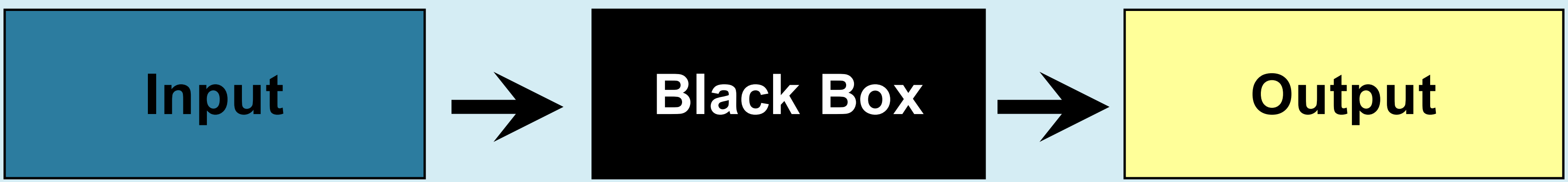
Spike Triggered Covariance: Space and Time

Frederic Theunissen

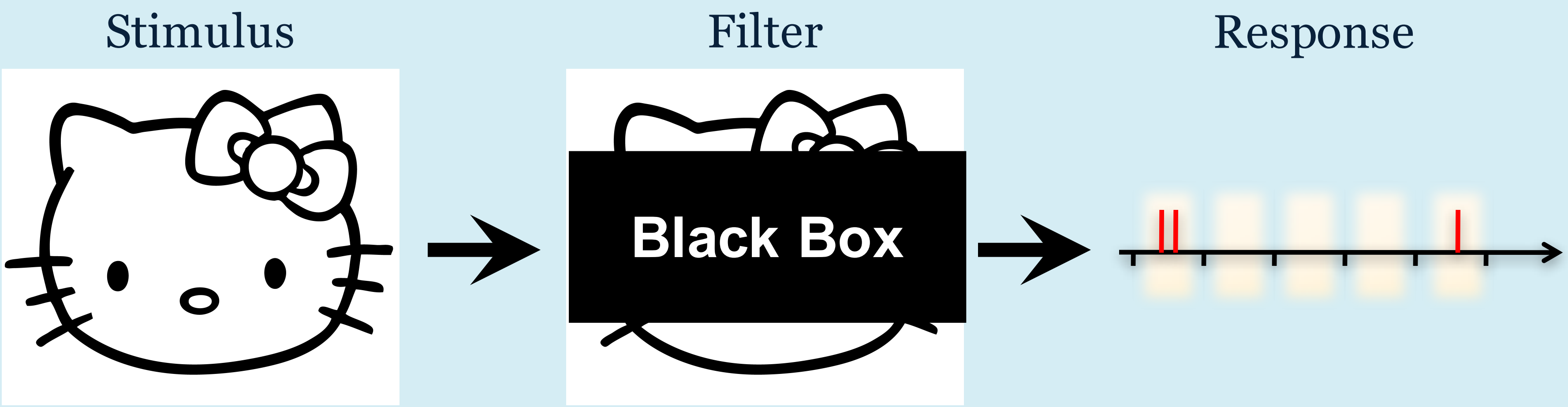
Neural Data Analysis

Summer 2016

Brain as Black Box

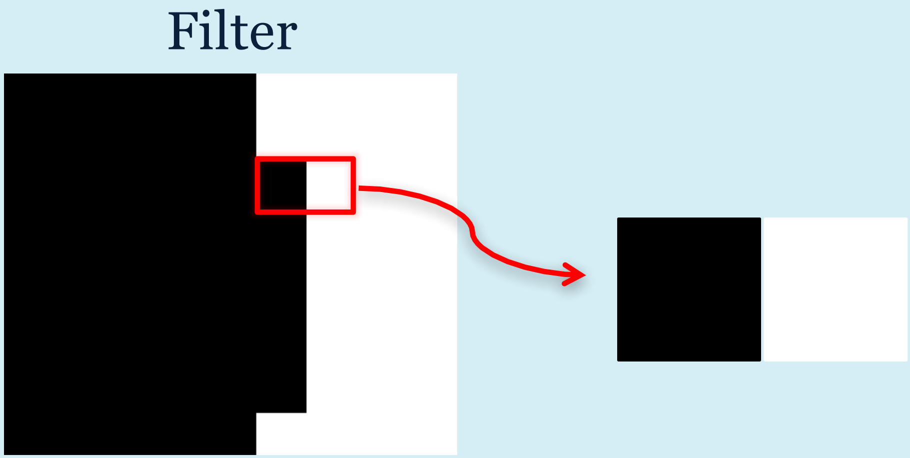


Filter Example

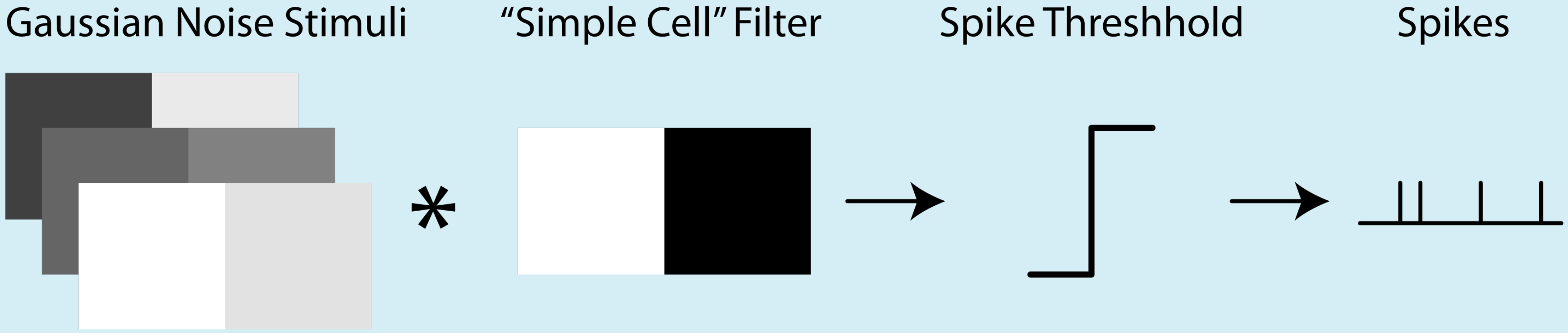


How do we find the filter from the stimulus and response?

