How complex and nonlinear are single neuron I/O transformations?

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1 Introduction

In this document, I argue that the question posed in the title can be assessed through the inference and analysis of bilinear state space models. These models can capture the same set of nonlinear input/output transformations that Volterra series expansions can; i.e. those with a *fading memory* property. Furthermore, their close resemblance to linear state space systems allows for the application of many of the same techniques. In particular:

1. Inference of parameters can be carried out via the same machinery as that of linear dynamical systems.
2. State dynamics are conditionally Gaussian, allowing for exact assessment of information theoretic quantities via sampling.

2 Volterra-Series based spike response model

We wish to reduce the detailed biophysical dynamics of compartment neuron models to one in which firing rate is explicit in terms of input spikes. We formulate a model in which the inputs are the times of the kth presynaptic spikes from presynaptic neuron j: $t_j^{(k)}$. The output are postsynaptic spikes $\hat{t}_i$. The classical spike response model involves a presynaptic spike filter (ϵ), a refractory term (η), and a term that filters external current injection (κ). Each of these in turn depends on the time since the last postsynaptic spike, $t - \hat{t}_i$. From these, an equation is constructed for the "membrane potential". To this membrane potential, a nonlinear escape probability function is applied, combined with probabilistic spiking:

$$
\begin{aligned}
u(t) &= \eta(t - t_i) + \epsilon(t - \hat{t}_i, \{t - t_j^{(k)}\}) + \int_0^\infty \kappa(t - \hat{t}_i, s) I^{\text{ext}}(t - s) ds \\
f(u) &= \exp(\beta(u(t) - \nu))\Delta t \\
p(y(t) = 1) &= \frac{f(u)}{1 + f(u)}
\end{aligned}
$$

where Δt is a discretization timescale and ν is a membrane potential threshold. In what follows, we neglect κ as we do not consider any external current sources besides the presynaptic spikes. We take the refractory kernel η to exhibit the phenomena of an action potential followed by hyperpolarization. To systematically capture the nonlinearities present in the input output transformation, the dependence on the presynaptic spikes is taken to be a Volterra series expansion;

$$
\begin{aligned}
\epsilon(t - \hat{t}_i, \{t - t_j^{(k)}\}) &= \int_0^\infty \sum_j h_j^{(1)}(\tau) n_j(t - \hat{t}_i - \tau) d\tau + \int_0^\infty \int_0^\infty \sum_{j,k} h_{j,k}^{(2)}(\tau_1, \tau_2) n_j(t - \hat{t}_i - \tau_1) n_k(t - \hat{t}_i - \tau_2) \\
&+ \int_0^\infty \int_0^\infty \int_0^\infty \sum_{j,k,l} h_{j,k,l}^{(3)}(\tau_1, \tau_2) n_j(t - \hat{t}_i - \tau_1) n_k(t - \hat{t}_i - \tau_2) n_l(t - \hat{t}_i - \tau_3) d\tau_1 d\tau_2 d\tau_3 + ... \\
n_j(t) &= \sum_k \delta(t - t_j^{(k)})
\end{aligned}
$$

Volterra series expansions can capture a wide range of nonlinear dynamics, specifically those with the fading memory property:

Definition 1. *Fading Memory Property [1]. Let $C(\mathbb{R})$ be the space of bounded continuous functions on $\mathbb{R}$, and $\mathcal{S}$ be an operator from $C(\mathbb{R}) \to C\mathbb{R}$. The operator $\mathcal{S}$ is said to have fading memory on $K \subseteq \mathbb{R}$ if there exists a decreasing function $w : \mathbb{R} \to (0, 1], \lim_{t\to\infty} w(t) = 0$ such that for each $u \in K$ and $\epsilon > 0$ there is a $\delta > 0$ such that for all $v \in K$:*

$$\sup_{t\leq 0} |u(t) - v(t)|w(-t) < \delta \to |Nu(0) - Nv(0)| < \epsilon$$

Intuitively, the fading memory property implies that the effect of differences in the input signal at long time lags into the past has vanishing effect on the present output. This requirement excludes chaotic systems and systems that can be induced into autonomous oscillation, both of which exist within the repertoire of single neuron dynamics [2,3]. Furthermore, since the refractoriness modeled by η depends only on the most recent spike, our model does not consider the role of spike adaptation. Nevertheless, Volterra series are widely to model noninearities in control systems and systems biology, and a similar Volterra series based spike response model has been applied previously to model single neuron spike trains (ref).

