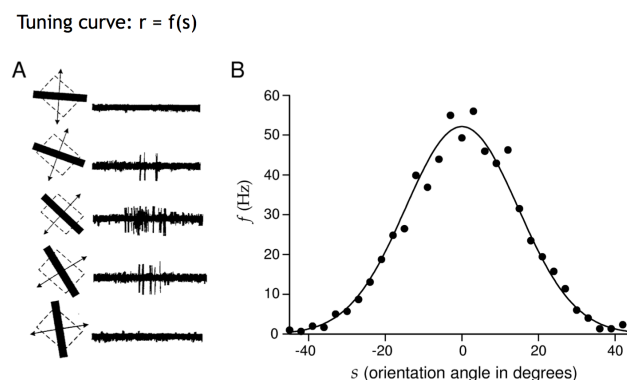


Task 7

Developing The Methods To Fit Receptive Field

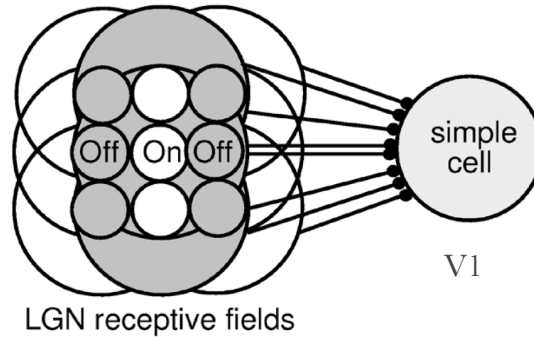
Introduction



Gaussian tuning curve of a cortical (V1) neuron

During 1950s, Torsten Wiesel and David Hubel discovered there is a particular kind of neuron in V1 cortex responds primarily to oriented edges and gratings. In the last task, it has been shown that these V1 neurons exhibiting orientation selectivity that can be fitted by linear model, and the neurons exhibiting directional selectivity can be further fitted by nonlinear-linear model (Von Mises Model) with additional second harmonic component. The resulting tuning curve therefore give us an intuitive picture of the neuron's behavior. However, in spite of its analytical simplicity, it lacks ability to capture other properties of the neurons. For instance, some of these cells exhibit size and position selectivity besides orientation selectivity. In hope of integrating other ineligible properties of neurons into the description, it is of our

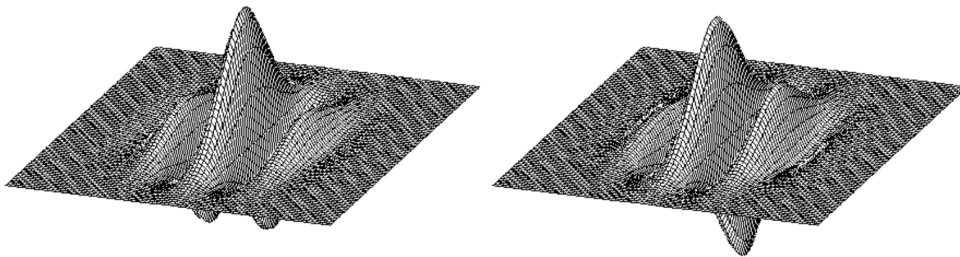
interests building a *receptive field* for the neurons. The receptive field of a neuron can be defined as the surface of an animal's body where the sensory neuron is evoked when stimuli is given. In auditory and visual systems, the notion is extended to the space surrounding an animal. The receptive fields of neurons directly receiving stimuli collectively form the receptive fields of neurons in higher order of the signal pathway.



In visual system, the receptive fields of retina ganglion cells and LGN neurons can be categorized as center-on, or center-off. They collectively form the receptive fields of V1 neurons. Torsten Wiesel and David Hubel discovered there are different kinds of orientational selective V1 neurons. ‘Simple cell’ responds to orientation and location of stimuli, while ‘complex cell’ is invariant to location of stimuli. The properties of simple cell are explained by the summation of LGN neuron receptive field as shown in the figure above.

The properties of simple cells are captured by 2D Gabor function, which is a Gaussian function modulated by a sinusoidal function.

