Implementing Spiking Neuron Model and Spike-Timing-Dependent Plasticity with Generalized Laguerre-Volterra Models

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Abstract—**To perform large-scale simulations of the brain or build biologically-inspired cognitive architectures, it is essential to have a succinct and flexible model of spiking neurons. The model should be able to capture the nonlinear dynamical properties of various types of neurons and the nonstationary properties such as the spike-timing-dependent plasticity (STDP). In this paper, we propose a generalized Laguerre-Volterra modeling approach for such a task. Due to its built-in nonlinear dynamical terms, the generalized Laguerre-Volterra model (GLVM) can capture various biological processes/mechanisms. Using Laguerre expansion of Volterra kernel technique, the model is fully represented with a small set of coefficients. The calculation of the model variables can be expressed recursively based on only the current and the one-step-before values and thus can be performed efficiently. In addition, we show that, using the same methodology, STDP can be implemented as a specific form of second-order Volterra kernel describing the causal relationship between pairs of input-output spikes and the changes of the feedforward kernels in the GLVMs.**

I. Introduction

LARGE-SCALE simulation of the brain and biologically-inspired cognitive architecture have become two of the most active and promising fields of computational neuroscience and neural engineering. Consistent with the "neuron doctrine" of Ramon y Cajal, their applications often involve building large-scale networks of spiking neuron models to (a) emulate the emergent population-level behaviors of the brain, or (b) mimic the higher-order cognitive functions to solve real life problems.

A successful spiking neuron model should keep a good balance between the biological realism and the computational efficiency. The former is required for biological interpretation and validation since it is elucidative to be able to relate the model variables to the observable biological processes/mechanisms. In addition, the biological processes/mechanisms are likely to be the indispensable components for achieving real brain-like functions, and thus have to be included into the model. On the other hand, the computational efficiency, obviously, is necessary for practical software/hardware implementations of the model. Furthermore, a succinct representation of neurons may also facilitate biological interpretations since it highlights the functional properties of the neuron.

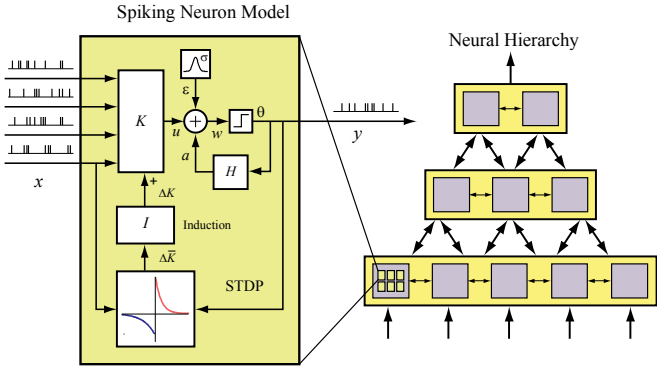

Figure 1. Spike neuron model with spike-timing-dependent plasticity as computational unit of a biologically-inspired cognitive architecture

In this study, we propose a generalized Laguerre-Volterra modeling approach for building spike neuron models for both large-scale simulations and biologically-inspired cognitive architectures. In our previous works [1, 2, 3], generalized Laguerre-Volterra model (GLVM) has been intensively used in (a) the identification of neural functional connectivities, and (b) the development of hippocampal memory prostheses. Due to its built-in nonlinear dynamical terms, a GLVM can capture accurately various biological processes/mechanisms such as post-synaptic potential (PSP), paired-pulse facilitation/depression, augmentation, spike generation, and output spike-triggered after-potential (AP), with a small set of model coefficients resulted from Laguerre expansion of the Volterra kernels. In addition, we extend the GLVM to include spike-timing-dependent plasticity (STDP) as a specific form of second-order Volterra kernel modeling the causal relationship between pairs of input-output spikes and the changes of the feedforward kernels in the GVMs. All model calculation can be performed efficiently in a recursive manner.

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978-1-4244-7929-0/14/$26.00 ©2014 IEEE

II. METHODOLOGY

A. Spiking neuron model

The spiking neuron model has a physiologically plausible structure (Fig. 1, left) that can be expressed as:

$$w = u(k,x) + a(h,y) + \varepsilon(\sigma), \quad y = \begin{cases} 0 & \text{when } w < \theta \\ 1 & \text{when } w \geq \theta \end{cases}$$

The variable x represents input spike trains; y represents output spike train; w represents the pre-threshold membrane potential of the output neurons, that is expressed as the summation of the post-synaptic potential u caused by input spike trains, the output spike-triggered after-potential a, and a Gaussian white noise ε with standard deviation σ. A threshold, θ, determines the generation of the output spike and the associated feedback after-potential (a). In this mode, the transformation from x to u is described as a set of feedforward Volterra kernels k. The transformation from y to a is described by a feedback Volterra kernel h.

