Wiener Kernel Estimation for Neural Systems with Natural Inputs

Garrett B. Stanley
Division of Engineering and Applied Sciences, Harvard University, Cambridge, MA 02138
gstanley@deas.harvard.edu

Abstract— **Wiener systems have been widely used as structural models of the nonlinear encoding from continuous stimuli to the discrete nature of neural activity. The majority of research related to Wiener system estimation has focused on technical issues related to Gaussian white noise (GWN) inputs. These artificial inputs are often not easily implemented experimentally, and recent evidence suggests that sensory systems may be particularly well adapted for processing of naturalistic sensory stimuli. It has been shown that for GWN inputs, the cascade of a linear system followed by a static nonlinearity can be identified through methods that mirror linear estimation. However, we have identified distortions associated with naturalistic stimuli that corrupt the second order statistics, and therefore the estimate of the linear component of the model.**

Keywords— **neural systems, estimation, Wiener kernels**

I. Introduction

Cross-correlation techniques for modeling nonlinearities have been used extensively in neural systems since they were first introduced by Lee and Schetzen [1]. Due to the discrete nature of neuronal activity in response to continuous sensory stimuli, the encoding mechanism is inherently nonlinear. One particularly effective model in early sensory systems is that the firing rate is the rectified output of the linearly filtered sensory input. This cascade of a linear system with a static nonlinearity is often referred to as a Wiener system, and has been utilized to capture the dynamics in a variety of sensory systems.

The theoretical properties of estimation techniques for Wiener systems have been discussed extensively [2], [3]. In particular, for Gaussian white noise (GWN) inputs, the estimation procedure mirrors that for a purely linear system [4]. Although white noise inputs are theoretically ideal for probing the characteristics of physical systems, they are often impractical to implement. Moreover, there is recent evidence that many sensory systems are particularly well adapted for processing of naturalistic stimuli [5], [6], [7]. The statistical characteristics of natural scenes have been studied extensively, although the impact on sensory processing is not yet clear [8], [9]. In this work, we therefore focus on the role of natural inputs in nonlinear neural systems. In particular, we address how the estimation of Wiener system models is affected by distortions introduced through the static nonlinearity, that are not present in the GWN input case.

II. Static Nonlinearities

Consider first a signal, $x(t)$, with zero mean, that is passed through a static nonlinearity, $f(\cdot)$, such that $y(t) = f(x(t))$. An important question has to do with how the static nonlinearity affects the correlation structure of the signal. Let us define the following auto-covariance function:

$$\phi_{xx}(m) \quad = \quad E\{x(t)x(t+m)\}$$

and cross-covariance function:

$$\phi_{xy}(m) \quad = \quad E\{x(t)y(t+m)\} \quad = \quad E\{x(t)f(x(t+m))\}$$

and the corresponding auto- and cross-spectra, $S_{xx}(\omega)$ and $S_{xy}(\omega)$. It is commonly accepted that the static nonlinearity, when an odd function, produces only a scaling of the covariance structure of GWN signals, so that $\phi_{xx}(t) \propto \phi_{xy}(t)$ [2], [4]. We explicitly tested this proposal in an attempt to determine the nature of this scaling for a variety of signal classes. The results are shown in Figure 1.

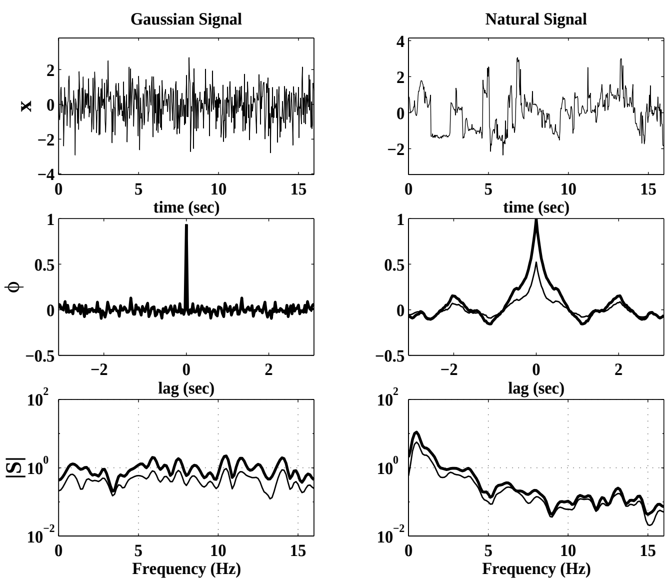

Fig. 1. Effects of static nonlinearity on signal correlation structure. The left column shows a realization of GWN, x, which was subsequently passed through a unity gain half-wave rectification. The auto-covariance, ϕ_{xx}, and cross-covariance, ϕ_{xy}, are shown in the center plot, with thick and thin lines, respectively. The corresponding auto-, S_{xx}, and cross-spectra, S_{xy}, are shown in the bottom plot. The right column shows the corresponding plots for a natural time-varying stimulus.