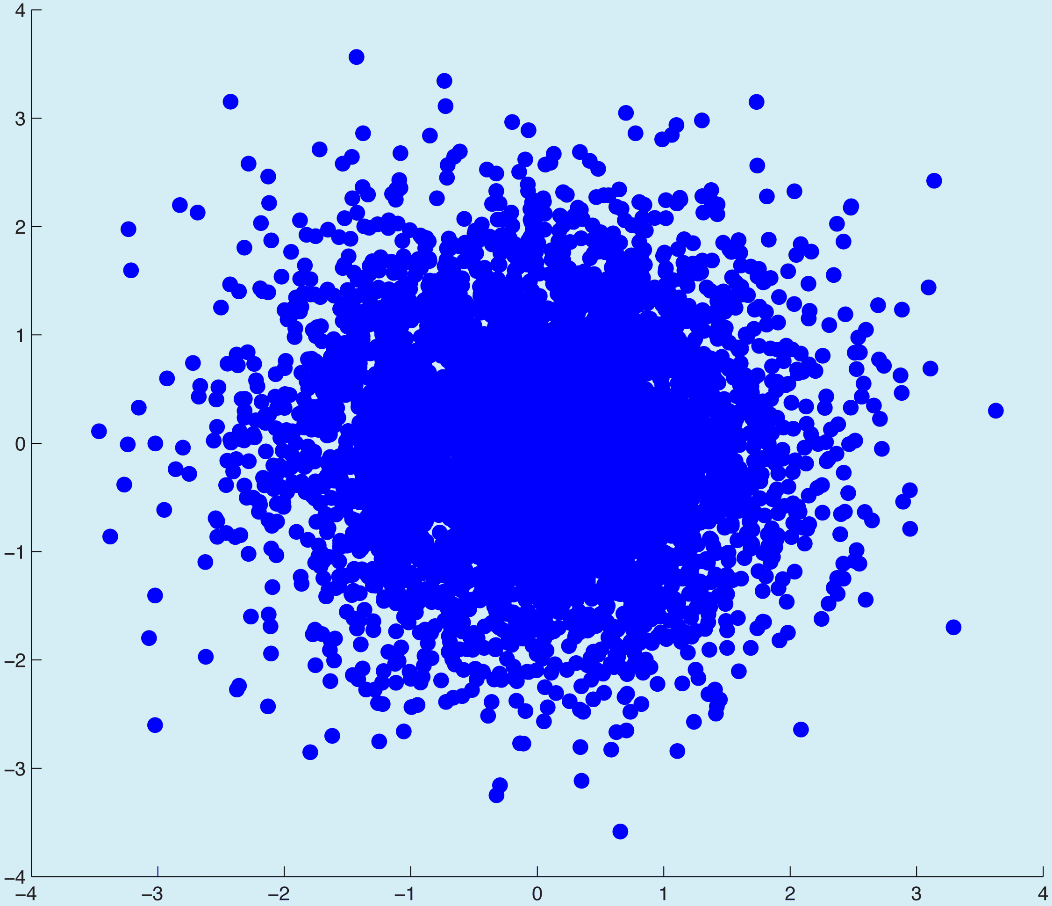
Two Pixel Filter Example



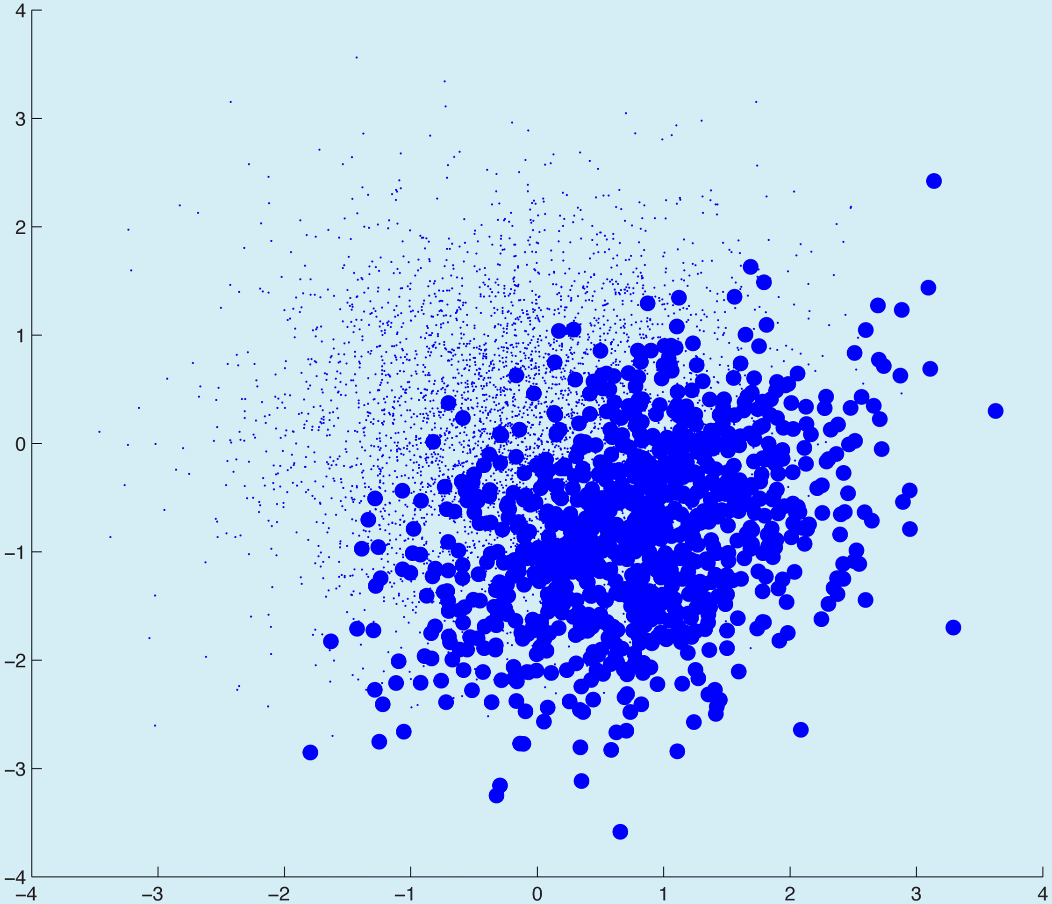
Two pixel Model Simple Cell



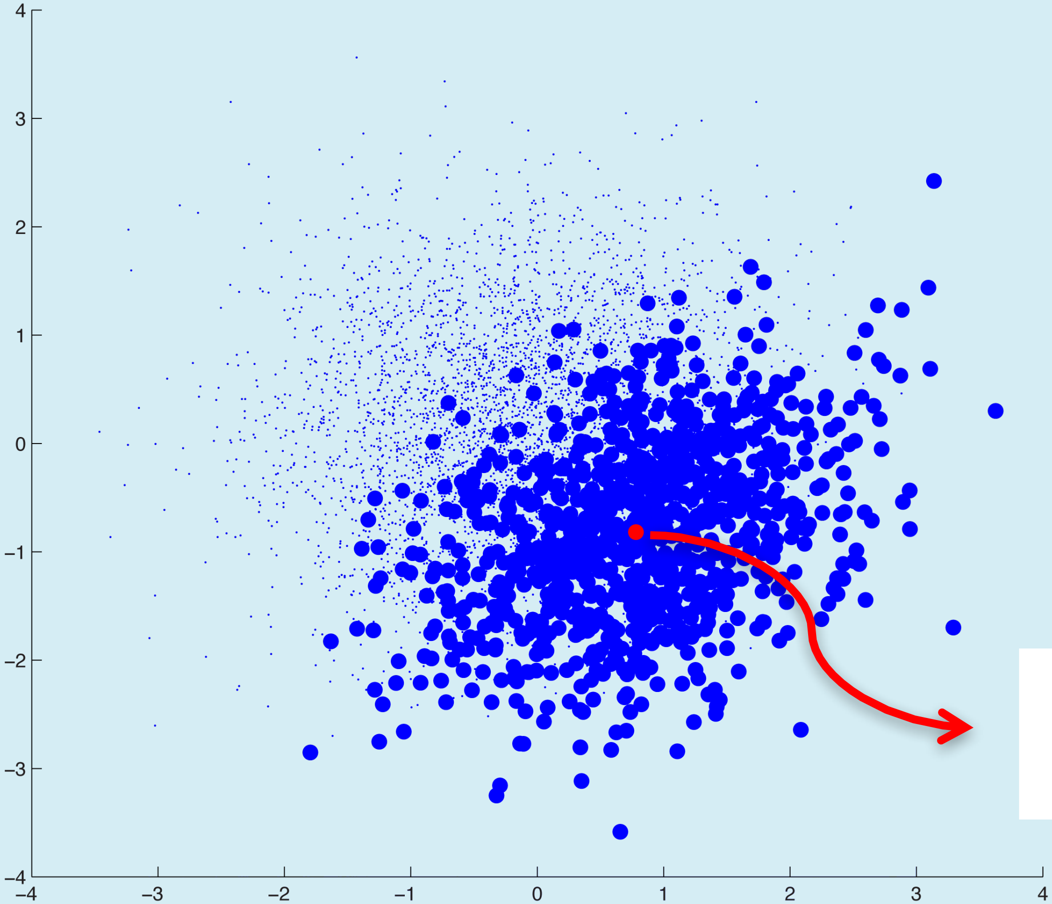
Two Pixel Gaussian Noise

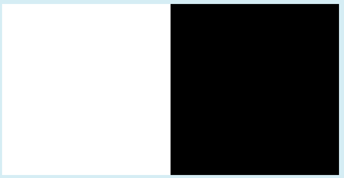