$$\begin{aligned} u(t) &= k_0 + \sum_{n=1}^{N}\sum_{\tau=0}^{M_k} k_1^{(n)}(\tau)x_n(t-\tau) \\ &+ \sum_{n=1}^{N}\sum_{\tau_1=0}^{M_k}\sum_{\tau_2=0}^{M_k} k_{2s}^{(n)}(\tau_1,\tau_2)x_n(t-\tau_1)x_n(t-\tau_2) \\ &+ \sum_{n_1=1}^{N}\sum_{n_2=1}^{n_1-1}\sum_{\tau_1=0}^{M_k}\sum_{\tau_2=0}^{M_k} k_{2x}^{(n_1,n_2)}(\tau_1,\tau_2)x_{n_1}(t-\tau_1)x_{n_2}(t-\tau_2) \\ &+ \ldots \\ a(t) &= \sum_{\tau=1}^{M_h} h(\tau)y(t-\tau) \end{aligned}$$

First order kernel k_1 can be interpreted as the PSP elicited by a single input spike; second order self-kernel k_{2s} can be interpreted as the paired-pulse facilitation/depression function. Second order cross-kernels k_{2x} describe the pair-wise nonlinear interactions between each unique pair of inputs as they affect u. The feedforward kernels provide a quantification of the synaptic strength between the input neurons and the output neuron.

To reduce number of parameters and avoid overfitting, Laguerre basis functions b are utilized in model estimations.

$$b_j(\tau) = \begin{cases} \alpha^{(j-\tau)/2}(1-\alpha)^{1/2}\sum_{k=0}^{\tau}(-1)^k\binom{\tau}{k}\binom{j}{k}\alpha^{\tau-k}(1-\alpha)^k \\ \qquad (0 \leq \tau < j) \\ \alpha^{(\tau-j)/2}(1-\alpha)^{1/2}\sum_{k=0}^{j}(-1)^k\binom{\tau}{k}\binom{j}{k}\alpha^{j-k}(1-\alpha)^k \\ \qquad (j \leq \tau \leq M) \end{cases}$$

Laguerre parameter α controls the rate of exponential decay of the basis functions. The larger α is, the slower b decay. With input and output spike trains x and y convolved with b:

$$v_j^{(n)}(t) = \sum_{\tau=0}^{M_k} b_j(\tau)x_n(t-\tau) \ , \ v_j^{(h)}(t) = \sum_{\tau=1}^{M_h} b_j(\tau)y(t-\tau)$$

u and a can be rewritten into:

$$\begin{aligned} u(t) &= c_0 + \sum_{n=1}^{N}\sum_{j=1}^{J} c_1^{(n)}(j)v_j^{(n)}(t) \\ &+ \sum_{n=1}^{N}\sum_{j_1=1}^{J}\sum_{j_2=1}^{j_1} c_{2s}^{(n)}(j_1,j_2)v_{j_1}^{(n)}(t)v_{j_2}^{(n)}(t) \\ &+ \sum_{n_1=1}^{N}\sum_{n_2=1}^{n_1-1}\sum_{j_1=1}^{J}\sum_{j_2=1}^{J} c_{2x}^{(n_1,n_2)}(j_1,j_2)v_{j_1}^{(n)}(t)v_{j_2}^{(n)}(t) + \ldots \\ a(t) &= \sum_{j=1}^{J} c_h(j)v_j^{(h)}(t) \end{aligned}$$

c are the kernel coefficients. Given the kernels are smooth and continuous functions, the number of basis functions J can be much smaller than the memory length (M_k and M_h). Since v and vv can be calculated from the known x, y and b. The Volterra series essentially expresses the nonlinear relationship between u and x into a linear relationship between u and [v, vv]. The joint effect of the threshold θ and the Gaussian noise ε is equivalent to a *probit* link function that maps the value of $u + a$ into the probability of y is equal to 1. The whole model thus can be expressed as a generalized linear model with the nonlinearity structured in the Volterra series. Therefore, this MISO model can be termed as a generalized Laguerre-Volterra model (GLVM).