The figure shows a comparison of the effects of a half-wave rectification on the second order statistical properties of GWN and a natural time-varying visual stimulus derived from a single pixel of a visual movie. Note that all signals were normalized to unity variance. The half-wave rectification had unity gain, so that $f(x) = x$ for $x \geq 0$, $f(x) = 0$ else. The nonlinear mapping of GWN produced a scaling of the covariance function, as expected, which tended to a factor of 2. The same roughly held for the natural input. In both cases, the scaling predicts that $\sqrt{2} \cdot y$ would have identical statistical characteristics as the original signal x. However, we have found distortions in the spectra that cannot be attributed to a simple scaling.

III. Wiener Systems

A commonly used model for a neural system is the cascade of a linear dynamic system with a static nonlinearity, often referred to as a Wiener system, as shown in Figure 2. The input

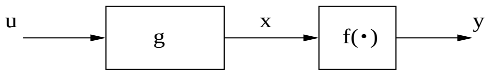

Fig. 2. The Wiener System Cascade

$u(t)$ passes through a linear system g whose output is $x(t)$, which then passes through the static nonlinearity $f(\cdot)$, producing output $y(t)$:

$$y(t) \quad = \quad f(x(t)) \quad = \quad f\left(\int_0^\infty g(\tau)u(t-\tau)d\tau\right)$$

The nonlinearity is often representative of nonlinear characteristics of the cell membrane, typically consisting of a rectification property, often practically manifesting itself in the mapping from a continuous input to a non-negative firing rate of the neuron. From the previous discussion on the effects of the static nonlinearity on correlation structure, we might infer that the estimation of the linear block of the Wiener system can be obtained from the cross-covariance between the stimulus and the resulting firing rate of the neuron:

$$\phi_{ux}(m) \quad = \quad \int g(\tau)\phi_{uu}(m-\tau)d\tau \quad \propto \quad \phi_{uy}(m)$$

We can then write $\hat{g} \propto \Phi_{uu}^{-1}\phi_{uy}$, where Φ_{uu} is the Toeplitz structure of the input auto-covariance, and ϕ_{uy} is a vector form of the cross-covariance. Figure 3 shows an example of estimates utilizing both GWN and natural inputs. Using the input, the output of a biphasic, second-order linear system was simulated, and subsequently passed through a half-wave rectification. The linear block was then estimated through cross-correlation techniques described above, from both the linear output x and the nonlinear output y. The GWN case exhibits the same scaling as we previously demonstrated in Figure 1. The estimate derived from the natural time-varying input, however, exhibits more interesting characteristics. The linear kernel estimated from ϕ_{uy}, as shown with the thin line in the upper right plot, exhibits distortions that are not present in the estimate derived from ϕ_{ux} (thick line).

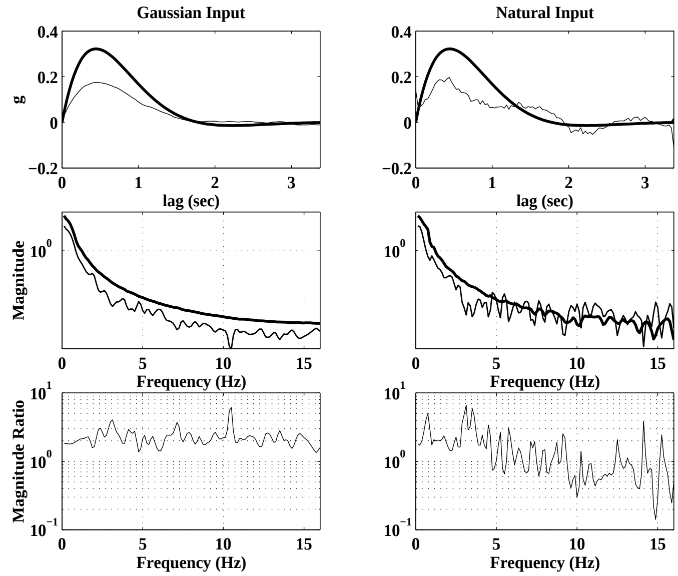

Fig. 3. Effects of static nonlinearity on cross-correlation estimation of linear block. The left column shows the estimation of first order kernel from ϕ_{ux} (thick line) and from ϕ_{uy} (thin line). The center plot shows the corresponding transfer function magnitudes, and the bottom plot shows the ratio of magnitudes as a function of frequency. The right column shows the corresponding plots for a natural time-varying stimulus.

IV. Discussion

The majority of research related to Wiener system estimation for physiological systems has focused on technical issues related to GWN inputs. These artificial inputs are often not easily implemented experimentally, and recent evidence exists that sensory systems may be particularly well adapted for processing of naturalistic sensory stimuli. It has been shown that for GWN inputs, the cascade of a linear system followed by a static nonlinearity can be identified through methods that mirror linear estimation, although the relationship with strongly non-white processes remains unclear.

We have shown here that the effect of the static nonlinearity is a scaling of the correlation structure that was previously postulated. However, natural time-varying stimuli often exhibit statistical characteristics that are non-white, non-Gaussian, and often non-stationary. When the Wiener system is driven with such a stimulus, the result is that distortions are introduced into the estimation scheme. The fact that the distortions are not present in the corresponding linear estimate demonstrates that it stems from the static nonlinearity, rather than deficiencies in the excitation properties of the input. This limitation may perhaps affect current studies in which natural sensory stimuli are used to probe the underlying dynamics, and therefore must be more carefully analyzed.

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