

# Laguerre-Volterra Identification of Spike-Timing-Dependent Plasticity from Spiking Activity: A Simulation Study

Brian S. Robinson, *Student Member, IEEE*, Dong Song, *Member, IEEE*, Theodore W. Berger, *Fellow, IEEE*

**Abstract**— This paper presents a Laguerre-Volterra methodology for identifying a plasticity learning rule from spiking neural data with four components: 1) By analyzing input-output spiking data, the effective contribution of an input on the output firing probability can be quantified with weighted Volterra kernels. 2) The weight of these Volterra kernels can be tracked over time using the stochastic state point processing filtering algorithm (SSPPF) 3) Plasticity system Volterra kernels can be estimated by treating the tracked change in weight over time as the plasticity system output and the spike timing data as the input. 4) Laguerre expansion of all Volterra kernels allows for minimization of open parameters during estimation steps. A single input spiking neuron with Spike-timing-dependent plasticity (STDP) and prolonged STDP induction is simulated. Using the spiking data from this simulation, the amplitude of the STDP learning rule and the time course of the induction is accurately estimated. This framework can be applied to identify plasticity for more complicated plasticity paradigms and is applicable to in vivo data.

## I. INTRODUCTION

The characterization of plasticity as a function of neural activity is an essential research front- it has profound effects on the computational nature of neural networks and could yield insights into learning and memory. Several experimental studies have investigated how the relative timing of pre and post-synaptic spiking influences synaptic weight. In [1], it was observed that when the presynaptic spike was before the postsynaptic spike there was potentiation and when post was before pre, there was depression. Furthermore, the shorter the interval between spike pairs, the larger the magnitude of the change in weight. This relationship has been termed spike-timing-dependent plasticity (STDP). Many open questions remain about a generalizable activity-dependent plasticity rule because observed learning rule characteristics change between different neural regions and different experimental paradigms[2].

In this paper, we propose a general methodology for learning rule identification that has many attractive potential features. First of all, it may be applied to in vivo spiking data between any two synaptically coupled neurons. A wide range of potential shapes of weight change as a function of spike timing can be captured. Additionally, the time course of plasticity induction can be identified. This framework can also be extended to consider nonlinear spike triplet and higher order interactions on synaptic weight.

The successful identification of an activity-dependent plasticity rule for a particular synapse is important in evaluating underlying plasticity mechanisms as well as in the implementation of a cognitive neural prosthesis. Previous research towards a cognitive prosthesis is focused on functionally replacing a neural region by replicating its input output spiking system characteristics [3]. There have been promising animal experimental results with a static system that indicate that such a cognitive prosthesis can instantiate functionality of a neural region in a learned memory task [4]. Implementation of identified plasticity rules could allow the dynamic nature of a neural region to be captured by the cognitive prosthesis.

The framework proposed in this paper is an extension of the nonlinear input output modeling put forth in the cognitive prosthetic research effort [5],[6]. In this previous work, output firing probability is affected by the precise timing of input and output spiking events. These effects are captured in Volterra kernels, which are capable of capturing nonlinear spiking interactions. These Volterra kernels are expanded with Laguerre basis functions in order to minimize the amount of open parameters and to ease estimation[7]. A methodology for tracking changes in these Volterra kernels over time has also been investigated in [8] by using SSPPF [9].

Plasticity learning rules can be captured in a similar manner. The tracked change in weight over time can be considered the plasticity system output and all spike timings can be considered as the system inputs. Volterra kernels can then be estimated that characterize the effect of spike timing on the change of weight. Laguerre expansion of these plasticity Volterra kernels is again used to decrease the open parameters and assist with estimation. The plasticity Volterra kernels can separately capture the effect of relative spike timing on the amplitude of the change in weight from the plasticity induction time course.

In this paper, we will present a simple example of how to extract a learning rule from spiking neural data with this methodology. We will simulate a single input spiking neuron with STDP and prolonged plasticity induction. With only the spiking data, we are able to accurately reconstruct the Volterra kernels that describe the STDP amplitude and induction accurately. This method is generalizable to more nuanced STDP kernel shapes and higher level interactions between spikes.