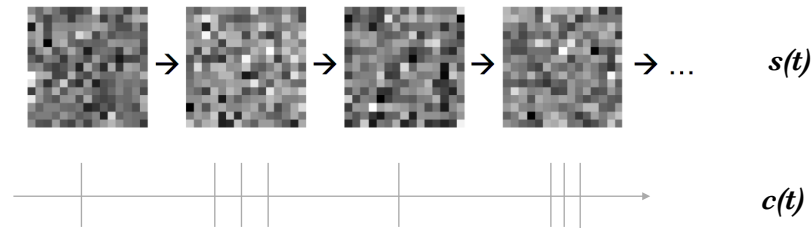
$$g(x, y; \lambda, \theta, \psi, \sigma, \gamma) = \exp\left(-\frac{x'^2 + \gamma^2 y'^2}{2\sigma^2}\right) \exp\left(i\left(2\pi\frac{x'}{\lambda} + \psi\right)\right)$$



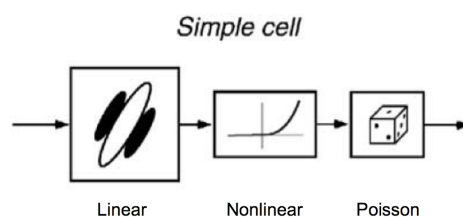
Real part and imaginary part of the impulse response of a Gabor filter

In this task, we aim to answer the following questions. How do we estimate the receptive fields of sensory neurons in higher level cortical area, whose receptive fields do not directly connect to the outside world ? What is the quality of the estimation ? How do we explain the estimation ?

Method



In this lecture, we tried to fit the receptive field of simple neuron by fitting the nonlinear-linear Poisson model, where vector $\mathbf{c}(t)$ represents spike counts estimation in each time frame during stimulation. The estimator is Poisson probability distribution parameterized by $\mathbf{r}(t)$, the mean spike count and the variance. \mathbf{w} and $\mathbf{s}(t)$ individually represents linear filter of the D by D stimuli and the D by D stimuli to the retina. The matrix \mathbf{w} and matrix $\mathbf{s}(t)$ are firstly reshaped as D^2 by 1 vector, and the linear filter is applied on the stimuli by taking their scalar product. The scalar is then passed to an exponential function, which distinctly differentiates excited state and silent state of the neuron.



$$c_t \sim \text{Poisson}(r_t)$$

$$r_t = \exp(\mathbf{w}^T \mathbf{s}_t)$$

To fit our model to the real V1 simple cell receptive field, we use *maximum likelihood method*, which is the joint distribution of Poisson probability estimation of the spike count at each time frame :

$$L(\mathbf{w}) = \log \prod_t \frac{r_t^{c_t}}{c_t!} \exp(-r_t)$$

And the log-likelihood:

$$\log L(w) = \sum_{t=1}^T c_t \log(r_t) - r_t - \log c_t!$$

The gradient of log-likelihood:

$$\frac{\partial}{\partial w} \log L(w) = \sum_{t=1}^T c_t s_t - s_t \cdot \exp(w' \cdot s_t)$$

Results

Task 1. **Fit instantaneous receptive fields.** In the first part, the receptive field influences the spike count instantaneously just as in the above equations. We will use *Maximum Likelihood* to fit the receptive field. First calculate and implement the log-likelihood function of w and its gradient with respect to w .

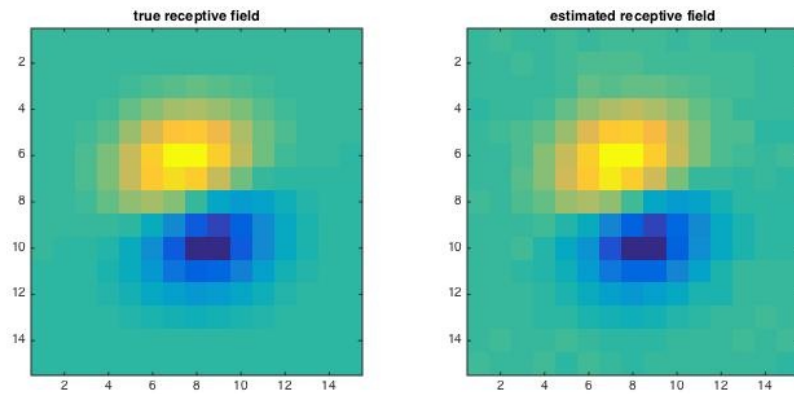


Figure 1: Visualize the true and the estimated receptive field on the same scale.

