

# Adaptation of temporal receptive fields of Macaque V1 neurons<sup>1</sup>

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## Abstract

Traditional view of macaque V1 neurons is that they are static spatiotemporal filters. This study shows that V1 neurons' temporal receptive fields (kernels) are dynamic and adaptive. We used stimuli that share the temporal statistical characteristics of natural stimuli to investigate the linear and the nonlinear components of the receptive fields. We found that the temporal frequency tuning of the receptive fields of the neurons change according to the statistical context of the stimulus environment. This adaptation might have play a role in maximizing information encoding (Brenner, et al., 2000; Wainwright, 1999).

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

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## 1 Introduction

We applied system identification techniques to study the temporal receptive cell or kernels of V1 neurons using naturalistic stimuli. Earlier workers have applied classical Wiener kernel method, which required white noise input and a large amount of data, to study neurons in salamander retina (Smirnakis, et al., 1997) and flowfly visual neurons (Rieke et al. 1997). Wiener kernel method has also been used to deduce the first order kernel of anesthetized cats (Stanley et al. 1999) and the first and second order spatial temporal kernels of anesthetized monkeys (Jacobson et al. 1993, Gaska et al 1994). However, V1

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neurons are known to tune to specific range of spatial and temporal frequency, white noises do not elicit strong response in the neurons and are not necessarily the optimal stimuli for probing at the neural system. An alternative type of stimuli is then of naturalistic stimuli that approximate what the neurons are developed and evolved to detect. Here, we utilized a sinusoidal grating stimuli with non-white temporal noise with a temporal power spectrum close to  $1/f$  – characteristics of natural stimuli (van Hateren 1992) – to investigate the potential adaptation of the neurons in response to the statistical structures of the stimulus environment.

## 2 Method

In order to recover the first and second order kernels of the neurons, and to study their potential variations under different stimulus environment, we developed a method based on the refinement of Korenberg’s (1988) fast orthogonalization algorithm for kernel identification, which is useful for characterizing systems using non-white and non-Gaussian stimuli with limited amount of data. The basic idea of this method is to assume the transfer function can be expressed in terms of the Volterra series, and apply the least means square regression method to obtain the best coefficients of the series relating the input and the output, taking into account the non-white nature of the stimuli.

We used sinusoidal grating as stimuli (Figure 1). During the experiment, the receptive field of the recorded neurons were roughly placed at the center of the grating stimulus. The sinusoidal grating underwent a random walk in a direction perpendicular to the grating. The step sequence was drawn from a Gaussian distribution and then low-passed and shaped so that their power spectrum approximated  $1/f$ . For each neuron, we select a particular sinusoidal grating with the direction and spatial frequency that the cell is optimally tuned to. The shaping of the power-spectrum was achieved by varying the  $\sigma$  of the GWN and the upper limit of the frequency band of the stimuli.

Each experimental trial began by turning on both a fixation dot and the sinusoidal grating moving back and forth along one-dimension with steps according to the specified noise distribution. 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.

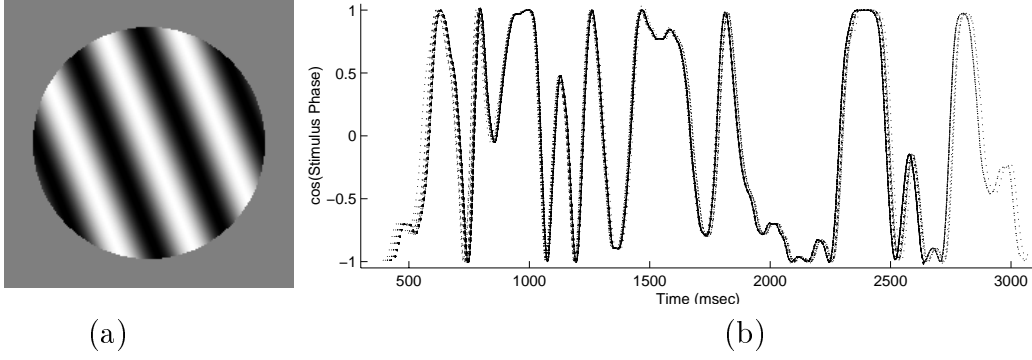


Fig. 1. (a) Example sine wave grating. The orientation and spatial frequency were chosen according to the optimal tuning of the cell. The diameter of the stimulus was  $5^\circ$ . (b) The series of repeated input signals presented to the monkey are shown as overlaid plots. The input signal used by the 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 results presented here are the first and second 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

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

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

$$[1 \ x(t-1) \ \cdots \ x(t-L) \ (x(t-1) \ x(t-1)) \ (x(t-1) \ x(t-2)) \ \cdots \\ (x(t-L) \ x(t-L))]$$

The standard solution for this regression problem is  $H = (X'X)^{-1} X'Y$ . Because of the correlations in our input signal  $x(t)$ , though, the matrix  $(X'X)$  is ill conditioned. Instead of directly inverting this matrix, we use the singular value decomposition  $USU' = (X'X)$  where  $US^{-1}U' = (X'X)^{-1}$  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 recorded from 30 neurons from one monkey using standard single-unit chronic recording technique and 10 neurons from a second monkey using chronically implanted micro-electrode array (Bionics, Inc, Utah) which allow a more extensive investigation of each neuron. Figure 2a shows the first and second order kernels of a typical cell recovered from the random 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. Figures 2b show the average neural response to the repeated trials and the predicted response based on both the first and second order kernels. The prediction was generally accurate. We found the second order kernels carry significant amount of information that yield an improvement of at least 20 percent in predicting the neuronal responses.

