# Estimation of temporal kernels for neurons in the primary visual cortex [1]

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**Abstract**

We applied system identification techniques to characterize the functional properties of neurons in Macaque V1. Instead of using a pure white noise input, we used as input a sinewave grating undergoing a pseudo-random walk in phase. Temporal correlation was introduced to the stimulus sequence so that it induced a more natural perception of a smooth apparent motion. We compared the kernels derived from an exact orthogonalization method using SVD against those derived from the classical Wiener kernel method. We found that the kernels from the exact method give a more accurate prediction of the neural responses to the dynamic stimulus sequence. We also found that a combination of the first and second order kernel provided a significantly better prediction of the neural responses than the first order kernel alone.

*Key words:* V1; receptive field; Wiener kernel; Volterra series

## 1 Introduction

White noise methods for analyzing the function of neurons have been employed by researchers over the past two decades [1-7]. However, when looking at the *in vivo* behavior of neurons to more natural stimuli, the use of white noise methods presents several problems. First, a true Gaussian noise has no temporal structure, while our neural systems all deal with temporally correlated signals. In other words, it is hard to construct an input signal which is

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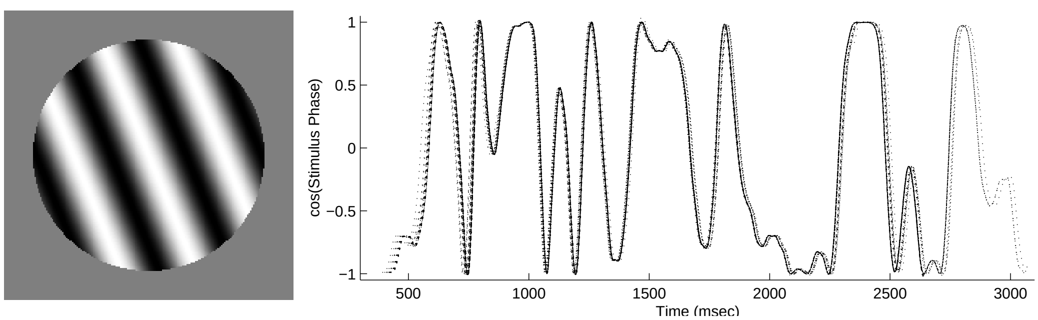
white noise yet appears natural. Second, the convergence of an estimate using white noise input is slow and an *in vivo* experiment with awake behaving monkeys only allow a limited amount of data to be collected. In this work, we attempted to address both of these issues by deriving a method to obtain the first order and second order temporal response kernel of V1 neurons that can predict accurately the neurons' response to this class of stimuli.

## 2 Methods

### *2.1 Stimulus Design*

Since we are interested in natural stimuli, can we use a stimulus that looks natural, yet contains a high noise component? We have decided to use a gray-scale sine wave grating. An example of our stimulus is given in Figure 1. This stimulus elicits a strong response from neurons in the primary visual cortex, which we take as evidence that our stimulus is in some sense *natural.* In each experimental session, the sine wave grating's orientation and spatial frequency was chosen in such a way that the neuron' response and its modulation by the grating stimulus would be maximized.




(a) (b)

Fig. 1. (a) Example sine wave grating. The orientation and spatial frequency were chosen according to the optimal tuning of the cell. The diameter of the stimulus was 5°. (b) The series of repeated input signals presented to the monkey are shown as overlaid plots. The input signal used by the kernels is the cosine of the phase, as opposed to using the phase directly. A phase of zero (cosine of 1) corresponds to the neuron's maximum response. This phase alignment is determined empirically from the data, and computed once for each cell.

The noise component of our stimulus is the phase of the grating, which undergoes a random walk with step sizes $x(t)$ drawn from a Gaussian distribution, $x(t) \sim N(0, \sigma)$. However, our visual system relies on a temporal correlation in the input in order to form a coherent motion percept. A pure random walk produces a jittering perception that does not excite the neurons significantly. In order to induce a perception of coherent motion, we apply a low pass Butterworth digital filter to a true Gaussian white noise signal. This removes the high frequency components of the input signal and creates the desired temporal correlation.

