tau_1 \dots d\tau_{n-2m} d\lambda_1 \dots d\lambda_m \quad (3) \end{aligned}$$

where P is the power level of the GWN input signal and h_n is the n-th order Wiener kernel. Note that the Wiener kernels are not equal to the Volterra kernels; whereas the latter do not depend on the input power, the former do.

III. Estimation of Volterra-Wiener models

In order to estimate the Volterra kernels using input-output measurements, Wiener suggested the use of Gaussian White Noise (GWN) as an effective test stimulus [11]. GWN exhibits frequency content over the entire frequency range, therefore it probes the enire dynamic range of any system. Pseudorandom (quasi-white) stimuli have therefore been widely used in quantitative neurophysiology in order to achieve efficient estimation of nonlinear neuronal models [2], [3], [1], [4].

Among the many methods that have been proposed for Volterra-Wiener model identification [12], [10], one of the first methods that found applicability in neuronal models (e.g. in [13]) is the cross-correlation approach proposed in [14]. According to this method, the Wiener kernels of a system excited with GWN are obtained as expected values of the output and the first and higher order cross-correlations between the input and output signals, i.e.:

$$\begin{aligned} \hat{h}_0 &= E[y(t)] \\ \hat{h}_1(\tau) &= (1/P)E[y(t)x(t-\tau] \\ \hat{h}_2(\tau_1, \tau_2) &= (1/2P^2)E[y_2(t)x(t-\tau_1)x(t-\tau_2)] \quad (4) \end{aligned}$$

where $y_2(t) = y(t) - \hat{h}_0 - \int_0^\infty \hat{h}_1(\tau)x(t-\tau)d\tau$ corresponds to the second-order residuals. This method requires long data records in order to achieve good estimates and it is also influenced by noise. Therefore, improvements such as the fast orthogonal search algorithm [12] have also been used.

One of the major issues in nonlinear systems identification is the number of required free parameters. For a Q-th order system with a memory of M, the least squares formulation of the Volterra series requires the estimation of Q^M parameters, which becomes very large for high order systems with large memory. One way to reduce this number is to express the Volterra kernels in terms of the Laguerre discrete-time basis as shown below for the first and second-order kernels:

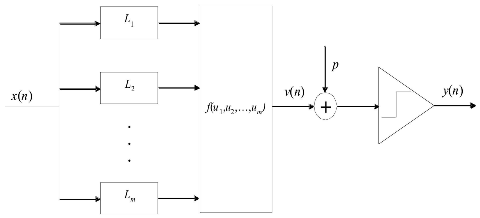

Fig. 3. Wiener-Bose model of a spider mechanoreceptor.

$$k_1(m) = \sum_{j=0}^{L} c_j b_j(m)$$

$$k_2(m_1, m_2) = \sum_{j_1=0}^{L} \sum_{j_2=0}^{L} c_{j_1 j_2} b_{j_2}(m_1) b_{j_2}(m_2) \tag{5}$$

In matrix form this representation can be written as:

$$\mathbf{y} = \mathbf{V}\mathbf{c} + \epsilon, \tag{6}$$

where $\mathbf{y}$ is the vector of output observations, $\mathbf{V}$ is a matrix containing the convolution of the input with the Laguerre functions $v_j = x * b_j$ and higher-order products between them $v_{j_1} v_{j_2} \ldots v_{j_Q}$ and $\mathbf{c}$ is the vector of the unknown expansion coefficients. The number of free parameters in this formulation is L^Q and, since typically $L << M$, it is reduced considerably. The least-squares estimate of $\mathbf{c}$ is given by [15]:

$$\hat{\mathbf{c}}_{LS} = (\mathbf{V}^T\mathbf{V})^{-1}\mathbf{V}^T\mathbf{y}. \tag{7}$$

One way to extract the most important components of the Volterra kernels is to perform singular value decomposition of the matrix consisting of the linear and nonlinear kernels and selecting the singular vectors that correspond to the most significant singular values [16]. These constitute a minimum set of linear filters followed by a static nonlinearity (Wiener-Bose model). In this way, one may obtain representations that are possibly more amenable to physiological interpretation. Results from this approach applied to a mechanoreceptor system are presented in the next section.

IV. Example: Mechanoreceptor System

In order to illustrate some of the concepts outlined above, we present an application of the Volterra-Wiener framework to the study of a sensory (mechanoreceptor) system. Specifically, we studied the encoding of mechanical displacements into action potentials in two types of spider mechanoreceptors by using a Wiener-Bose model, shown in Fig. (3) and the Laguerre expansion of kernels [6]. The stimulus was pseudorandom displacements (graded) whereas the output was the recorded output potentials (binary). Since the output is binary, the output of the static nonlinearity $f(u_1, u_2, ..., u_M)$, which maps the values of the convolutions of the input with the linear filters to the occurrence of action potentials, is compared to a threshold p.

