Adaptation of the temporal receptive fields of Macaque V1 neurons [1]

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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. In order to study the adaptation of the kernels to a variety of stimuli, we developed a regression approach to recover kernels using naturalistic stimuli. Using this technique, we studied how the kernels of the V1 neurons in macaque monkeys adapt to the frequency bandwidth of naturalistic signals. We found that the temporal frequency tunings and the gains of the receptive fields of the neurons change according to the statistical context of the stimulus environment.

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

1 Introduction

We refined and applied a system identification technique based on the approach of Korenberg [2] to study the adaptation of the temporal receptive cell of macaque V1 neurons to naturalistic stimuli. Earlier work on the adaptive behavior of neurons in salamander retina [7] and blowfly visual neurons [6,1] typically used Gaussian white noise as input. However, the fact that neurons are adaptive to the variance of the Gaussian white noise in those studies also suggests that their input-output relationship between white noise and natural stimulus might in fact be different. Wiener kernel (white noise) method [10,3,5] has been used deduce the first order kernel of anesthetized cats [8] and the first and second order spatial temporal kernels

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of anesthetized monkeys [4]. But this method requires white noise input and a large amount of data, hence inappropriate for awake monkey experiment. Here, we would like to study the kernels of the neurons in response to naturalistic stimuli with different stimulus statistics in awake behaving monkeys.

2 Method

Korenberg's (1988) [2] fast orthogonalization algorithm for kernel identification is useful for characterizing systems using non-white and non-Gaussian stimuli with a limited amount of data. We refined this method using single-value decomposition to stabilize the algorithm. 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, as described below.

Let $x(t)$ be the input signal and the cell's response be $y(t)$. A linear system in terms of the first and the second order kernels with memory length L is then given by

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

where h_0 corresponds to the mean firing rate, h_τ is the first order kernel, and h_{τ_1,τ_2} the second order kernel. We restrict all τ'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

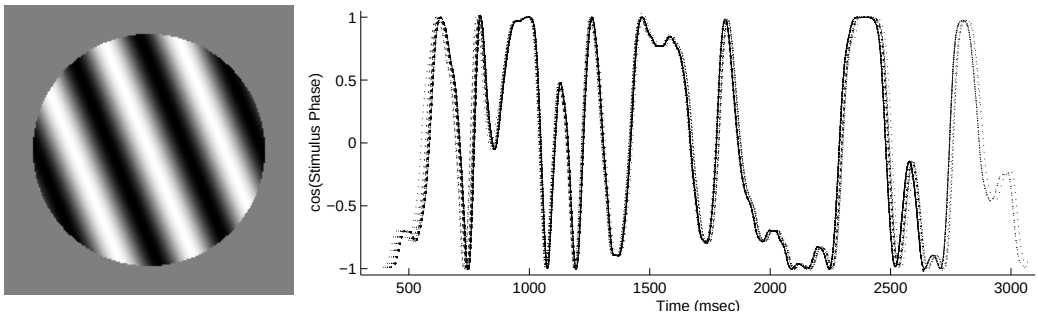
$$[1\ x(t-1)\ \cdots\ x(t-L)\ (x(t-1)\ x(t-1))\ (x(t-1)\ x(t-2))\ \cdots\ (x(t-L)\ x(t-L))]$$

The standard solution for this regression problem is $H = (X'X)^{-1} X'Y$. Because of the temporal correlations in the input $x(t)$, typical of naturalistic stimulus, 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 eigenvalues, where n is chosen so that we account for 99% of the variance in X. In essence, the kernel is obtained by the normalizing the cross-correlation of the input and output with the covariance matrix of the input. The use of SVD and selecting the n largest eigenvectors is a type of principle component regression.

3 Experiment

In order to focus our study on the temporal receptive field, we used a moving visual stimulus with its movement limited to one dimension. The stimulus was a sinusoidal grating (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 distribution such that the temporal correlations of the cos(phase) variation (which is also the intensity variation at a point in the receptive field) exhibited the $1/f$ spectrum, i.e. the power spectrum of the natural stimulus. The movement of this stimulus thus has the same statistics on temporal correlations as natural stimuli [9] and is called 'naturalistic'.

To investigate the potential adaptation of the neurons in response to the statistical structures of the stimulus environment, in different blocks of the experiment, we used the signals that have been filtered to have different frequency bandwidths. The lower end of the frequency band tested was fixed at 0.1 Hz, and the higher end can be one of the following frequencies: 6, 9, 12, 15, 18, 21, 24, and 27 Hz. Generally, we attempted to study a neuron's response to as many frequency bandwidth signals as possible in so far we could maintain the neuron and that the monkey was willing to work.



(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.