### 2.2 *Experimental procedure*

In each recording sessions, the orientation tuning and the spatial frequency tuning of the neurons was first determined so that the sinewave grating that would elicit the maximum modulation and responses was used. The receptive fields were roughly placed at the center of the grating stimulus. Their center were typically between 2° and 4° eccentricity away from the fovea. Their size ranged from 0.5° to 1°.

Each experimental trial began by turning on both a fixation dot and the randomly moving stimulus simultaneously. The monkey needed to maintain fixation for 2200 msec at the fixation dot before it received a juice reward. Both the fixation dot and stimulus were removed from the screen for a fixed period of time before the next trial began. There were two types of stimulus presentation, random and repeated. The random trials were ones where the stimulus motion was different each trial. The repeated trials used one particular movement sequence drawn from the same sample as the random trials. The monkey was presented with 10 random sequences followed by 2 repetitions of one sequence, for a total of 40 times, providing us with neural responses to 400 trials of unique random sequences, and 80 trials of a particular stimulus sequence. Kernels estimated using only the random trials were used to estimate the average post-stimulus time histograms of the repeated stimulus sequence.

### 2.3 *Kernel Estimation*

Wiener kernel methods are typically used when both a large amount of data can be generated and the input to the system is true Gaussian noise. Because we are interested in the *in vivo* behavior of visual neurons, we are limited in the amount of data which can be collected. In addition, our input signal is correlated in time and thus not true Gaussian white noise. Our method attempts to recover the temporal kernels from the responses of neurons to limited amount of non-white noise data. We define the kernels in terms of Volterra series expansion, and use Least Mean Square regression method to estimate the coefficients of these terms based on the input signals and the output responses. By casting the kernel estimation problem into an optimization problem, we can correct for the correlations in the input and reduce the amount of data required.

The results presented here are the first and second order kernels, although there is no inherent limitation in the method restricting us from estimating higher order kernels. Our input signal is $x(t)$ and the cell's response is $y(t)$. Our linear system with memory length $L$ is then

$$y\left(t\right) = h_0 + \sum_{\tau=1}^{L} h_\tau x\left(t-\tau\right) + \sum_{\tau_1=1}^{L} \sum_{\tau_2=\tau_1}^{L} h_{\tau_1,\tau_2} x\left(t-\tau_1\right) x\left(t-\tau_2\right) \tag{1}$$

where $h_0$ corresponds to the mean firing rate, $h_\tau$ is the first order kernel, and $h_{\tau_1,\tau_2}$ the second order kernel. We restrict all $\tau$'s to be positive, so we only consider causal filters. This equation is easily expressed in matrix form as $Y = XH$, where time is now indexed by matrix row in $Y$ and $X$. $H$ contains the concatenation of the terms