## II. METHODS

### A. Model Structure – Spiking Neuron System

A single input single output (SISO) spiking neuron was simulated as outlined in Fig. 1. An output spike  $y$  is generated every time  $w$ , (the subthreshold membrane

---

B. S. Robinson, D. Song and T. W. Berger are with the Center for Neural Engineering, Department of Biomedical Engineering, University of Southern California, Los Angeles, CA 90089 USA (e-mail: bsrobins@usc.edu; dsong@usc.edu; berger@bmsr.usc.edu)

potential) passes the threshold  $\theta$ . The subthreshold membrane potential,  $w$ , is calculated by summing  $u$  (the synaptic potential),  $a$  (the after-potential), and  $n$  (Gaussian white noise). Every spike from  $x$  increases the synaptic potential,  $u$ , with the time course and amplitude of the feedforward kernel  $K_I$ . Every spike from the output spike train  $y$  decreases the after potential,  $a$ , according to the feedback kernel  $H$ . Refer to [5], [6] for more details about this modeling framework.

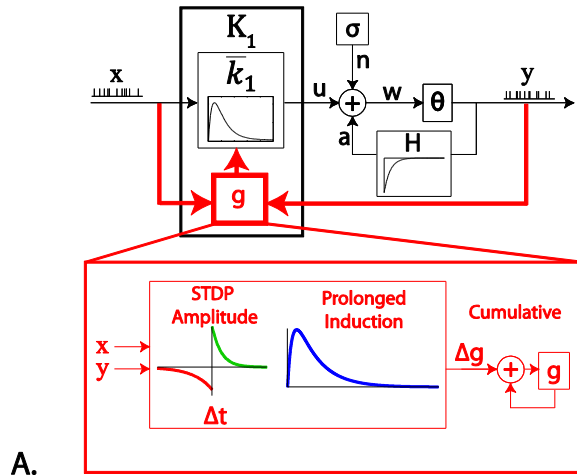


Figure 1. A. SISO spiking neuron model structure with  $K_I$  weight modulated by STDP with prolonged induction. B. Conceptual example of how  $x$  and  $y$  spike pairs affect weight change  $\Delta g$  over time with respect to order of  $x$  and  $y$  spikes as well as interspike interval. The weight,  $g$ , is the cumulative sum of  $\Delta g$ .

The amplitude of  $K_I$  is modulated over time by the synaptic weight ( $g$ ) and has the shape according to the normalized feedforward kernel  $\bar{k}_1$ , ( $\bar{k}_1$  is defined to have a maximum amplitude of one).

$$K_I = g\bar{k}_1 \quad (1)$$

During simulations the input spike train will be a generated 5Hz Poisson process. Simulations will be iterative with a 1ms time step.

### B. STDP Model Structure

The change in synaptic weight ( $\Delta g$ ), is a function of the input and output spike times ( $x$  and  $y$ ) as outlined in Fig. 1. At every time step, the synaptic weight equals the previous synaptic weight plus  $\Delta g$ . The premise of the implemented rule is based on STDP as discussed in [10]. If  $x$  spikes before  $y$ ,  $g$  will increase and if  $y$  spikes before  $x$ ,  $g$  will decrease.

The amplitude of the weight change,  $\Delta g$ , depends on the interval of time between  $x$  and  $y$  spike pairs. The STDP amplitude kernels ( $K_{Axy}$  and  $K_{Ayx}$ ) implemented in the model have time constants and relative amplitudes from [10] and can be seen in Fig 2.  $K_{Axy}$  is the kernel that describes the amplitude of spike pairs when  $x$  is before  $y$  and  $K_{Ayx}$  is for  $y$  before  $x$ .

In the model, the change in synaptic weight has a prolonged induction time of  $\sim 30$  seconds which is the approximate time scale that it takes for long-term potentiation induction in experimental studies[11]. See Fig 2 for the  $\Delta g$  induction kernel ( $K_\psi$ ) used in the model.

