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RANDOM PERTURBATIONS OF VOLTERRA DYNAMICAL SYSTEMS IN NEUROSCIENCE

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Abstract. Nonlinear Volterra integral equations can arise in systems whenever there is feedback and filtering. Usually these are analyzed by deriving equivalent differential models and then using standard dynamical systems methods. However, the presence of noise in these models usually puts them beyond differential equations, and one must consider the Volterra integral equations directly. The purpose of this paper is to apply a random perturbation method to a canonical network from mathematical neuroscience that has parametric noise, and to demonstrate how the results can be used to estimate the loss of information due to cycle slipping, which corresponds to noise-induced spurious firing in the network.

1 Introduction Noise in systems can be modeled in several different ways: For example, Langevin's equation describes a linear physical system to which white noise is added, and the linear theory for it has been extended to nonlinear stochastic differential equations with additive white noise [1]. This approach is referred to as being based on *additive noise.* Another approach was derived from work of Bogoliubov [2, 3] on averaging in nonlinear oscillatory systems. In this approach, parameters in the system are allowed to be random processes, and methods based on averaging and ergodic theory provide useful predictions from the model. This approach is referred to as being based on *parametric noise.* A third approach is to derive models, such as Markov chains, for the system's state variables as being random variables, and then to use methods of probability theory for analysis, e.g. see [4].

In this paper, we study a model in mathematical neuroscience that is derived elsewhere [6]. There is a solid deterministic basis for this model and additive noise does not adequately describe the separate variation of parameters encountered. Therefore, we consider the problem with parametric noise. In particular, we investigate here how noise can induce spurious firing in a neural network, possibly resulting in the corruption of information processing by the system. We do this using recently derived perturbation methods for Volterra equations perturbed by parametric noise [5].

2 A Model Neural Network The phase-locked loop arises in mathematical neuroscience as a canonical model of excitable neural tissue of Type I [6]. Consider a network of M such electronic circuits that are connected through bandpass filters as described in Figure 1.

A mathematical model for a phase-locked loop is posed in terms of voltages put out by the VCO having a fixed wave form, say $\cos\theta$, and a variable phase $\theta(t)$. The circuits are designed so modeling is in terms of the phase variable.

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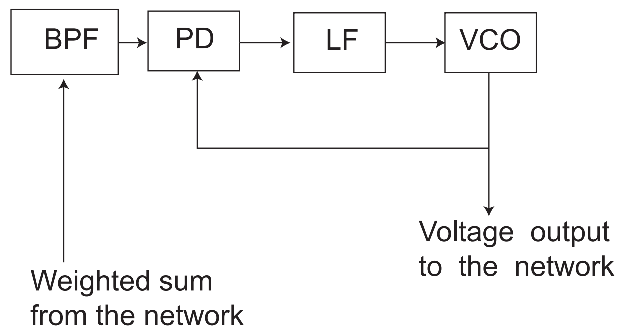

Figure 1: A phase-locked loop circuit as being an element in a network. BPF denotes a band-pass filter, PD denotes a phase detector, LF denotes a loop filter, and VCO denotes a voltage controlled oscillator.

Filters are described as being linear time-invariant systems of the form

$$v_{out}(t) = \int_0^t h(t-t')\, v_{in}(t')\, dt'$$

where v_{in} is an input signal, $h(t)$ is the filter's impulse response function (its Laplace transform, $H(s)$, is the filter's transfer function), and v_{out} is the filter's output. For example, a bandpass filter has a transfer function whose support (which is in the frequency domain) describes the pass bands; namely, those frequencies that do and do not get through the filter. Using these ideas and the methodology of canonical models for neural networks [6], we can derive the following network model:

$$\begin{aligned} \tau_j \ddot{\theta}_j(t) + \dot{\theta}_j(t) &= \omega_j \\ &+ \cos\theta_j(t) \int_0^t h_{BPF}(t-t') \sum_{i=1}^{M} C_{j,i} \cos\left(\theta_i(t') + \psi_{j,i}\right)\, dt' \end{aligned} \tag{1}$$

for $j = 1, \ldots, M$, where $\dot{\theta} = d\theta/dt$ and where

1. τ_j is the time constant of the (low-pass) loop filter in j^{th} node.
2. $\cos\theta_j(t)$ is the voltage put out by the j^{th} VCO; θ_j is its phase.
3. ω_j is the center frequency of the j^{th} VCO.
4. $C_{j,i}$ is the strength of connection from the i^{th} node to the j^{th} node and $\psi_{j,i}$ is the orientation of the connection.
5. h_{BPF} is the impulse response function for the bandpass filter.

We refer to the model as being a Volterra Dynamical System (VDS, a dynamical system involving Volterra integro-differential equations). At this point, the model can be analyzed using standard methods of dynamical systems provided the bandpass filter is described by an equivalent ordinary differential equation, which is typical in engineering applications [7]. However, when the system includes parametric noise, we must proceed in a different way. (Because of space restrictions here, we describe the method by using an abstract model and later discuss how to specialize the results to the network model (1).)

