Nonlinear reverse correlation with synthesized naturalistic noise

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Abstract

Reverse-correlation is the most widely used method for mapping receptive fields of early visual neurons. Wiener kernels of the neurons are calculated by cross-correlating the neuronal responses with a Gaussian white noise stimulus. However, Gaussian white noise is an inefficient stimulus for driving higher-level visual neurons. We show that if the stimulus is synthesized by a linear generative model such that its statistics approximate that of natural images, a simple solution for the kernels can be derived.

Key words: Vision, Reverse correlation, Spike-triggered average, Spike-triggered covariance, Independent component analysis

1 Introduction

Reverse-correlation is a system analysis technique for quantitatively characterizing the behavior of neurons. The mathematical basis of reverse correlation is based on the Volterra/Wiener expansion of functionals: If a neuron is modeled as the functional $y(t) = f(x(t))$, where $x(t)$ is the (one dimensional) stimulus to the neuron, any nonlinear f can be expanded by a series of functionals of increasing complexity. The parameters in the terms of the expansion, called *kernels*, can be calculated by cross-correlating the neuronal responses to the stimulus, provided that the stimulus is Gaussian and white[4].

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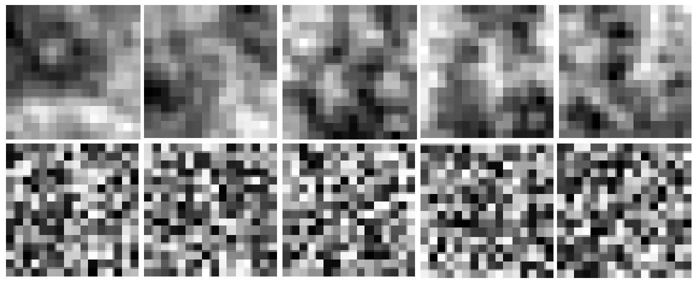

Fig. 1. The stimuli (vector x, upper row) are synthesized by linearly transforming a white noise cause (vector s, lower row) via a linear generative model: $x = A\ s$. Matrix A is learned from samples of natural images.

One of the many limits of this technique is that Gaussian white noise is an inefficient stimulus for driving higher order neurons, since visual features that are known to activate these areas appear very rarely in Gaussian white noise. The goal of this paper is to show that if we generate more "interesting" stimuli by training a linear generative model from natural images, solutions to the kernels can be obtained easily. Computer simulation is used to show that this stimulus design converges faster than white noise. We are currently collecting physiological data using this stimulus.

2 Stimulus synthesis

Instead of using Gaussian white noise for reverse correlation, we can linearly transform white noise such that the the statistics of the transformed images approximate those of natural images. This should produce a better stimulus for higher-order visual neurons since it contains more features found in nature.

More specifically, let the stimulus $x(t) = (x_1(t) \ldots x_n(t))^T$ be synthesized by:

$$x(t) = A\ s(t)$$

where $s(t) = (s_1(t) \ldots s_n(t))^T$ is white. The vector $s(t)$ is called the *cause* of the stimulus $x(t)$. The constant matrix A can be learned from patches of natural images by various algorithms, for example, Infomax Independent Component Analysis (Infomax ICA)[1]. In this case, the distribution of the causes $s_1(t) \ldots s_n(t)$ is required to be supergaussian. We use the Laplace distribution.

Examples of the synthesized stimuli are illustrated in Figure 1. Visual features that occur very rarely in white noise, such as localized edges, corners, curves, and sometimes closed contours, are much more common after the A transformation.

3 Kernel calculation

To calculate the kernels, one can follow Wiener and orthogonalize the Volterra series with respect to the distribution of the new stimulus, instead of Gaussian white noise. Here we provide a much simpler solution, using a trick that is similar to the treatment of non-white inputs in [3]. Instead of directly solving for the kernels of system f, we consider system f', which is formed by combining system f with the linear generative model: $f' = f \circ A$. The kernels of system f' can be calculated by the standard cross-correlation method, because its input $s(t)$ is white [1]. After f' is identified, we consider a new system f'', formed by combining f' with the inverse of the generative model: $f'' = f' \circ A^{-1}$. The kernels of system f'' can be easily obtained by plugging $s(t) = A^{-1}x(t)$ into the kernels of f', and expressing the kernels as functions of $x(t)$ instead of $s(t)$. But since $f'' = f' \circ A^{-1} = f \circ A \circ A^{-1} = f$, system f'' is equivalent to f. We therefore calculate kernels of f by transforming the kernels of f'.

Let the column vector $\phi(\tau) = (\phi_1(\tau) \ \ldots \phi_n(\tau))^T$ be the first-order kernels of f', obtained by cross-correlating system response with white noise $s(t)$. The first-order kernels of the original system f, $h(\tau) = (h_1(\tau) \ \ldots h_2(\tau))^T$, are simply

$$h(\tau) = A^{-T} \ \phi(\tau)$$

The second-order kernels of system f,

$$h_{ij}(\tau_1, \tau_2), \qquad i, j = 1 \ldots n, \quad h_{ij}(\tau_1, \tau_2) = h_{ji}(\tau_1, \tau_2)$$

can be calculated from $\phi_{ij}(\tau_1, \tau_2)$, kernels of system f', by the following equa-

[1] Note that $s(t)$ is Laplacian distributed, instead of Gaussian distributed. Kernels higher than the first order need to be calculated according to [2].