The kernels quantitatively describe the input-output nonlinear dynamics of the neuron. A more intuitive representation is the single-pulse and paired-pulse response functions (r_1 and r_2) derived from the kernels.

$$r_1^{(n)}(\tau) = k_1^{(n)}(\tau) + k_{2s}^{(n)}(\tau,\tau)$$

$$r_{2s}^{(n)}(\tau_1,\tau_2) = 2k_{2s}^{(n)}(\tau_1,\tau_2)$$

$$r_{2x}^{(n_1,n_2)}(\tau_1,\tau_2) = k_{2x}^{(n_1,n_2)}(\tau_1,\tau_2)$$

$r_1^{(n)}$ is essentially the postsynaptic potential (PSP) elicited by a single spike from the n^{th} input neuron; $r_2^{(n)}$ describes the joint nonlinear effect of pairs of spikes from the n^{th} input neuron in addition to the summation of their first order responses, i.e., $r_1^{(n)}(\tau_1) + r_1^{(n)}(\tau_2)$. $r_{2x}^{(n_1,n_2)}(\tau_1,\tau_2)$ represents the joint nonlinear effect of pairs of spikes with one spike from neuron n_1 and one spike neuron n_2.

B. Implementation of STDP

STDP is essentially a specific form of synaptic learning rule that maps the pair-wise interactions between input and

output spikes to the changes of the synaptic weight. In the GLVM, synaptic weight is represented as the first-order feedforward kernel k_1 and the learning rule can be expressed in a Volterra form as:

$$\Delta k_1(t) = \sum_{\tau_x=0}^{M_L}\sum_{\tau_y=0}^{M_L} L_2^{(x,y)}(\tau_x,\tau_y)x(t-\tau_x)y(t-\tau_y)$$

L_2 is the second-order cross kernel between input x and output y for the learning rule. It is determined by the STDP function [4], which provides the steady-state LTP/LTD magnitude, and the STDP induction function I, which describes the transience of the STDP. With appropriate L_2 shape, k will be changed by the timings of the input and output spikes. In turn, k governs the generation of output spikes based on the input spikes. The spiking neuron model and the STDP then can be implemented with a recursive manner.

C. Recursive model calculation

A nice property of the Laguerre basis functions is that they can be calculated recursively as:

$$L_j(\tau) = \begin{cases} j=0,\tau\ge 0 & \sqrt{\alpha^{\tau}(1-\alpha)} \\ j>0,\tau=0 & \sqrt{\alpha}L_{j-1}(0) \\ j>0,\tau>0 & \sqrt{\alpha}\left[L_j(\tau-1)+L_{j-1}(\tau)\right]-L_{j-1}(\tau-1) \end{cases}$$

Even more conveniently, v, the convolutions of L and x, also can be calculated recursively as:

$$v_j(t) = \begin{cases} j=0,t>0 & \sqrt{\alpha}v_0(t-1)+\sqrt{1-\alpha}x(t) \\ j\ge 0,t=0 & \sqrt{\alpha^j(1-\alpha)}x(t) \\ j>0,t>0 & \sqrt{\alpha}v_j(t-1)+\sqrt{\alpha}v_{j-1}(t)-v_{j-1}(t-1) \end{cases}$$

In this recursive formula, the jth-order v at time t depends on only the one-step-before value of v, the current value of the one-order-lower v, and the one-step-before value of the one-order-lower v. The calculation is strictly local, with the arbitrarily long memory length M embedded. This formula has great advantages in hardware implementation [5].

III. Results

A. GLVM for spiking neurons

We have implemented the GLVMs for spiking neurons in Matlab®. The code uses the recursive calculation and can simulate various biological processes with its kernels functions (Fig. 2). Figure 2 shows biological processes/mechanisms captured by the model.

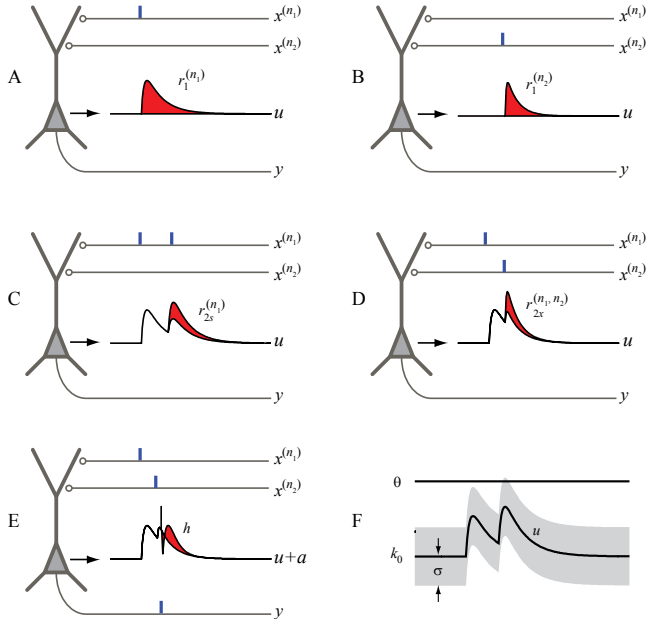

Figure 2. Various biological processes/mechanism captured by the GLVM of spiking neurons