In this task, the true receptive field is a Gabor function, and the data is generated by nonlinear linear Poisson model, so the estimated receptive field looks almost identical to the true receptive field after fitting. On the other hand, it is still discernible the noise surrounding

the excitatory area and inhibitory area. It is due to the error tolerance criterion of the minimization scheme, and can be further reduced by lowering the error tolerance.

2. Fit receptive fields with time lag. In the second part, there is also a temporal component to the receptive field, i.e. the spike rate of the neuron is not instantaneously influenced by the stimulus but by stimulus values in the past. To fit receptive fields, you can keep the formula for the maximum likelihood fit the same, but augment the stimulus space by adding stimulus values from the past as additional dimensions.

In this task, we consider the situation when the receptive field not only sensitive to instantaneous input, but also the previous inputs. To do this, we have to expand our receptive field to time dimension, making it a D by D by t steps array. Like the previous manner, we reshape the array to a $D^2 * \#time\ frames$ by 1 column vector. The result is quite successful. The estimated receptive field shows the same temporal decay as the generative receptive field. Since maximum likelihood method is sensitive to the value of data, the maximization result deteriorate as the data size increase, explaining the stronger noise in time-dependent receptive field than instantaneous receptive field.

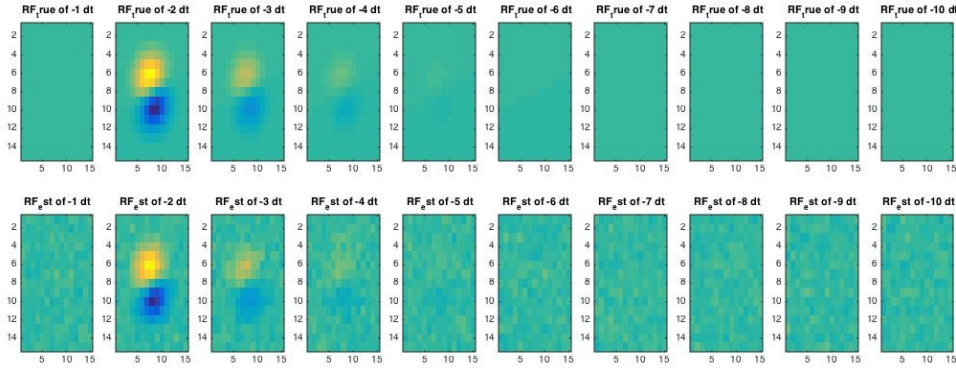


Figure 2: Estimate the receptive field with 10 time steps and visualize the true and the estimated receptive fields for each time step separately. Use the same color map for all panels.

3. Decompose the receptive field into its temporal and spatial component.

The receptive field of the neuron used here consists of a spatial component (the Gabor filter) and a temporal component. Both are independent and the resulting spatial-temporal

component is thus called separable. As discussed in the lecture, you can use singular-value decomposition to separate these two.

The singular value decomposition (SVD) of a real rectangular matrix M factorizes the matrix into components USV' , where the S matrix is diagonal, and composed of real, non-negative numbers. U, V' are orthogonal matrix whose column representing left eigenvectors. The numbers on the diagonal of S are called the singular values of M . Here we use the convention that the singular values are sorted in descending order.

$$M_{ij} = (USV')_{ij} = S_{1,1}U_{i,1}V_{1,j} + S_{2,2}U_{i,2}V_{2,j} + \dots$$

Therefore, The first term of the series is a low-rank approximation to the original matrix, provided the matrix is factorizable, and the first term is distinctly larger than the rest singular values. If the receptive field is truly separable, then the first singular value should be the only non-zero value. From Figure 3.a, we can see that indeed the only non-zero singular value is the first one. The minimization error accounts for the small singular values of estimated receptive field.