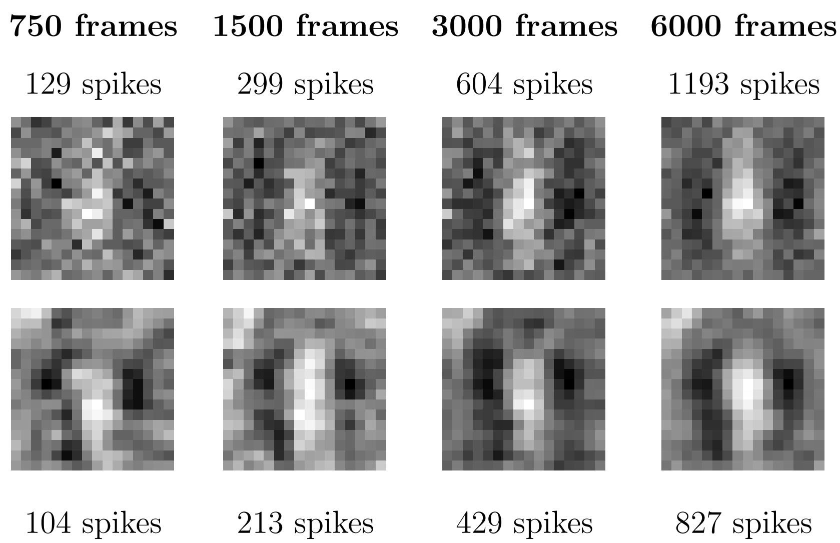

Fig. 2. Examples of learned receptive field of a simulated simple cell. Upper row: traditional reverse correlation with respect to a m-sequence. Lower row: reverse correlation with respect to the synthesized naturalistic noise.

tion:

$$\begin{bmatrix} c_{11}h_{11}(\tau_1,\tau_2) & \dots & c_{1n}h_{1n}(\tau_1,\tau_2) \\ \vdots & & \vdots \\ c_{n1}h_{n1}(\tau_1,\tau_2) & \dots & c_{nn}h_{nn}(\tau_1,\tau_2) \end{bmatrix} = A^{-T} \begin{bmatrix} c_{11}\phi_{11}(\tau_1,\tau_2) & \dots & c_{1n}\phi_{1n}(\tau_1,\tau_2) \\ \vdots & & \vdots \\ c_{n1}\phi_{n1}(\tau_1,\tau_2) & \dots & c_{nn}\phi_{nn}(\tau_1,\tau_2) \end{bmatrix} A^{-1}$$

where $c_{ij} = 1$ if $i = j$, and $c_{ij} = \frac{1}{2}$ if $i \neq j$. A useful technique for studying nonlinear system is to inspect the eigenvectors of the *spike-triggered covariance matrix* [5,6]. This equation gives the correct way to calculate the spike-triggered covariance matrix with respect to the synthesized stimulus. Higher order kernels can also be derived with the same procedure.

4 Simulation results

Figures 2 are results of linear reverse correlation, using a simulated simple cell. The simple cell is modeled as a linear gabor filter, followed by rectification, a static sigmoid nonlinearity, and gaussian additive noise. Spikes are generated by a Poisson spike generator. Although this version of synthesized noise elicited less spikes than m-sequence, the reconstructed receptive fields are better. The M-sequence took much more spikes to establish clear inhibitory

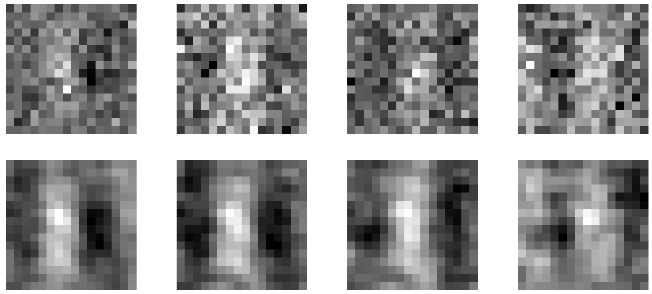

Fig. 3. Example of second-order kernels. See text for more detail. Upper: m-sequence reconstruction 3000 frames, 11072 spikes. Lower: synthesized noise reconstruction. 3000 frames, 12862 spikes.

(dark areas) subfields. Figure 3 shows some examples of second order kernels. Recall that there is a second-order kernel for each pair of pixels. To simplify visualization, we picked four reference points (pixel number 103 to 106, on the central row of the 16-by-16 stimulus), and calculate the second-order kernels between the reference points and every other point in the stimulus. The Upper row displays the second-order kernels using m-sequence (3000 frames, 11072 spikes). The lower row displays the second-order kernels calculated using the synthesized noise (3000 frames, 12862 spikes). It is very clear that the structured approach to stimulus synthesis and reconstruction make the algorithm much more resistant to noise.

5 Discussions

In this paper, we demonstrated that if we linearily transform white noise by a linear generative model trained to approximate natural images, first order kernels (spike-triggered average) and second-order kernels (spike-triggered covariance) can be calculated very easily. It is possible to use natural images directly for reverse correlation and calculate the kernels by regression. However, regression requires the inversion of the correlation matrix of natural images, which is sometimes not invertible. The synthesis matrix A is almost always invertible. Compare to the storage and manipulation of natural images, it is also a lot easier to generate stimuli and estimate kernels during experiments.

The synthesis model is motivated by our knowledge of the receptive field structure of simple cells. The vector s (the "causes") can be interpreted as a representation of the stimulus x in the cortex. Kernels calculated with respect to s might offer a different way of analyzing reverse correlation data.

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Hsin-Hao Yu is a graduate student at the Department of Cognitive Science, UC San Diego. He is interested in studying the hierarchical structure of feature selectivity in the visual cortex, by combining machine learning techniques with physiological recordings. He received his B.A. degree in Applied Mathematics from National Chiao-Tuing University (Hsin-Chu, Taiwan).