Spike Triggered Stimuli

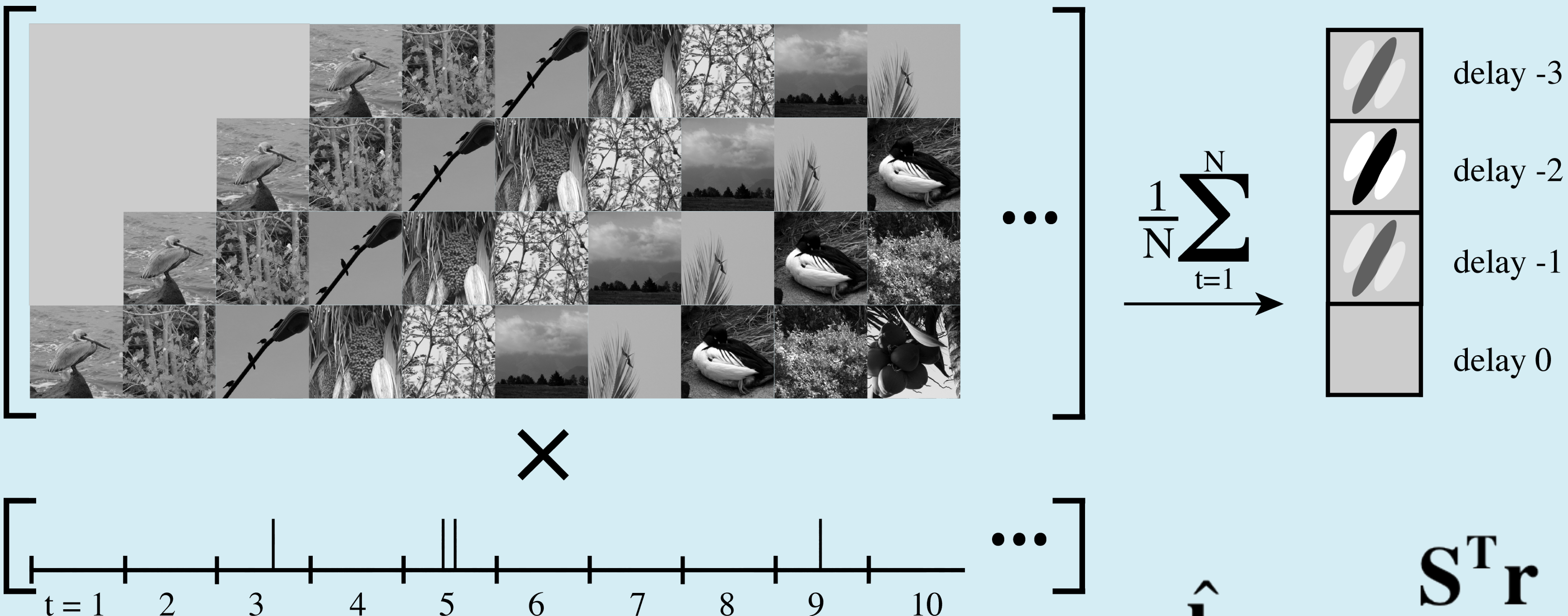


Average of Spike Triggered Stimuli





The Spike Triggered Average



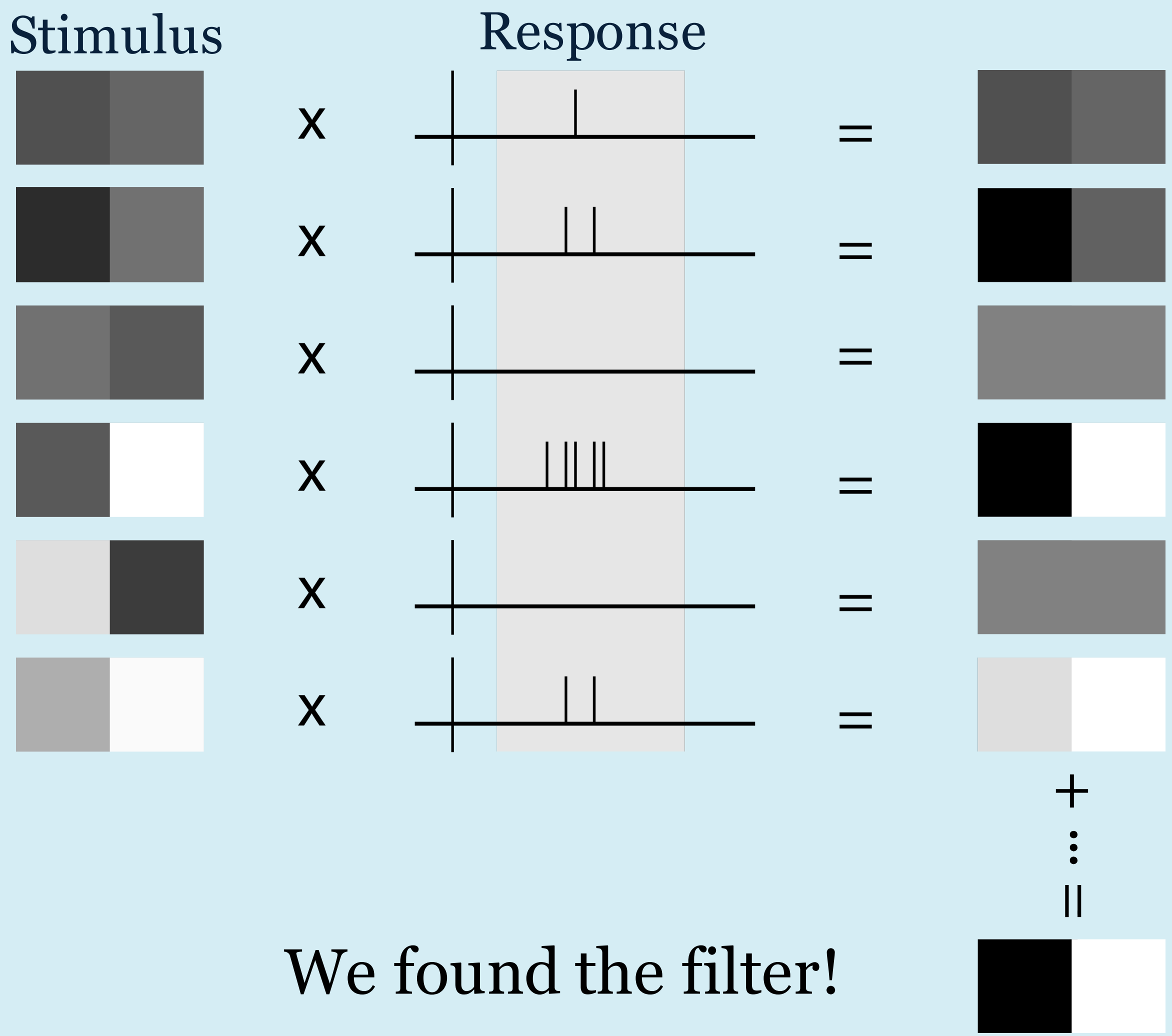
$$\hat{\mathbf{h}}_{STA} = \frac{\mathbf{S}^{\mathbf{T}}\mathbf{r}}{N}$$