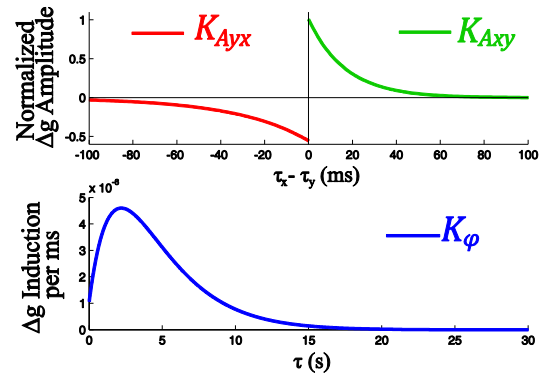


Figure 2.  $\Delta g$  STDP Amplitude and Induction Kernels.

The change in weight,  $\Delta g$ , as a function of time can be written in the Volterra kernel framework as,

$$\Delta g(t) = \sum_{\tau_x=1}^{M_\psi} \sum_{\tau_y=0}^{\tau_x-1} K_{Axy}(\tau_x - \tau_y) K_\psi(\tau_y) x(t - \tau_x) y(t - \tau_y) + \sum_{\tau_y=1}^{M_\psi} \sum_{\tau_x=0}^{\tau_y-1} K_{Ayx}(\tau_x - \tau_y) K_\psi(\tau_x) x(t - \tau_x) y(t - \tau_y) \quad (2)$$

where  $x$  is the input spike train,  $y$  is the output spike train,  $\tau_x$  and  $\tau_y$  are the time history intervals evaluated for  $x$  and  $y$  spiking, and  $M_\psi$  is the memory of  $K_\psi$ . The term  $x(t - \tau_x)y(t - \tau_y)$  in (2) equals one when the  $\tau_x$  and  $\tau_y$  combinations correspond to  $x$  and  $y$  spiking pairs in memory  $M_\psi$  and zero otherwise.

### C. Tracking Weight Change

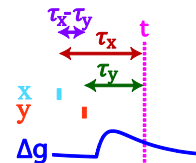


Figure 3. Visualization of  $\tau$  variables at time  $t$  used in (2)

The input kernel,  $K_I$ , and the feedback kernel,  $H$ , can be tracked over time from  $x$  and  $y$  spike timing data alone by tracking their Laguerre coefficients using SSPFP [8] and [9]. The tracked input kernel,  $\hat{K}_I$ , can be represented as,

$$\hat{K}_I = \hat{g}\bar{k}_1 \quad (3)$$

The tracked weight,  $\hat{g}$ , at any point in time can be calculated as the amplitude of  $\hat{K}_1$ , because the amplitude of  $\bar{k}_1$  is equal to 1. The tracked weight change,  $\Delta\hat{g}$ , is essential to the estimation of the learning rule and is calculated as,

$$\Delta\hat{g}(t) = \hat{g}(t) - \hat{g}(t-1) \quad (4)$$

#### D. STDP Estimation

In order to reduce the number of estimated parameters for the STDP kernels, each kernel can be expanded with Laguerre basis functions,

$$K(\tau) = \sum_{j=0}^L c^j b_j(\tau) \quad (5)$$

where  $b_j(\tau)$  is the Laguerre basis function of order  $j$ ,  $c^j$  is the corresponding Laguerre coefficient, and  $L$  is the total order of basis functions used. Because of the linear nature of the Volterra kernel and Laguerre expansion,  $\Delta g$  can also be represented as

$$\begin{aligned} \Delta g(t) = & \sum_{j_A=0}^{L_A} \sum_{j_\psi=0}^{L_\psi} c_{xy}(j_A, j_\psi) V_{xy}^{(j_A, j_\psi)}(t) \\ & + \sum_{j_A=0}^{L_A} \sum_{j_\psi=0}^{L_\psi} c_{yx}(j_A, j_\psi) V_{yx}^{(j_A, j_\psi)}(t) \end{aligned} \quad (6)$$