The first and second order kernels, obtained by the Laguerre expansion technique from the displacement/output action potential data, are shown in Fig. (4). Singular value decomposition of the matrix containing the first and second-order kernels revealed three significant singular values in this case and the corresponding singular vectors yielded the impulse responses of the linear filters $\mu_1, \mu_2 and \mu_3$, shown in Fig. (4) in the time and frequency domains (termed the principal dynamic modes of the system - PDMs). The first (most significant) singular vector has a high-pass (differentiating) characteristic, suggesting that its output depends primarily on the displacement velocity and secondarily on the displacement magnitude. The second filter has a band-pass characteristic with a peak at around 180 Hz and a high-frequency plateau, implying dependence on the magnitude of displacement (position) in addition to the resonant behavior around 180 Hz. The third filter has a low-pass characteristic that implies dependence only on the integrated (cumulative) displacement/position over a 6 ms time-window.

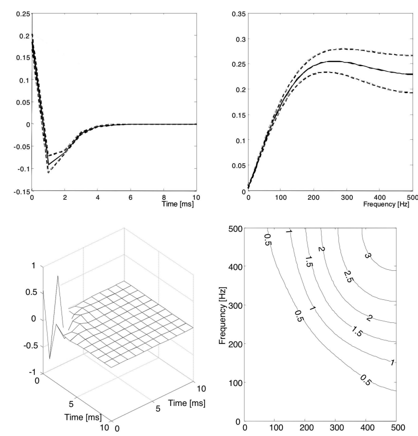

Fig. 4. First and second-order Volterra kernels of mechanoreceptor neuron

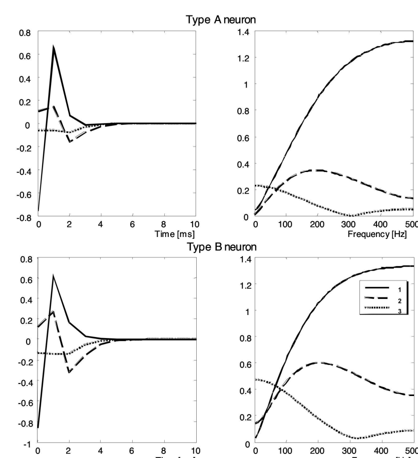

Fig. 5. Principal Dynamic Modes for one Type A and one Type B mechanoreceptor neuron (time and frequency domain). The first, second and third PDM exhibit high-pass, band-pass and low-pass characteristics respectively.

The combinations of PDM output values that gave rise to action potentials at the mechanoreceptor output are shown in the three-dimensional scatter plot of Fig. (6), where the PDM output values that corresponded to action potentials are shown in blue, while those that did not are shown in red. The construction of the three-input static nonlinear function $f(u_1, u_2, ..., u_M)$ was obtained by three-dimensional histogramming, yielding the probability of firing for the mechanoreceptor neuron. The one-dimensional marginal probabilities $p(u_1),\ p(u_2),\ p(u_3)$ are shown in Fig. (7) In general, these marginal projections are asymmetric with respect to their arguments. The predictive capability of these models were found to be very good, with most output action potentials being predicted correctly both for training and validation data. The total performance was assessed by constructing ROC curves by varying the threshold p between zero and one [6].

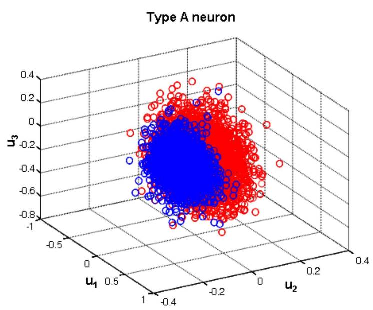

Fig. 6. Scatter plot of the PDM output values that correspond to action potentials (blue) for a mechanoreceptor neuron.

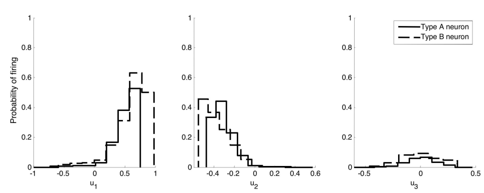

Fig. 7. One-dimensional marginal probability of firing functions obtained from the three-dimensional static nonlinearity $f(u_1, u_2, u_3)$.

V. DISCUSSION

Volterra-Wiener models have been used extensively in physiological systems modeling, including several applications to neuronal systems. They provide a complete characterization of the system of interest without placing any a priori assumptions on system structure, i.e. they are data-driven, and they can be used to approximate mappings of any given complexity. As shown above, they can be expressed in equivalent forms that are amenable to interpretation - it was found that mechanoreceptors can encode several different properties of a mechanical stimulus (velocity, position, cumulative position). On the other hand, one should be careful regarding the chosen estimation method, as the number of free parameters may increase exponentially for high-order systems, requiring very large amounts of experimental data. Moreover, the accurate estimation of these models requires rich, broadband stimuli that excite the system over a wide range of frequencies. Therefore, particular care should be taken in the experimental design. However, with the increased computational power that is available and the improved estimation and experimental methods, the Volterra-Wiener approach provides a comprehensive framework in order to study neuronal function, which is typically characterized by complex and nonlinear behavior - particularly in the central nervous system. Some recent applications of the Volterra-Wiener theory have included the study of hippocampal neurons [9], the study of nonlinear interactions in the spectrotemporal receptive fields of the primary auditory cortex [8] and the study of visual cell responses to natural images [5].

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