$$[h_0 \; h_1 \; \cdots \; h_L \; h_{1,1} \; h_{1,2} \; \cdots \; h_{L,L}]'$$

And row $t$ of $X$ is similarly

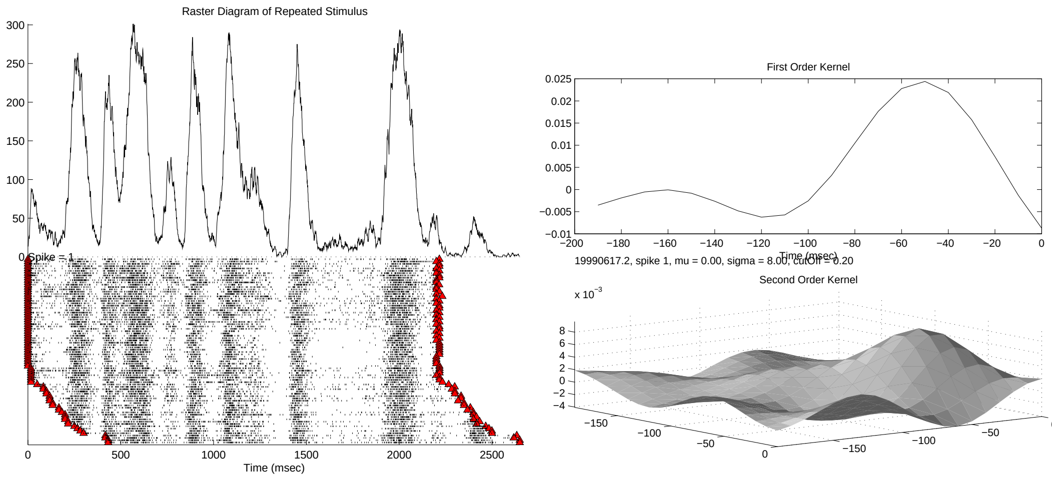
$$\begin{array}{l}[1 \; x\left(t-1\right) \; \cdots \; x\left(t-L\right) \; \left(x\left(t-1\right) \; x\left(t-1\right)\right) \; \left(x\left(t-1\right) \; x\left(t-2\right)\right) \; \cdots \\ \left(x\left(t-L\right) \; x\left(t-L\right)\right)]\end{array}$$

The standard solution for this regression problem is $H = \left(X'X\right)^{-1} X'Y$. Because of the correlations in our input signal $x\left(t\right)$, though, the matrix $\left(X'X\right)$ is ill conditioned. Instead of directly inverting this matrix, we use the singular value decomposition $USU' = \left(X'X\right)$ where $US^{-1}U' = \left(X'X\right)^{-1}$ and $S$ is a diagonal matrix. We include the first $n$ largest dimensions as ranked by their eigenvalue, where $n$ is chosen so that we account for 99% of the variance in $X$.

## 3 Results

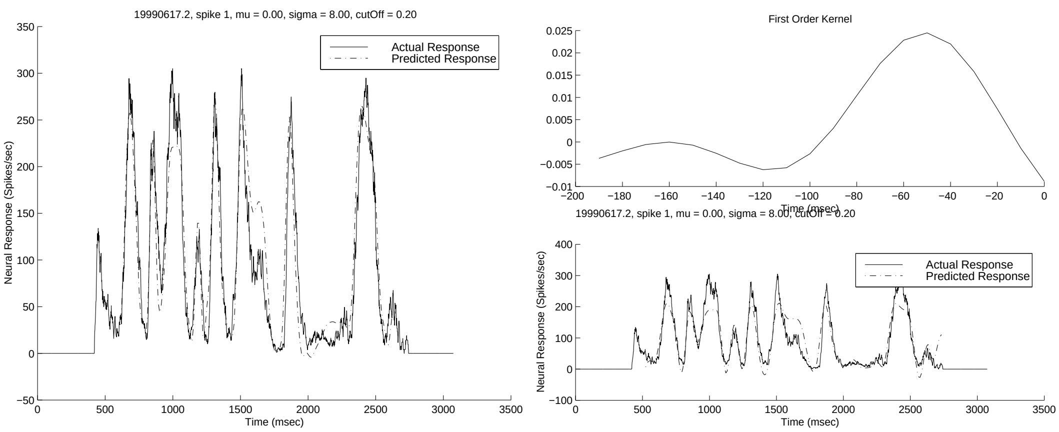
We have collected data for various noise parameters, primarily from simple cells in V1. Figure 1b shows the cosine of the phase during the 80 test trials. Figure 2a shows the raster of the response of a neuron to the corresponding sine wave grating. Figure 2b shows the first and second order kernels estimated from the input and output of all the non-repeated trials. The kernels have an enforced latency of 50 msec and a memory length of $L = 200$ msec. Coefficients are estimated at 10 msec intervals. The kernels are applied to the input to yield a predicted response of the neuron for the repeated trials. Figure 3 shows both the average neural response and the estimated response based on first order kernels and a combination of the first and second order kernels. As can be seen, with the second order kernel, the estimate is generally accurate.