Where  $V_{xy}$  represents the x before y spiking data filtered through the Laguerre basis functions, and  $V_{yx}$  represents y before x as defined as,

$$V_{xy}^{(j_A, j_\psi)}(t) = \sum_{\tau_x=1}^{M_\psi} \sum_{\tau_y=0}^{\tau_x-1} b_{Axy}^{(j_A)}(\tau_x - \tau_y) b_\psi^{(j_\psi)}(\tau_y) x(t - \tau_x) y(t - \tau_y) \quad (7)$$

$$V_{yx}^{(j_A, j_\psi)}(t) = \sum_{\tau_y=1}^{M_\psi} \sum_{\tau_x=0}^{\tau_y-1} b_{Ayx}^{(j_A)}(\tau_y - \tau_x) b_\psi^{(j_\psi)}(\tau_x) x(t - \tau_x) y(t - \tau_y) \quad (8)$$

The coefficients  $c_{xy}$  and  $c_{yx}$ , are defined as

$$c_{xy}^{(j_A, j_\psi)} = c_{Axy}^{(j_A)} c_\psi^{(j_\psi)} \quad (9)$$

$$c_{yx}^{(j_A, j_\psi)} = c_{Ayx}^{(j_A)} c_\psi^{(j_\psi)} \quad (10)$$

In order to reconstruct the learning rule, the  $c_{xy}$  and  $c_{yx}$  coefficients must be estimated which is a total of  $2(L_A + 1)(L_\psi + 1)$  coefficients. The coefficients  $c_{xy}$  and  $c_{yx}$  can be estimated as  $\hat{c}_{xy}$  and  $\hat{c}_{yx}$  by performing linear regression using (6) with the estimated  $\Delta\hat{g}$  value from (4) and the filtered x and y spiking data,  $V_{xy}$  and  $V_{yx}$  according to (7) and (8). The sets of Laguerre basis functions,  $b_{Axy}$ ,  $b_{Ayx}$ , and  $b_\psi$  have separate poles in this simulation.

In order to reconstruct the estimated  $\hat{K}_{Axy}$ ,  $\hat{K}_{Ayx}$ , and the  $\hat{K}_\psi$  kernels,  $\hat{c}_{Axy}$ ,  $\hat{c}_{Ayx}$ , and  $\hat{c}_\psi$  estimates must be obtained from the estimated  $\hat{c}_{xy}$  and  $\hat{c}_{yx}$  values. The estimated coefficients may be normalized without loss of accuracy by setting:

$$\hat{c}_{Axy}^{(0)} = 1 \quad (11)$$

With substitution of (11) into (9) and (10), the remaining coefficients can be obtained from the following equations:

$$\hat{c}_\psi^{(j_\psi)} = \hat{c}_{xy}^{(0, j_\psi)} \quad (12)$$

$$\hat{c}_{Axy}^{(j_A)} = \hat{c}_{xy}^{(j_A, j_\psi)} / \hat{c}_\psi^{(0, j_\psi)} \quad (13)$$

$$\hat{c}_{Ayx}^{(j_A)} = \hat{c}_{yx}^{(j_A, j_\psi)} / \hat{c}_\psi^{(0, j_\psi)} \quad (14)$$

#### E. Ensuring Simulation Stability

The modeled system is prone to instability. As  $g$  increases,  $x$  spikes will increasingly cause  $y$  spikes which will cause  $g$  to increase even faster. Similarly, as  $g$  decreases,  $x$  spikes will become less causal for  $y$  spikes, which will cause  $g$  to decrease even faster. To prevent this system instability, when  $g$  crosses above or below specified thresholds, the  $x$  spiking shifts from a random Poisson train to patterned inputs. When  $g$  crosses below a threshold,  $x$  spiking increases to 50Hz bursts which causes  $y$  spiking and an increase in the  $g$  value. When  $g$  crosses above a certain threshold,  $x$  spiking will only occur within 10ms after  $y$  spikes, which causes a decrease in the  $g$  value. Thus, stability is achieved without altering the model structure.