3 Random Perturbations of a Volterra Dynamical System Consider the system

$$\dot{x}(t) = \omega(y(t/\varepsilon)) + \int_0^t k(t-t', y(t'/\varepsilon), x(t'))\, dt' \tag{2}$$

where x, ω, and k are vector-valued functions, and k is continuously differentiable in the t and x arguments. y is a vector of random processes that satisfies certain natural conditions to be listed below, and ε is a small parameter that describes the ratio of the time scale on which the system responds (slow) to that on which noise acts (fast). y takes values in a measurable space $Y \subset R^N$.

We suppose that y satisfies the following conditions (explanations of these terms may be found in [5]):

1. It is a stationary or a Markov random process.
2. It is an ergodic process (in the sense of Birkhoff) having ergodic measure, say ρ, in Y.
3. It satisfies a strong mixing condition.
4. ω and k are measurable on Y with respect to ρ.

When these conditions are satisfied, we can obtain a useful approximation to the solution $x(t)$:

$$x(t) = \bar{x}(t) + \sqrt{\varepsilon}\, \tilde{x}(t) + r(t, \varepsilon) \tag{3}$$

where $\bar{x}$ solves the averaged equation

$$\dot{\bar{x}}(t) = \bar{\omega} + \int_0^t \bar{k}(t-t', \bar{x}(t'))\, dt' \tag{4}$$

and

$$\bar{\omega} = \int_Y \omega(y)\rho(dy), \qquad \bar{k}(t,x) = \int_Y k(t,y,x)\rho(dy).$$

The random process $\tilde{x}$ is a diffusion process that satisfies a (linear) equation

$$\dot{\tilde{x}}(t) = z(t) + \int_0^t L(t-t')\, \tilde{x}(t')\, dt' \tag{5}$$

where z is a Gaussian process having $Ez = 0$ and its second moments are given by an explicit formula (e.g., see [5], p. 18) involving the linearization of $\bar{k}$ about $\bar{x}(t)$, ρ, and the function

$$R(y, B) = \int_0^\infty \left(P(t', y, B) - \rho(B)\right)\, dt'$$

for any $y \in Y$ and any measurable set $B \subset Y$. Here $P(t, y, B)$ is the probability that the process $y(t)$ starting at point y lies in the set B at time t. The function L can be found in terms $\bar{k}$ and $\bar{x}$ [5]. The equation for $\tilde{x}$ shows it to be a Gaussian process, which can be determined directly from z using the resolvent kernel for L.

The remainder, or error term, $r(t, \varepsilon)$, is of order $o(\sqrt{\varepsilon})$, meaning that $r(t,\varepsilon)/\sqrt{\varepsilon}$ converges to zero as $\varepsilon \to 0$ in a stochastic sense (e.g., weak convergence in C).

The following sample calculation can help one to better understand the approximation: Consider the differential equation

$$\dot{x}(t) = \omega(y(t/\varepsilon))$$

where ω and y are as above. The solution of this problem is

$$\begin{aligned} x(t) &= x(0) + \int_0^t \omega(y(t'/\varepsilon))\,dt' \\ &= x(0) + t\,\bar{\omega} + \int_0^t \left(\omega(y(t'/\varepsilon)) - \bar{\omega}\right)\,dt', \end{aligned}$$

and the law of large numbers shows the last integral is small in a probabilistic sense as $\varepsilon \to 0$. In fact,

$$\int_0^t \left(\omega(y(t'/\varepsilon)) - \bar{\omega}\right)\,dt' = \sqrt{\varepsilon}\,\sqrt{\varepsilon}\int_0^{t/\varepsilon} \left(\omega(y(t')) - \bar{\omega}\right)\,dt'$$

and by a central limit theorem we have

$$\sqrt{\varepsilon}\int_0^{t/\varepsilon} \left(\omega(y(t')) - \bar{\omega}\right)\,dt' \to W(t)$$

as $\varepsilon \to 0$ where W is a diffusion process. As a result,

$$x(t) = t\,\bar{\omega} + \sqrt{\varepsilon}\,W(t) + r(t,\varepsilon)$$

where r can be estimated to be of order $o(\sqrt{\varepsilon})$ in a probabilistic sense. Note that the first term in this expression satisfies $\dot{\bar{x}} = \bar{\omega}$.

4 Discussion and Conclusions The perturbation method for Volterra Dynamical Systems with parametric noise can be used to analyze aspects of the network in system (1). The result of the analysis is an approximation of the form

$$\theta_j(t) = \bar{\theta}_j(t) + \sqrt{\varepsilon}\,\tilde{\theta}_j(t) + r_j(t,\varepsilon) \tag{6}$$

for the voltage phase at each node $j = 1, \dots, M$. This can be used to evaluate the impact of parametric noise on the neural network. First of all, the system can be averaged. This system for $\bar{\theta} = \{\bar{\theta}_j\}$ may or may not be analytically tractable, but at least there are good numerical methods available for simulating its solution [8]. Second, the next order term solves a linear Volterra dynamical system that is forced by a Gaussian process, whose statistics depend on the nature of the parametric noise in the model. Explicit formulas for these are given in [5]. This equation can be analyzed using the resolvent kernel methods for linear Volterra equations to determine properties of the random processes $\tilde{\theta} = \{\tilde{\theta}_j\}$.