In other cells, a more rectified response can be seen. There does appear to be a common temporal structure for the kernels, a center-surround organization in time. Figure 6a compares the prediction errors of the Wiener kernel method and the prediction errors due to the exact kernel method we used. The mean improvement index of (Wiener MSE - Exact MSE)/(Wiener MSE + Exact MSE) is equal to 0.305 with standard deviation of 0.172. The Wiener kernels are approximated using cross-correlation techniques with proper weighting to adjust for the non-whiteness of the noise signals. Figure 6b compares the




(a) (b)

Fig. 2. (a) The raster of the cell's response to the repeated sequence, along with the average PSTH across all trials. (b) The first and second order kernel computed for the neuron. The second order kernel has been shown as a symmetric surface, when in reality only the upper triangular coefficients are estimated




(a) (b)

Fig. 3. (a) The average response over the 80 repeated trials is shown, smoothed by a 10 msec moving average filter. The estimate for this response, using the first and second kernels presented above, is also shown, showing high correlation. (b) The first order exact kernel with its prediction of the response.

errors based on prediction using both the first and second order kernels against the errors based on prediction using only the first order kernels. We have therefore demonstrated the temporal kernels extracted using the exact method is able to predict the responses of the neurons, and that the first and second kernels provides sufficient information to provide a fairly accurate description of the behaviors of V1 neurons. The exact kernel method, however, has higher computational complexity than the other approximation methods. Finding the covariance matrix is an $O(N^2 * M)$ operation, where N is the number of "columns" per record and M is the number of record. Finding the matrix inverse is an $O(N^3)$ operation. We will run into problems when we start looking at higher order kernels because N itself is a polynomial of order $n^k$, where n is the number of time samples and k is the order of the kernel.

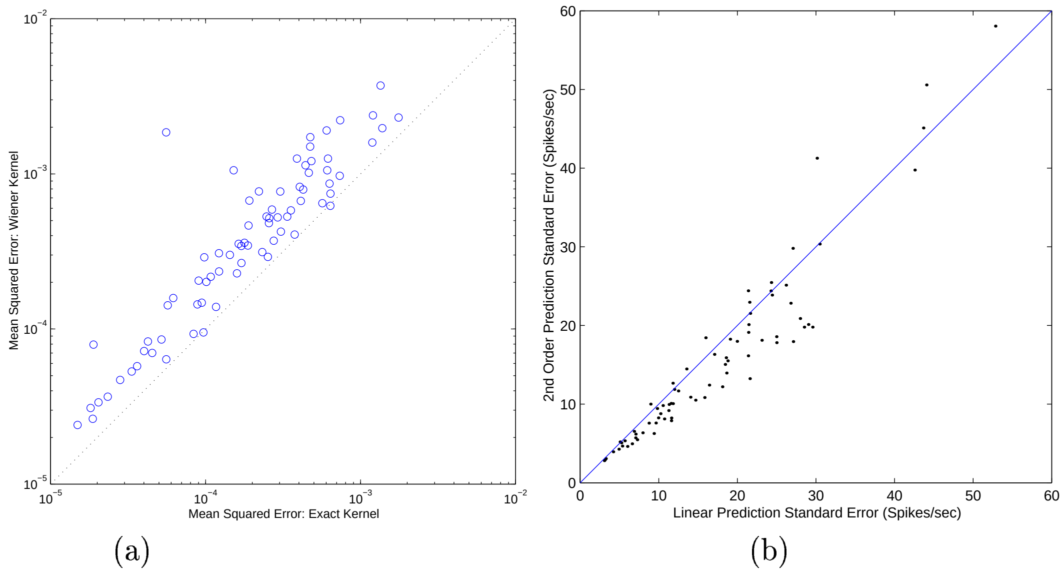



Fig. 4. (a) Population comparison of the performance of Wiener and Exact kernel estimates, showing the mean square error of the Wiener kernel is greater than that of the Exact kernel. (b) Population comparison of the performance of Exact first order kernel against the Exact first+second order kernels.

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