Spike Triggered Methods as Regression

$$\hat{\mathbf{h}}_{STA} = \frac{\mathbf{S}^{\mathrm{T}}\mathbf{r}}{N}$$

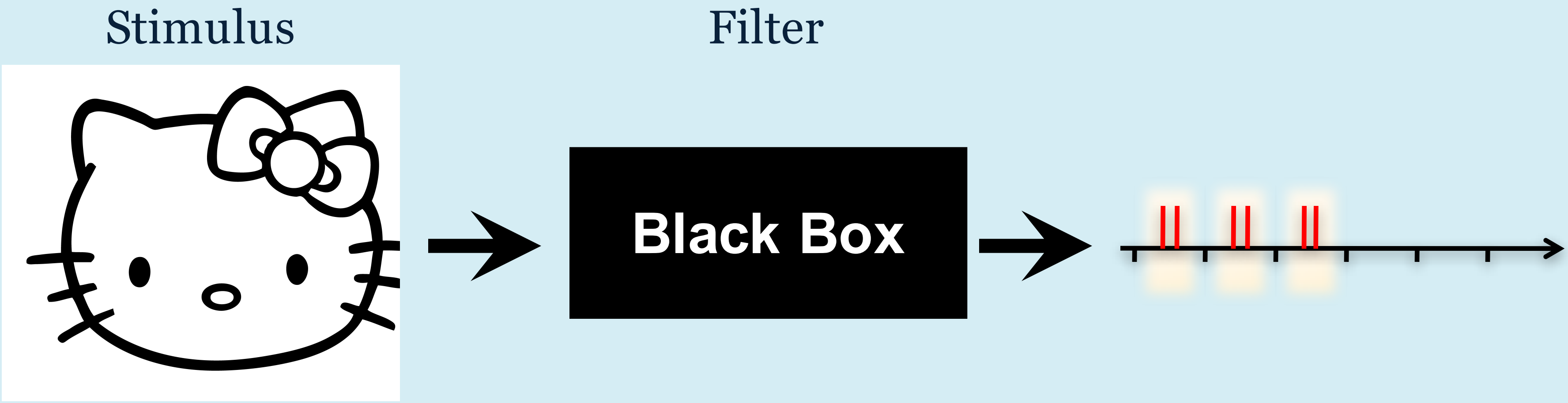
$$\hat{\mathbf{h}}_{cSTA} = \left(\mathbf{S}^{\mathrm{T}}\mathbf{S}\right)^{-1}\mathbf{S}^{\mathrm{T}}\mathbf{r}$$