The main impediment to the use of Volterra series is the number of parameters, which baloons as the system order expands. While this can be mitigated through implicit kernel based estimation, we will instead opt to use an equivalent representation of the dynamics. First, we quote another theorem from [1], which shows that a Volterra series can be equivalently represented via a linear dynamical system with nonlinear readout:

Theorem 1. *Approximation by finite dimensional LDS*

Let $\epsilon > 0$ and suppose that N is any *time invariant operator with fading memory on K. Then there is a finite Volterra series operator $\hat{N}$ such that for all $u \in K$,*

$$||Nu - \hat{N}u|| \leq \epsilon$$

where $\hat{N}$ is the I/O operator of the dynamical system

$$\dot{x} = Ax + Bu \quad y = p(x)$$

where $p(x)$ is some (polynomial) nonlinear function.

Further still, the I/O representation of the system may be expressed as a bilinear dynamical system with linear readout:

$$\dot{x} = Ax + Fu \otimes z + Bu \quad y = Cz$$

It is this latter representation that we will develop further, as there are robust methods for its inference and well motivated ways to measure the complexity of the resulting models.

3 Maximum Likelihood Inference of Bilinear Point Process Models

In this section, we develop regularized maximum likelihood inference techniques for bilinear state space models driving a spike response model. While we develop the procedure for fitting to a scalar point process output driven by multivariate point process input, the output can in principle be made multivariate as well. This bilinear dynamical system model could thus serve as a generalization of the LDS point process model [4] for application to electrophysiological population recordings. As we highlight in later sections, bilinear dynamical systems can capture a wide range of nonlinearities while still retaining a great degree of interpretability. Furthermore, at the heart of their inference lies a Kalman filter, and thus their inference may borrow the machinery of linear dynamical systems.

Our spike respones model takes on the following hierarchical form:

$$
\begin{aligned}
x_{t+1} &= Ax_t + F\mathbf{n}_t \otimes x_t + B\mathbf{n}_t \\
y_t &= Cz_t \\
\psi &= \eta(t - t_i) + y(t) \\
\lambda(t) &= \exp(\eta\psi(t) - \nu)\Delta t \\
p(o(t) = 1) &= \frac{f(u)}{1 + f(u)}
\end{aligned}
$$

Given input spike trains $\mathbf{n}$, we first focus on the procedure for inferring $y(t)$. This will be done using EM. We will follow the presentation in [5]. We add process noise to the state dynamics, as this can help address the effects of model mismatch and improve model fit, though in contrast to (ref), we do not include any measurement noise:

$$
\begin{aligned}
x_{t+1} &= Ax_t + F\mathbf{n}_t \otimes x_t + B\mathbf{n}_t + \nu \quad \nu \sim \mathcal{N}(0, Q) \\
y_t &= Cx_t
\end{aligned}
$$

Furthermore, we assume that the initial condition is normally distributed according to $x_0 \sim \mathcal{N}(\mu_0, P_0)$. For notational convenience, we stack the inputs and outputs together:

$$
Y \equiv \{y_1, y_2, ..., y_T\}, \mathbf{N} \equiv \{\mathbf{n}_1, \mathbf{n}_2, ..., \mathbf{n}_T\}
$$

. The, we can write down the likelihood:

$$
L(\theta) = \log p_\theta(Y) = -\frac{1}{2}\sum_{t=1}^{T} \log\det H_t P_{t|t-1} H_t^\top - \frac{1}{2}\sum_{t=1}^{T}(y_t - \hat{y}_{t|t-1})^\top \left[H_t P_{t|t-1} H_t^\top\right]^{-1}(y_t - \hat{y}_{t|t-1})
$$

where we have neglected some constants. Here $\hat{y}_{t|t-1}$ is the one step ahead optimal linear predictor and $P_{t|t-1}$ is the associated state covariance. Crucially. it is possible to map the filtering step (E step) associated with bilinear models to a time-varying instance of filtering a linear state space model via the modified state equations:

$$
\begin{aligned}
x_{t+1} &= A_t x_t + B\mathbf{n}_t \quad y_t = Cx_t \\
A_t &= A + F(u_t \otimes I_n)
\end{aligned}
$$

Thus, the E step reduces to Kalman filtering, the details of which we do not recapitulate here. We provide a working toy example of the full hierarchical inference procedure in the last section.