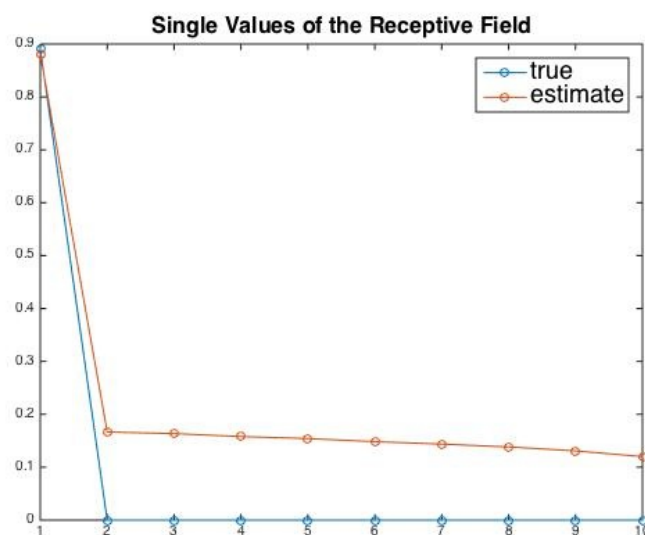
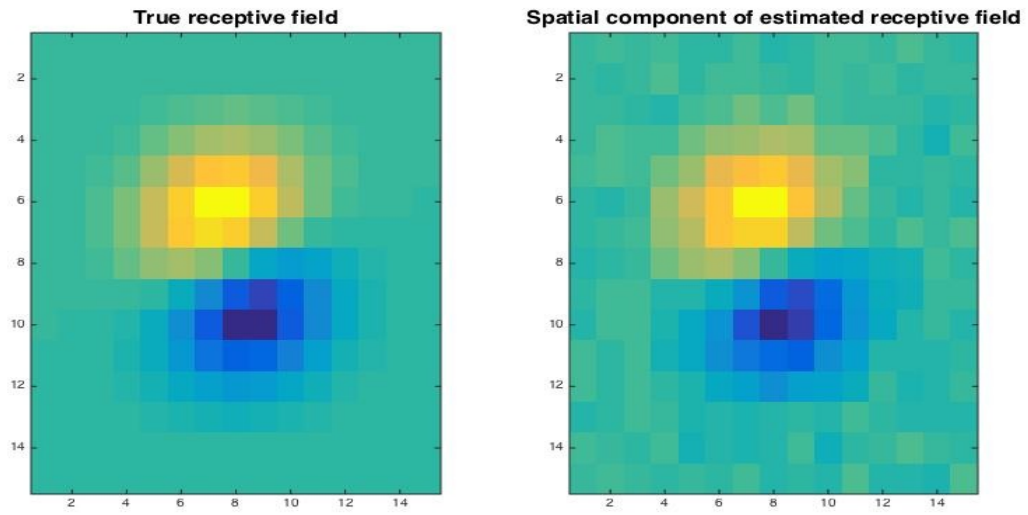
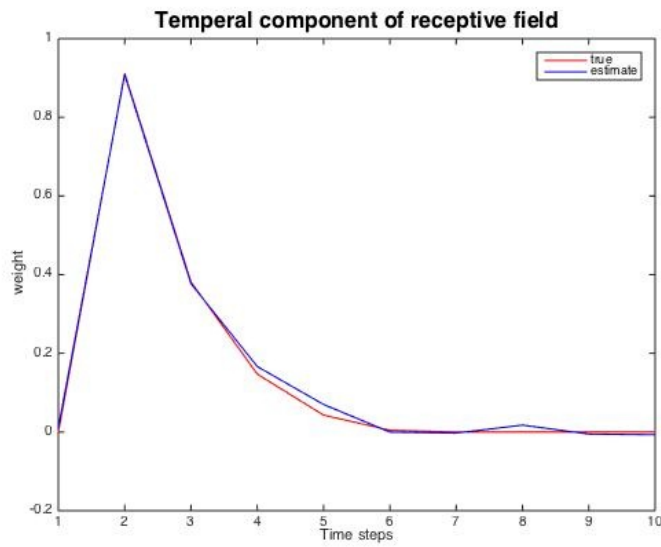


Figure 3: (a) Plot the spectrum of singular values. How many SVs prominently stick out from the rest?