Spike Triggered Average



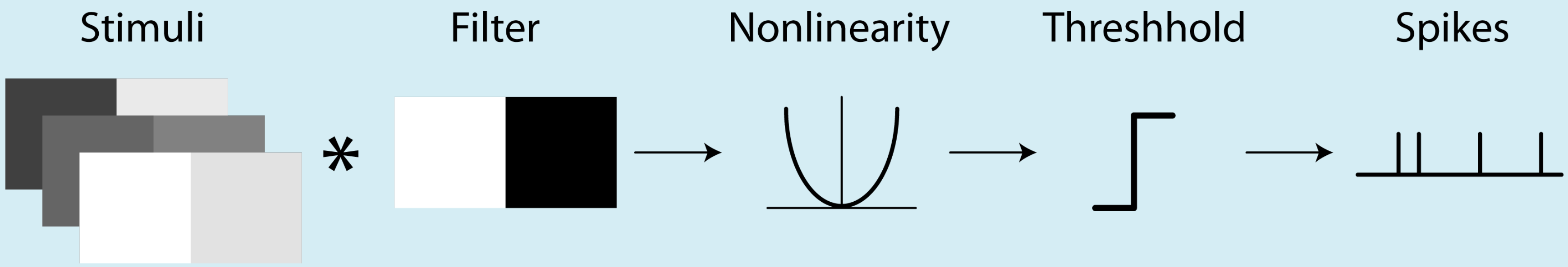
We found the filter!

Complex Filter Example

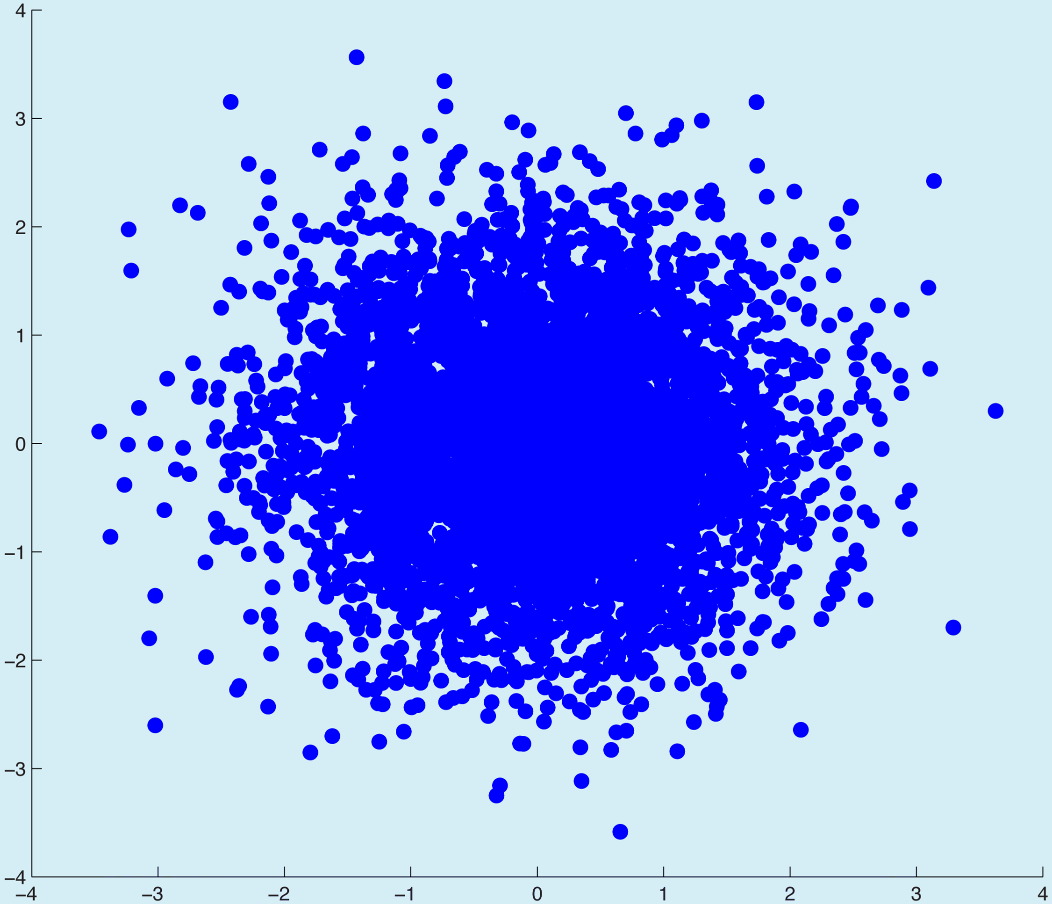


How can we find a phase invariant filter?