Interestingly, when we varied the power spectrum of the test signals, the recovered kernels were found to change also (Fig. 3a). This suggests the kernels might be adaptive to the statistical context of the stimuli. We computed the power spectral density of each kernel for signals of different frequency band and found that the frequency tuning of the cell shift with a change in the power spectrum of the signals (Figure 3b). To rule out this change is due simply to the method and the frequency structures of the stimulus, we applied the same method and stimulus a model of static first and second order kernels and showed that kernels can be recovered accurately using our methods. In conclusion, we found that the temporal receptive fields of V1 neurons are not static but dynamic, adapting to the statistical structures of the stimulus environment. Adaptation to temporal contrast and standard deviation of velocity noises have been reported earlier in salamander and primate retina (Smirnakis et al 1997, Chander and Chicklilnisky 2001) and flowfly visual neurons (Brenner et al. 2000, Fairhall et al. 2001). Our study shows that similar adaptation exists in macaque V1 neurons in the frequency domain.

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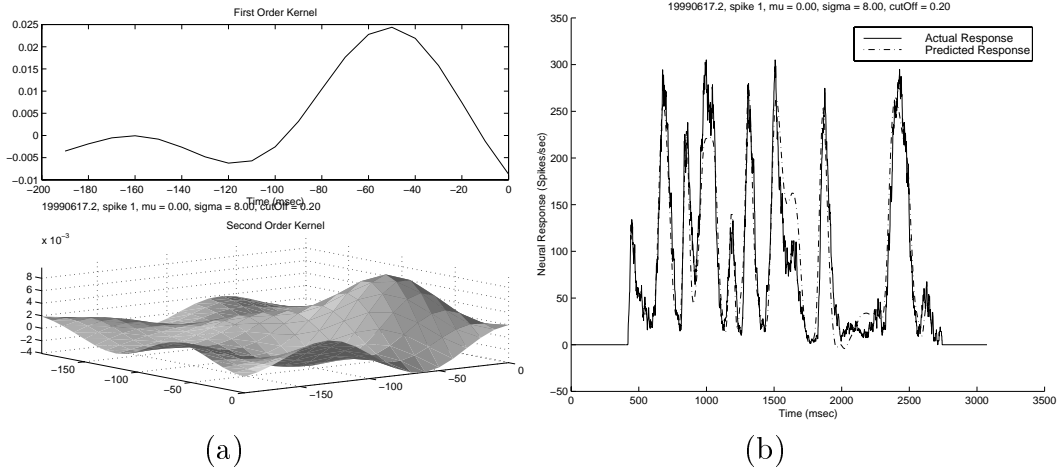


Fig. 2. (a) The first and second order kernel computed for the neuron. The second order kernel has been shown as a symmetric surface, when in reality only the upper triangular coefficients are estimated (b) The average response over the 80 repeated trials is shown, smoothed by a 10 msec moving average filter. The estimate for this response, using the first and second kernels presented above, is also shown, showing that the prediction is fairly accurate.

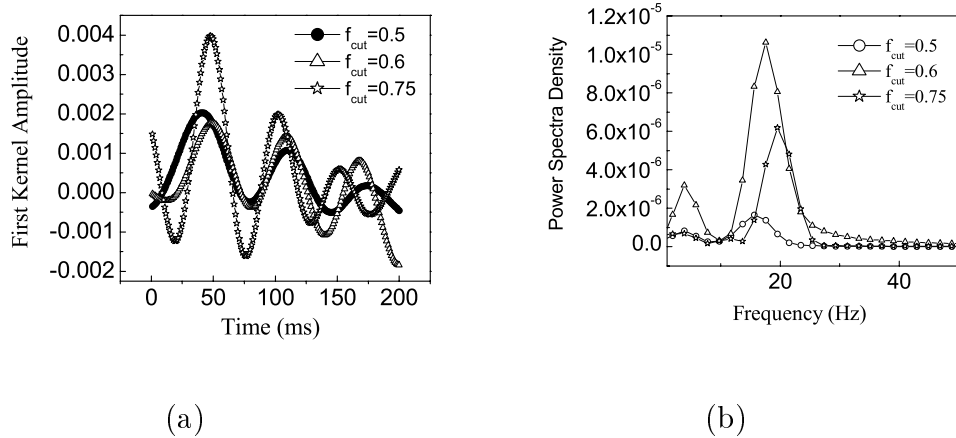


Fig. 3. (a) The temporal receptive fields of a cell recovered in the three noise stimulus environment show adaptation in the scale and amplitude of the cell's receptive field. (b) The power spectral density plots of the temporal receptive fields reveal adaptation in the frequency tuning.

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