4 Measuring the spectrum of energy transferred from input to output via balanced truncation

Once a state space system has been inferred from input/output data, a further set of questions one can pose are related to the distortion of properties of input/output transformations under compression of teh state space associated with the system. The distortion induced by such compression, a sort of rate distortion curve, can be measured by the performance of model reduction schemes. Formally, these procedures are posed in terms of optimization problems of projectons of the state space while attempting to preserve a transfer function norm. There are many possible norms one can associate to input/output transfer functions $H(s)$. In the linear case, the three most common are:

1. $\mathcal{H}_2 = \left(\int_{-\infty}^{\infty} d\omega ||H||_F^2\right)^{1/2}$

2. $\mathcal{H}_\infty = \sup_\omega ||H(\omega)||_F$

3. Hankel: $= \mathrm{Tr}(PQ)$

where P and Q are the controllability and observability Grammians, respectively. The interpretations, respectively, are the average gain across frequencies, or equivalently, the L_2 norm of the impulse response, the peak gain across frequencies, and the total energy (in L_2 sense) transferred from the past inputs to future outputs. For linear systems, there exist optimal methods to perform $\mathcal{H}_2$ and Hankel norm model reduction [6, 7]. A not necessarily optimal, but highly efficient and interpretable model reduction strategy is given by balanced truncation, which projects the state space along eigendirections associated with the largest eigenvalues of the product PQ. Most importantly, it has a direct extension to bilinear systems in terms of generalizations of the observability and controllability Grammians to nonlinear systems [8, 9]:

Definition 2. *The controllability energy functional is defined as the minimum amount of energy required to steer the system from $x(\infty) = 0$ to $x(0) = x_0$:*

$$L_c(x_0) = \min_{u \in \mathcal{L}_2^m(-\infty, 0])} \frac{1}{2} \int_{-\infty}^{0} ||u(t)||^2 dt$$

Similarly, the observability energy functional can be defined as the energy generated by the nonzero initial conditions $x(0) = x_0$ with zero control input:

$$L_0(x_0) = \frac{1}{2} \int_0^\infty ||y(t)||^2 dt$$

For linear systems, these functionals reduce to the usual observability and controllability Grammians. For bilinear systems, it can be shown that that these functionals also correspond to grammians which are derived from the following generalized Lyapunov equations:

$$\begin{aligned} AL_c + L_c A^\top + F^\top L_c F + BB^\top = 0 \\ A^\top L_o + L_o A + F^\top L_o F + C^\top C = 0 \end{aligned}$$

The spectrum of the product of these two Grammians can then be used to probe how many independent input/output channels there are that transfer significant amounts of energy.

5 Calculating the dynamical complexity of bilinear state space models

The "almost" linear character of bilinear models also permits accessible calculation of information theoretic quantities. Here, we detail how one may calculate the predictive informtion associated with the state space dynamics of a bilinear dynamical system model of single neuron input/output transformations. Recall that for a linear stochastic system, the mutual information between past and future is given by:

$$-\frac{1}{2} \log \det I - PQ$$

where P and Q are the solutions to the causal and acausal Kalman filters, respectively. Recall from the section above on inference that conditioned on the input, the posterior predictive density of y_t is Gaussian, which can furthermore be obtained through time dependent Riccati equations. From this, we can conclude that the time T predictive information, conditioned on a particular input $\mathbf{n}_t$, is given by:

$$I(y_{-T:0}; y(0:T) | \mathbf{n}_{-T:0}) = -\frac{1}{2} \log \det I - P_T Q_T$$

where P_T and Q_T are the causal and acausal solutions of the Riccati equations associated with filtering the bilinear system over time window T. The predictive information can then be obtained by averaging this quantity over the input distribution:

$$I(y_{-T:0}; y_{0:T}) = -\frac{1}{2}\Big\langle \log\det I - P_T Q_T \Big\rangle_{p(\mathbf{n})}$$

This provides the opportunity to assess how the dynamical complexity is modulted by the input distribution. In particular, one could imagine tuning the correlation between arrival times of presynaptic spikes. Similar calculations could be done relating to the mutual information between each presynaptic input and the output, or alternatively the dynamical memory trace of each input [10].

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