(b) Plot the first temporal component.



(c) Plot the first spatial component.

3.Real data: The bin width is 10 ms. Using the methods developed above, fit the receptive fields of the neuron for one time lag at a time (the ML fit is very sensitive to the number of parameters estimated and will not produce good results if you fit the full space-time receptive field for more than two time lags at once). V1 cells typically respond with a latency of 40–50 ms.

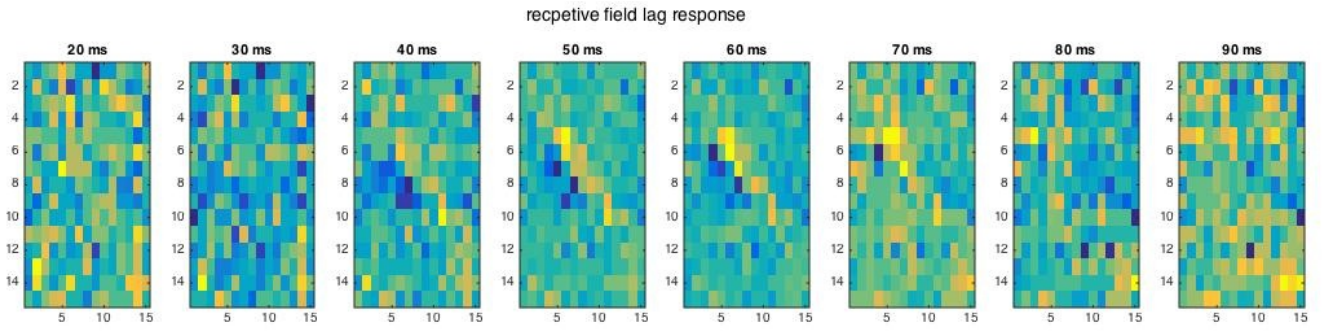


Figure 4: Visualize the raw receptive fields for time lags between 20 and 90 ms.

Is the real data spatial-temporal separable? We also applied singular value decomposition, and the singular value spectrum revealed that the real neuron data is not separable. However, it is suggested that it is possible that non-orthogonal decomposition may give rise to more natural result¹.