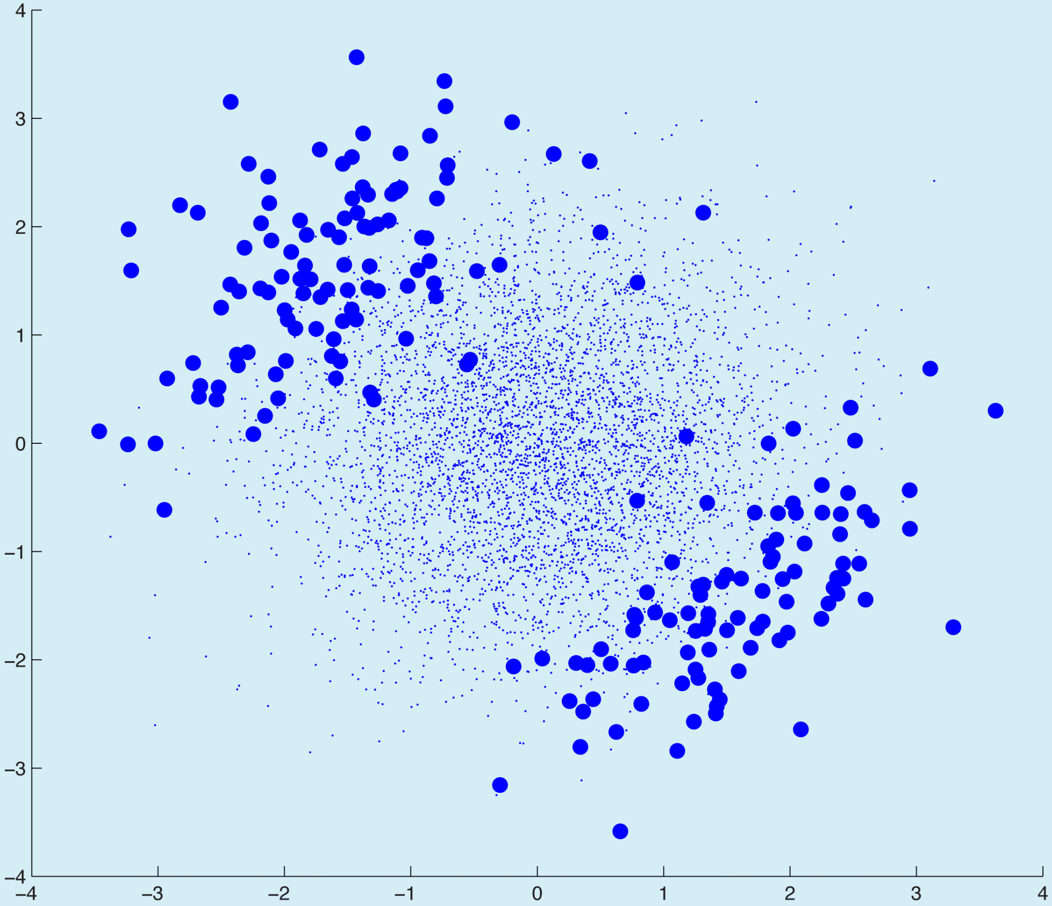
Two Pixel Model Complex Cell



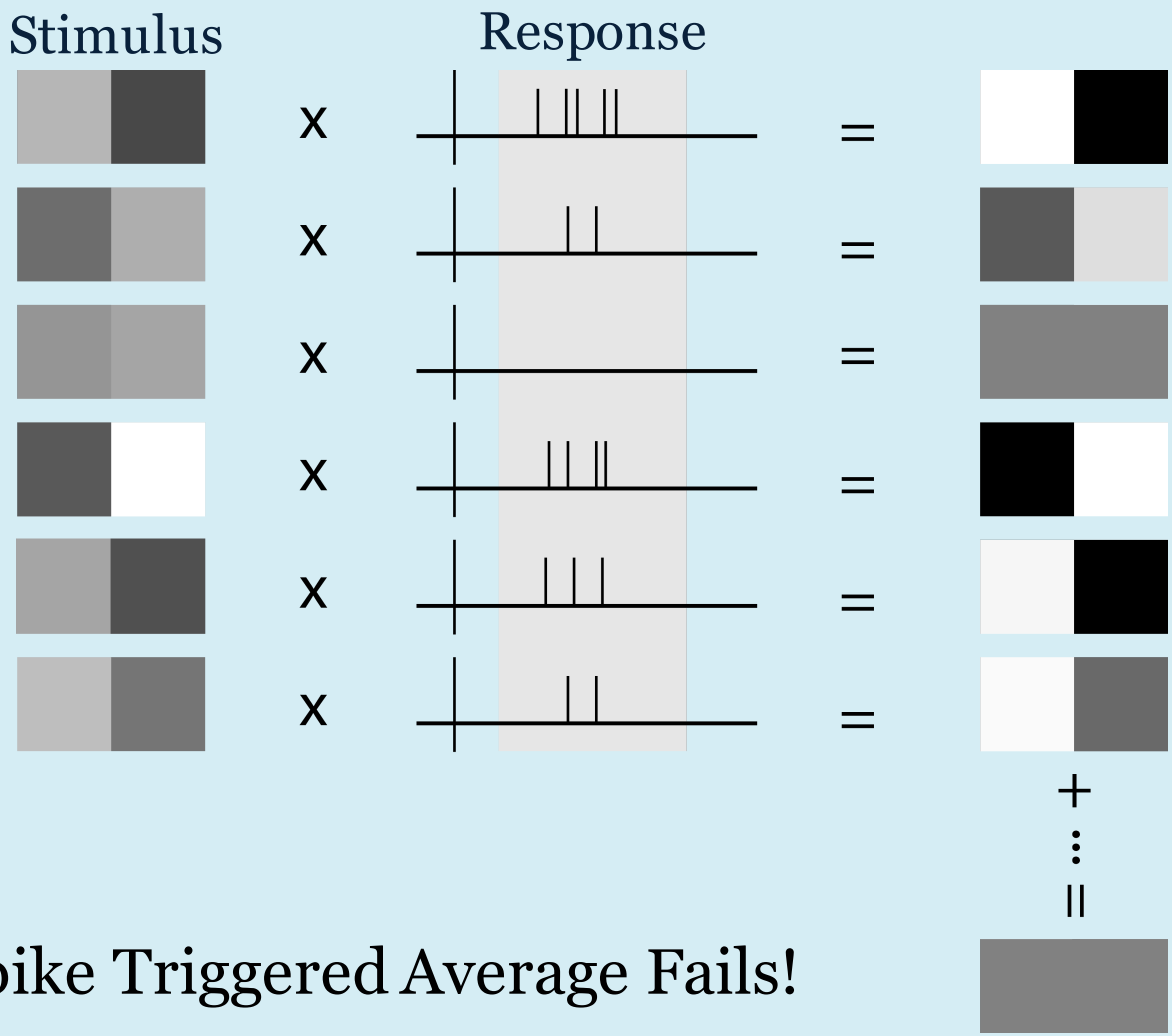
Two Pixel Gaussian Noise



Spike Triggered Stimuli



Spike Triggered Average



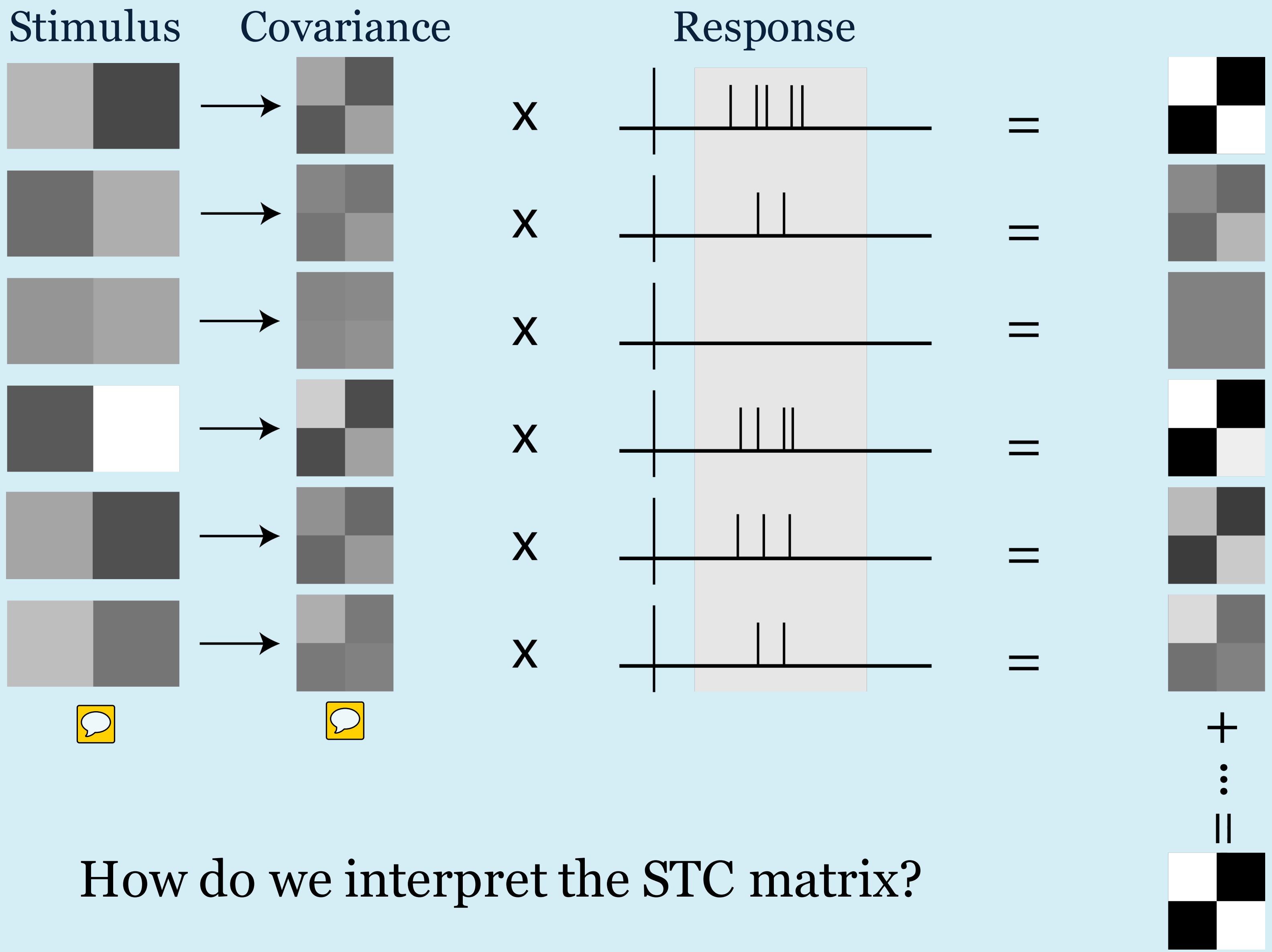
Spike Triggered Average Fails!

Can we use pixel interactions?

$$\begin{array}{cc} p1 & p2 \\ -1 & 1 \end{array} \quad \longrightarrow \quad \begin{array}{ccc} & p1 & p2 \\ p1 & 1 & -1 \\ p2 & -1 & 1 \end{array}$$

$$\begin{array}{cc} p1 & p2 \\ 1 & -1 \end{array} \quad \longrightarrow \quad \begin{array}{ccc} & p1 & p2 \\ p1 & 1 & -1 \\ p2 & -1 & 1 \end{array}$$