### III. RESULTS

The fluctuation of  $g$  during a 200s simulation can be seen in Fig 4A. Using the spiking data,  $\Delta\hat{g}$  was accurately estimated throughout the simulation, see Fig 4B. Using the spiking data and the estimated  $\Delta\hat{g}$ , all three plasticity kernels were able to be estimated accurately, see Fig 5.

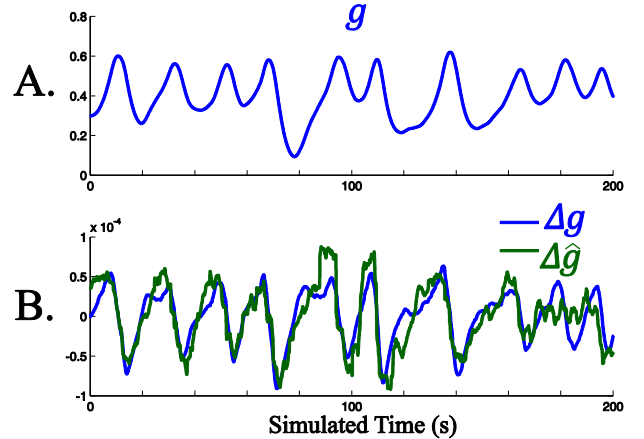


Figure 4. A. Weight fluctuation during a 200s simulation. B. Estimated  $\Delta\hat{g}$  closely resembles real  $\Delta g$ .

### IV. DISCUSSION

The simulation and estimation methodology presented demonstrates the ability to identify a STDP learning rule using only spiking neural data.

One simplification of the learning rule identification presented is that the poles of the different Laguerre basis functions of the simulation were known during estimation. Laguerre pole estimation can be incorporated in the future by using methodology presented in [12].

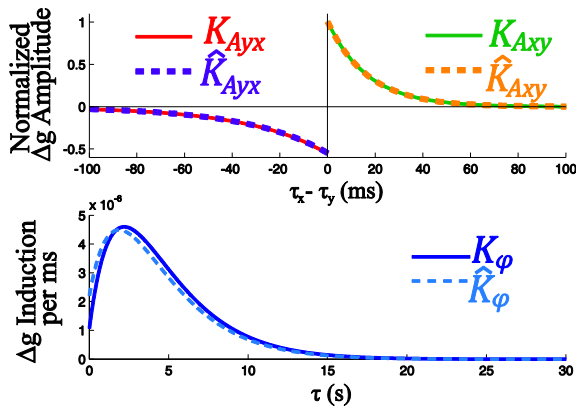


Figure 5. Estimated amplitude kernels ( $\hat{K}_{Axy}$  and  $\hat{K}_{Ayx}$ ) and induction kernel ( $\hat{K}_\phi$ ) closely resemble real kernels ( $K_{Axy}$ ,  $K_{Ayx}$ , and  $K_\phi$ ).

A limitation of the simulation example presented is that the system was prone to instability. In the future, weight saturation could be added to the model by adding a sigmoidal link function to the weight. This would limit system instability and model physiological processes that limit unbounded changes in weight. System identification could still be applied by using a generalized linear model (GLM) framework.

The simulated STDP amplitude kernels in this simulation had a shape that was based on [10], however the shape of this relationship reported in experiments varies between neural regions and experimental setup. This STDP shape has immense functional implications for learning in neural systems as well as understanding underlying mechanisms. By estimating this relationship with Volterra kernels and Laguerre basis functions, a wide variety of potential estimated shapes are possible with a small number of open parameters. Also, a separate relationship can be estimated from any coupled spiking pair of neurons. The ability to estimate the plasticity induction time course in this model is another useful tool in increasing the fidelity of the modeled system and investigating underlying plasticity mechanisms.