B. Laguerre-Volterra expression of STDP

We expand the learning rule kernel with three sets of Laguerre basis functions as:

$$\Delta k_1(t) = \sum_{j_A=1}^{L_A}\sum_{j_\psi=1}^{L_\psi} c_{xy}(j_A,j_\psi)v_{xy}^{j_A}(t)v_{xy}^{j_\psi}(t) + \sum_{j_A=1}^{L_A}\sum_{j_\psi=1}^{L_\psi} c_{yx}(j_A,j_\psi)v_{yx}^{j_A}(t)v_{yx}^{j_\psi}(t)$$

$$v_{xy}^{j_A}(t) = \sum_{\tau_x=1}^{M_\psi} b_{xy}^{j_A}(\tau_x-\tau_y)x(t-\tau_x)$$

$$v_{xy}^{j_\psi}(t) = \sum_{\tau_y=0}^{\tau_x-1} b_{xy}^{j_\psi}(\tau_y)y(t-\tau_y)$$

$$v_{yx}^{j_A}(t) = \sum_{\tau_y=1}^{M_\psi} b_{yx}^{j_A}(\tau_y-\tau_x)y(t-\tau_y)$$

$$v_{yx}^{j_\psi}(t) = \sum_{\tau_x=0}^{\tau_y-1} b_{yx}^{j_\psi}(\tau_y)x(t-\tau_x)$$

In the equations above, c are the sought learning rule coefficients. They are split into c_{xy} and c_{yx} to represent the two halves of the cross kernel for x preceding y and y preceding x, respectively. Subscript A represents the STDP amplitude. Subscript ψ represents the STDP induction. With appropriate coefficients, L_2 can be reconstructed as:

$$L_2^{(x,y)}(\tau_x,\tau_y) = \sum_{j_A=1}^{L_A}\sum_{j_\psi=1}^{L_\psi} c_{xy}(j_A,j_\psi)b_{xy}^{j_A}(\tau_x-\tau_y)b_{xy}^{j_\psi}(\tau_y) + \sum_{j_A=1}^{L_A}\sum_{j_\psi=1}^{L_\psi} c_{yx}(j_A,j_\psi)b_{yx}^{j_A}(\tau_y-\tau_x)b_{yx}^{j_\psi}(\tau_x)$$

Figure 3 shows the derivation of L_2 for the STDP and induction functions. With this equivalency, STDP is realized in the form of a second-order cross kernel between input x and output y, that can be implemented with the same recursive calculation for the GLVM of spiking neurons.

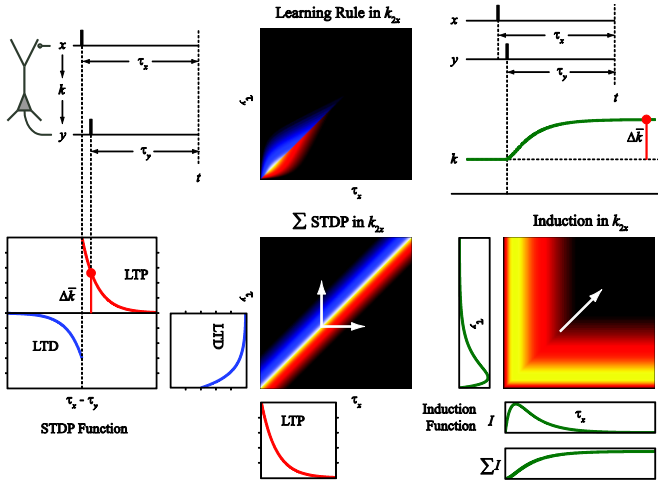

Figure 3. Relationship between the STDP function, the induction function (I), and the second-order cross kernel (k_{2x}) of input (x) and output (y). Left column: STDP function. Center middle: the integral of the STDP function in k_{2x}. Right column: the induction function I and its representation in k_{2x}. The integral of I describes the STDP dynamics. The STDP function determines the steady-state change of the synaptic weight k. Center top: the k_{2x} representation of the STDP function and the induction function. This k_{2x} is calculated as the element-wise product of the k_{2x} of STDP function and the k_{2x} of I. Note that I is not plotted in scale for better visualization. White arrows indicate the directions of the STDP and induction functions in the cross kernel.