For each neuron, we select a particular sinusoidal grating with the direction and spatial frequency that the cell is optimally tuned to. 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

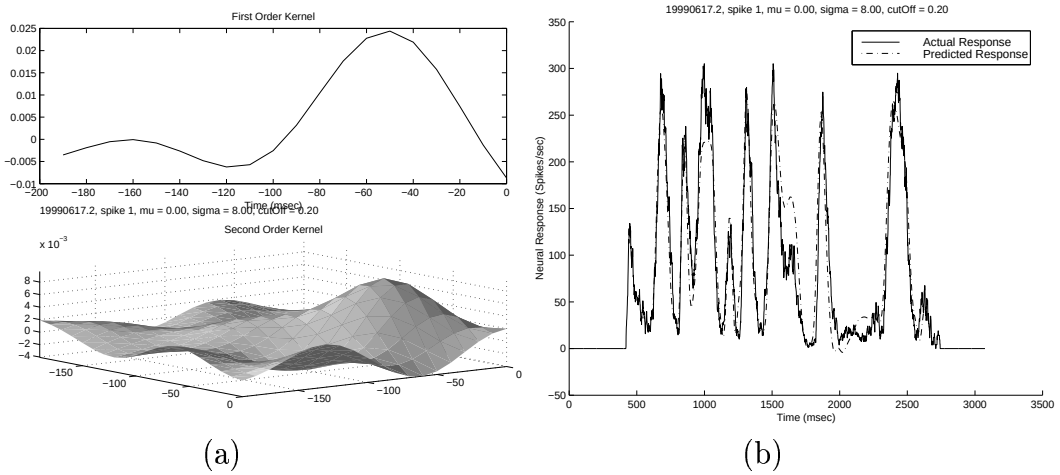
stimulus motion was different each trial. The repeated trials used over and over again a particular 2.2 second movement sequence drawn from the same distribution as the random trials. The monkey was presented with 10 random sequences followed by 2 repetitions of one sequence, for a total of 40 times, 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.

4 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). 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 L of 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 2b shows the average neural response (PSTH) to the repeated trials and the predicted response based on both the first and second order kernels. Note that the repeated trials were not in the training set. Nevertheless, the prediction was generally accurate. We found the second order kernels carry a significant amount of information that yield an improvement of at least 20 percent in predicting the neuronal responses.

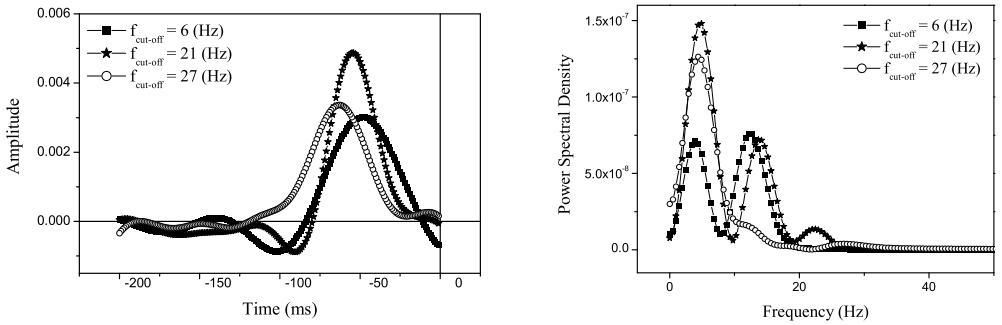
When the frequency bandwidth was varied, we found that the temporal kernels of the cells changed (Figure 3a,b). The gain of the kernel, obtained by integrating its power spectral density, reaches a maximum at an intermediate frequency bandwidth. The optimal frequency bandwidth varies from cell to cell. Figure 4a shows the kernel gains of three different cells as as a function of bandwidths. The kernel gain of each cell was normalized by the maximum gain of the cell. It clearly shows a tuning to the frequency bandwidth: some preferred a lower frequency bandwidth (e.g. cell d183) while others preferred a higher one (e.g. cell Di185). Figure 4b shows the distribution of the optimal frequency bandwidth for the 10 neurons we managed to study for a long time. We evaluate the strength of the gain modulation by computing the ratio (A-B)/(A+B) where A is the peak kernel gain, and B is the kernel gain for the 27 Hz frequency bandwidth signal (see Figure 4a). The distribution of the gain modulation relative to the highest frequency bandwidth signal was shown in Figure 4c.

The observed neuronal adaptation to frequency bandwidth may arise from the underlying temporal frequency tuning of the cells and the spectral statistics of the signals. The high frequency component of a wider band signal may exert a destructive interference on the cell's nonlinear spiking dynamics. While the causes and the purpose of frequency bandwidth adaptation remains to be elucidated, we have demonstrated in this work the feasibility and utility of our method for studying kernel adaptation in V1 neurons of awake macaque monkeys to non-white noise stimulus. This opens up a lot of opportunities for studying the adaptation of the neuronal kernels in awake monkeys under different behaviroal manipulations and training.



(a) (b)

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.



(a) (b)

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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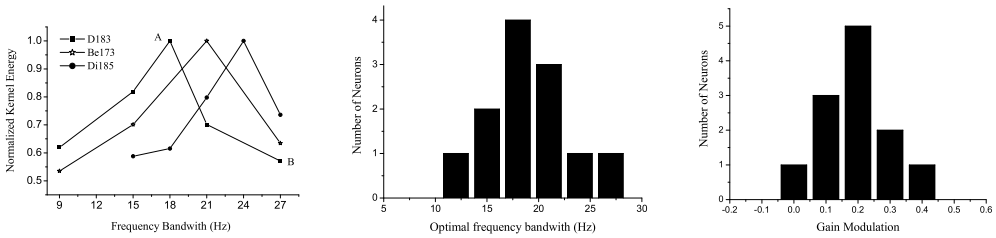

(a) (b) (c)

Fig. 4. (a) Three different cells' kernel gains for signals of different frequency bandwidths. Each cell's gain is normalized by its maximum gain across different bandwidths. (b) Distribution of cells in terms of their optimal frequency bandwidths. (c) Distribution of the strength of gain modulations.

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