The model presented is single-input single-output (SISO), however this framework could easily be extended to multiple-input single-output (MISO) by adding additional feedforward kernels. A multiple-input multiple-output (MIMO) model could be created by combining several MISO models. Furthermore, the plasticity model could be extended from spike pair interactions to triplets or higher level interactions by using a 2nd order or greater Volterra kernel for determining the amplitude of the change in weight. Also, in the example presented, there was one weight parameter for the first order feedforward kernel. If multiple weight parameters were tracked for the feedforward kernel, the spiking-activity dependent change in shape of the feedforward kernel could be analyzed.

In future experiments, the presented plasticity identification framework could be applied to in vivo data in order to characterize plasticity in different neural regions.

#### ACKNOWLEDGMENT

Computation for the work described in this paper was supported by the University of Southern California Center for High-Performance Computing and Communications ([www.usc.edu/hpcc](http://www.usc.edu/hpcc))

#### REFERENCES

- [1] G. Q. Bi and M. M. Poo, "Synaptic modifications in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type," *The Journal of neuroscience*, vol. 18, no. 24, pp. 10464–72, Dec. 1998.
- [2] K. A. Buchanan and J. R. Mellor, "The activity requirements for spike timing-dependent plasticity in the hippocampus," *Frontiers in synaptic neuroscience*, vol. 2, no. June, p. 11, Jan. 2010.
- [3] T. W. Berger, D. Song, R. H. M. Chan, S. Member, V. Z. Marmarelis, J. Lacoss, J. Wills, R. E. Hampson, S. A. Deadwyler, J. J. Granacki, and S. Member, "A Hippocampal Cognitive Prosthesis: Multi-Input, Multi-Output Nonlinear Modeling and VLSI Implementation," *IEEE transactions on neural systems and rehabilitation engineering*, vol. 20, no. 2, pp. 198–211, 2012.
- [4] R. E. Hampson, D. Song, R. H. M. Chan, A. J. Sweatt, M. R. Riley, G. a Gerhardt, D. C. Shin, V. Z. Marmarelis, T. W. Berger, and S. a Deadwyler, "A nonlinear model for hippocampal cognitive prosthesis: memory facilitation by hippocampal ensemble stimulation," *IEEE transactions on neural systems and rehabilitation engineering*, vol. 20, no. 2, pp. 184–97, Mar. 2012.
- [5] 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 bio-medical engineering*, vol. 54, no. 6 Pt 1, pp. 1053–66, Jun. 2007.
- [6] 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, no. 9, pp. 1340–51, Nov. 2009.
- [7] V. Z. Marmarelis, "Modeling methodology for nonlinear physiological systems," *Annals of biomedical engineering*, vol. 25, no. 2, pp. 239–51, 1997.
- [8] R. H. M. Chan, D. Song, and T. W. Berger, "Tracking temporal evolution of nonlinear dynamics in hippocampus using time-varying volterra kernels," *2008 30th Annual International Conference Proceedings of the IEEE EMBS*, vol. 2008, pp. 4996–9, Jan. 2008.
- [9] U. T. Eden, L. M. Frank, R. Barbieri, V. Solo, and E. N. Brown, "Dynamic analysis of neural encoding by point process adaptive filtering," *Neural computation*, vol. 16, no. 5, pp. 971–98, May 2004.
- [10] G. Bi and M. Poo, "Synaptic modification by correlated activity: Hebb's postulate revisited," *Annual review of neuroscience*, vol. 24, pp. 139–66, 2001.
- [11] B. Gustafsson and F. Asztely, "Onset Characteristics of Long Term Potentiation in the Guinea Pig Hippocampal CA1 Region in Vitro," *European Journal of Neuroscience*, vol. 1, no. 4, 2006.
- [12] R. H. M. Chan, D. Song, and T. W. Berger, "Nonstationary modeling of neural population dynamics," *2009 31st Annual International Conference Proceedings of the IEEE EMBS*, vol. 2009, pp. 4559–62, Jan. 2009.