Finally, cycle slipping in the network can be estimated in terms of the variance of these Gaussian random processes. The mean time between slips in a phase-locked loop is proportional to the signal-to-noise ratio [9] and the noise band width [10], and these can be estimated using either the formulas derived above or using spectral methods applied to computer simulations of $\tilde{\theta} = \{\tilde{\theta}_j\}$. In particular, the variance of the first order correction to the phases indicates the likelihood of cycle slipping. The simulation shown in Figure 2 is for the phase of a single node PLL. This is comparable to a pendulum with a sub-threshold torque applied to the support point. When noise is added to this torque, it can cause the pendulum to clock around - in this case, several times before being captured again by the equilibrium.

The results described here show that

1. The system obtained by using average values of the data provides an approximation to the expected value of the solution, and the formulas for $\bar{\omega}$ and $\bar{k}$ show how to correctly average the data.

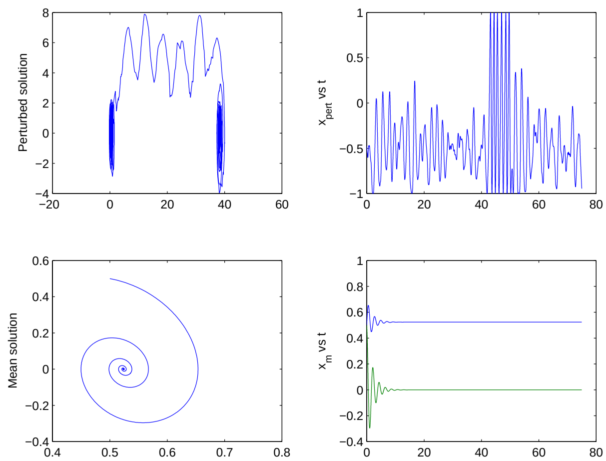

Figure 2: Simulation of a single node with parametric forcing with $\ddot{\theta} + \dot{\theta} = \omega(y_1(t/\varepsilon)) + A(y_2(t/\varepsilon))\cos\theta$, where y_1, y_2 are two-state Markov processes. Lower Left: $\bar{\theta}$ vs. $\dot{\bar{\theta}}$. Lower Right: $\bar{\theta}(t)$ and $\dot{\bar{\theta}}$ vs. t. The center frequency fluctuates between two values, say ω_1 and ω_2. In this simulation $(\omega_1 + \omega_2)/(2\bar{A}) < 1$ and $\omega_2/\bar{A} > 1$. The variance of $\tilde{\theta}$ is proportional to the band width, $\omega_2 - \omega_1$. Upper Left: θ vs. $\dot{\theta}$ for the perturbed system. Noise moves the trajectory from one potential well to another, and in the course of this it generates a spurious burst of voltage spikes, shown at the Upper Right. The larger the variance of $\tilde{\theta}$, the larger the number of cycle slips.

2. The errors however, can be large, although with low probability. In the context of the phase-locked loop network described above, large deviations of $\tilde{\theta}$ correspond to cycle slipping in the network, which would be observed as spurious firing of a node. We have outlined how the mean time between slips can be estimated.

3. The variance of $\tilde{\theta}$ in the approximation provides an estimate of the rate of cycle slipping. While the formula is not presented here in detail, it is an expression that involves only the linearization of the averaged system about the average solution, the ergodic measure ρ of the parametric noise, and the rate of convergence of the random process, which is described by the function $R(y, B)$. All of these components can be calculated explicitly. These formulas show how the statistics of the parametric noise are folded into the approximation to the solution.

4. The cycle slipping rate depends on large deviations of the phases from their means, and the methods of large deviation theory can be used to give further information. We do not pursue this here, but this is discussed in [5].

5. Computer simulations of this model can be performed using for each component of y a finite state, continuous time Markov process and using estimates of the other data (connection strengths, etc.), coming from biophysical experiments. The impact of this noise on a node's information processing capability is determined (in part) by its signal-to-noise ratio which can be estimated using standard spectral methods [9]. These spurious spikes can propagate through a network unless suitably filtered out, which can be done by the bandpass filter at each node if the passbands at each node suppress the higher frequency spurious bursts generated by noise. Synapses in biophysical neurons are known to have passbands that can do this [11].

One of the strong features of phase-locked loops is their stability in the presence of noise. A detailed discussion of cycle slipping for a single PLL and references to further literature are presented in [5], Chapter 10.

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