C. *Simulation of a GLVM of spiking neuron with STDP*

We have implemented the GLVM of spiking neuron with the STDP learning rule. In this model, the first-order feedforward kernel k_1 has a typical EPSP shape determined by 3 Laguerre basis functions. The peak amplitude is 0.3. The feedback kernel has a negative exponential shape fit with a single zeroth-order Laguerre basis function. The peak amplitude is -1. To run the simulation, input spike train x is fed into the model to generate output spike train y. The synaptic strength between the input and output neurons, i.e., k_1, is changed following the standard STDP rule and the induction function. In this simulation, the shape of k_1 remains the same; only the amplitude is changed. The left (LTD) half of the STDP function is a single exponential (fit with one zeroth-order Laguerre basis function) with time constant and peak amplitude at 33.7 ms and -0.018. The right (LTP) half of the STDP function is a single exponential (fit with one zeroth-order Laguerre basis function) with time constant and peak amplitude at 16.8 ms and 0.032. Both sides share the same induction function determined by 3 Laguerre basis functions. The total length of simulation is 200 s. Figure 4 shows how the peak amplitude of k_1 fluctuates over time following the STDP functions.

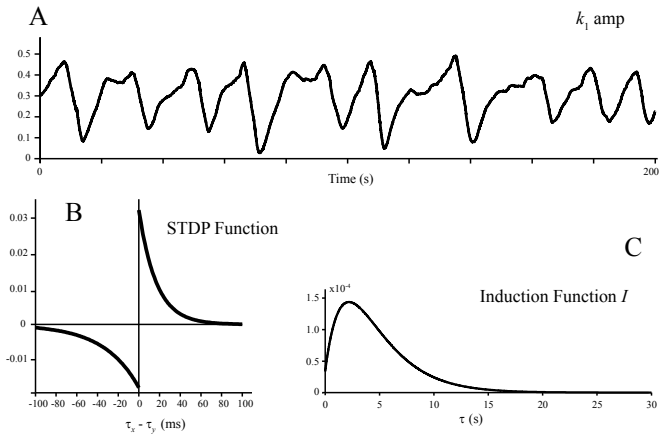

Figure 3. Simulation of a GLVM of spiking neuron with STDP

IV. Discussion

This paper presents a GLVM approach for building spiking neuron model with STDP. Different from the previous identification models on STDP [6, 7], the aim of this model is to serve as the computational unit for large-scale brain simulations and biologically-inspired cognitive architectures, taking advantages of its flexibility and succinctness.

References

[1] D. Song, R. H. M. Chan, V. Z. Marmarelis, R. E. Hampson, S. A. Deadwyler, and T. W. Berger, "Nonlinear dynamic modeling of spike train transformations for hippocampal-cortical prostheses," *IEEE Transactions on Biomedical Engineering*, vol. 54, pp. 1053-1066, 2007.

[2] D. Song, R. H. M. Chan, V. Z. Marmarelis, R. E. Hampson, S. A. Deadwyler, and T. W. Berger, "Nonlinear modeling of neural population dynamics for hippocampal prostheses," *Neural Networks*, vol. 22, pp. 1340-1351, 2009.

[3] D. Song, R. H. M. Chan, V. Z. Marmarelis, R. E. Hampson, S. A. Deadwyler, and T. W. Berger, "Sparse generalized Laguerre-Volterra model of neural population dynamic," *Proceedings the IEEE EMBS Conference*, pp. 4555-4558, 2009.

[4] G. Bi, and M. M. Poo, "Synaptic modifications in cultured hippocampal neurons: Dependence on spike timing, synaptic strength, and *postsynaptic* cell type," *Journal of Neuroscience*, vol. 18, pp. 10464-10472, 1998.

[5] T. W. Berger, D. Song, R. H. M. Chan, V. Z. Marmarelis, J. LaCoss, J. Wills, R. E. Hampson, S. A. Deadwyler, and J. J. Granacki, "A hippocampal cognitive prosthesis: Multi-input, multi-output nonlinear modeling and VLSI implementation." *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, pp. 198-211, 2012.

[6] B. S. Robinson, D. Song, and T. W. Berger, "Laguerre-Volterra identification of spike-timing-dependent plasticity from spiking activity: a simulation study," *Proceedings of the IEEE EMBC Conference*, pp. 5578-5581, 2013.

[7] D. Song, B. S. Robinson, R. H. M. Chan, V. Z. Marmarelis, R. E. Hampson, S. A. Deadwyler, and T. W. Berger, " Identification of functional synaptic plasticity from ensemble spiking activities: a nonlinear dynamical modeling approach," *Proceedings of the IEEE EMBC Neural Engineering Conference*, pp. 617-620, 2013.