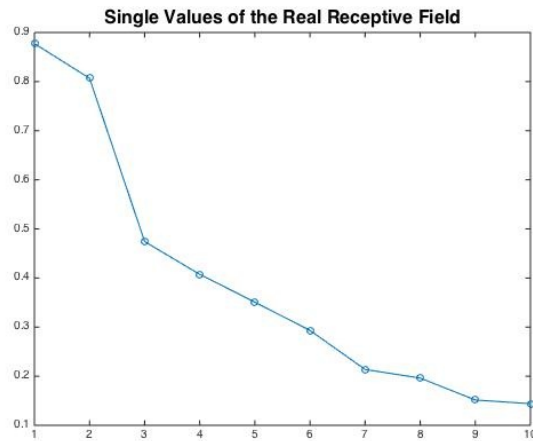
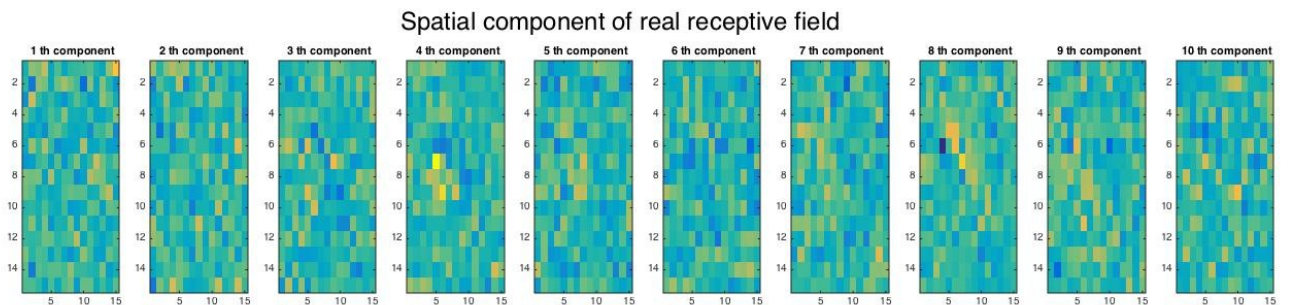
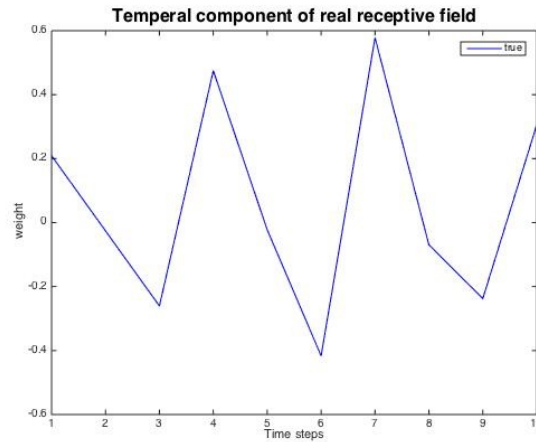


Figure 5. (a) Singular values of real neuron data. The second value is certainly non-zero.



¹ <http://xcorr.net/2011/09/20/using-the-svd-to-estimate-receptive-fields/>

(b) *The first spatial component does not present any filter. The fourth and the 8th component shows a faint sign of filter.*



(c) *The first temporal component indicates the influence of stimuli do not decay with time, which is implausible because V1 neuron should not respond to inputs infinite long time ago.*

Discussion

In this task, we achieve several goals.

Firstly, we showed that the nonlinear linear Poisson model is a simple and efficient way to obtain receptive field of neurons. It doesn't have a close form solution for maximum value, but it has a close form solution for first derivative, which facilitate the computational speed in minimizing log likelihood. However, the model is constrained by data's dimensionality. That is, the times of computation increase D fold when one more dimension is added. There are other problems regarding to maximum likelihood method. The method is so sensitive to the number of parameter estimated, so the larger the data, the worse the estimation. It is also cursed by dimensionality. The demand for samples increase exponentially as dimensionality increase in order to achieve equal quality of optimization.

Secondly, we extended the idea of receptive field to temporal dimension. The neurons may not respond most strongly to the instantaneous input, but the input several millisecond ago. The delay phenomena are particularly prevalent in higher-level cortical area, whose input have to pass several intermediate stations before reaching them. For instance, we showed the

V1 neuron's response started building up from 20 ms and peaked at 60 ms after stimulation in the last task.

We also showed the singular value decomposition is an easy and effective way to decompose spatial-temporal separable receptive field. The method provides a simple gauge of separability —there should be only one non-zero singular value for separable receptive field.

Finally, we analysis the data from real V1 neuron data, which is not spatial-temporal separable. Suppose the neuron is directional tuned, then the time order of the position of stimulus becomes an important trait of the receptive field, and subsequently accounting for the spatial-temporal correlation of the receptive field.

Summary

The task demonstrated a few neural data analysis techniques to analyze the receptive field of neurons. The receptive field of directional or orientational tuned V1 neurons can be estimated by linear-nonlinear Poisson model with maximum likelihood fitting. The fitting result is constrained by the size of the data. The spatial and temporal component of the receptive field can be uncoupled by singular value decomposition, provided they are separable. These techniques are theoretically sound as shown in the fitting of toy model. Lastly, we applied the technique to the real neuron data. It indicated that the V1 simple cells response most strongly to stimuli occurring 40 to 60 millisecond a head of the recording time.