Spike Triggered Covariance

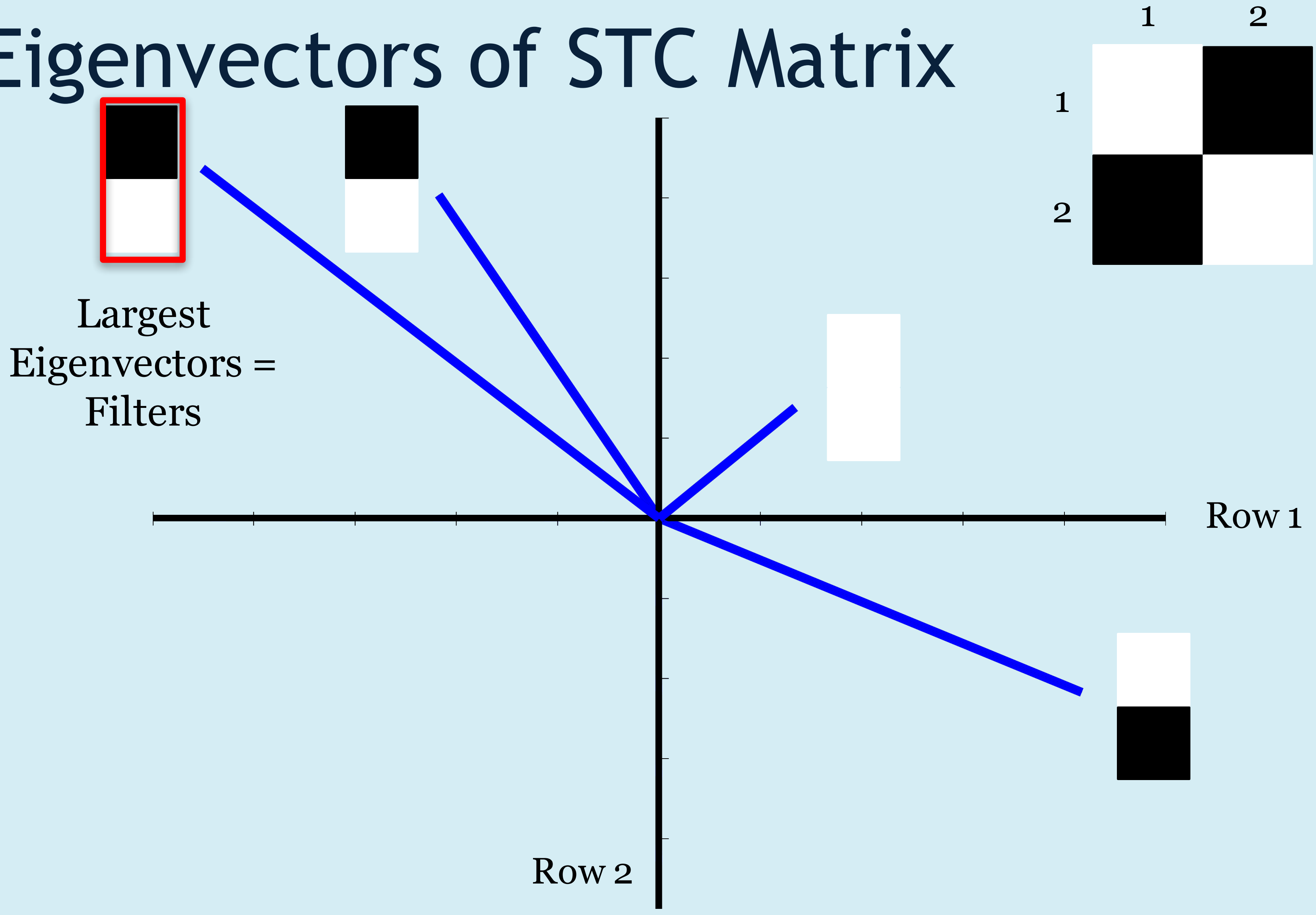


How do we interpret the STC matrix?

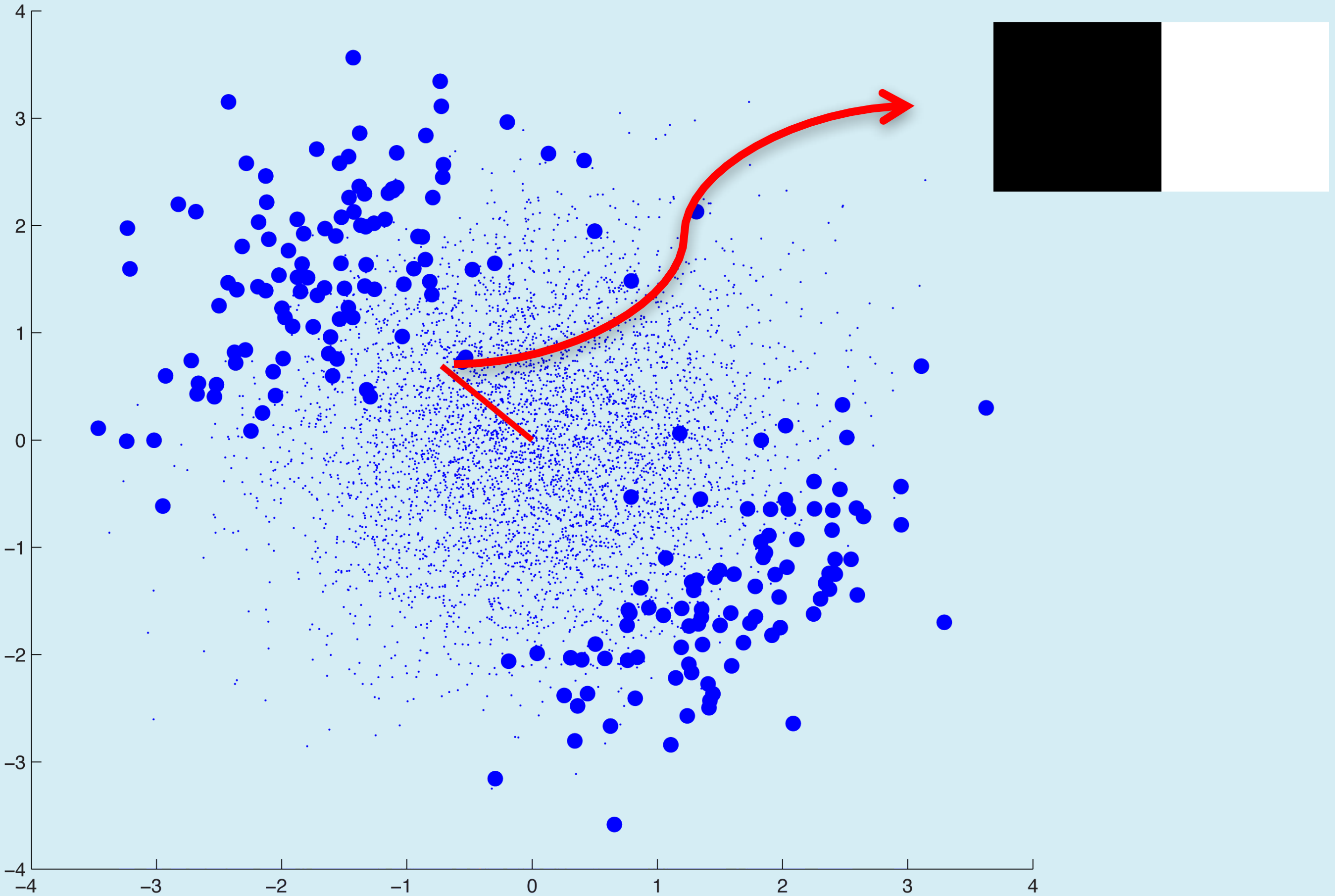
Interpreting the STC Matrix

- STC matrix is large and complex
- Need a way to reduce dimensionality but retain the information
- PCA can find directions that account for most variance

Eigenvectors of STC Matrix

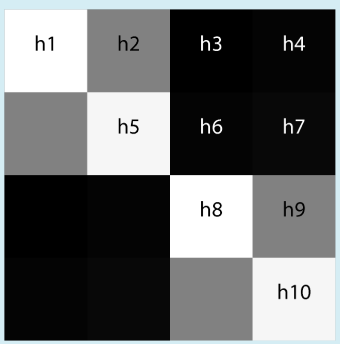


First PC of Spike Triggered Stimuli



Spike Triggered Covariance Analysis

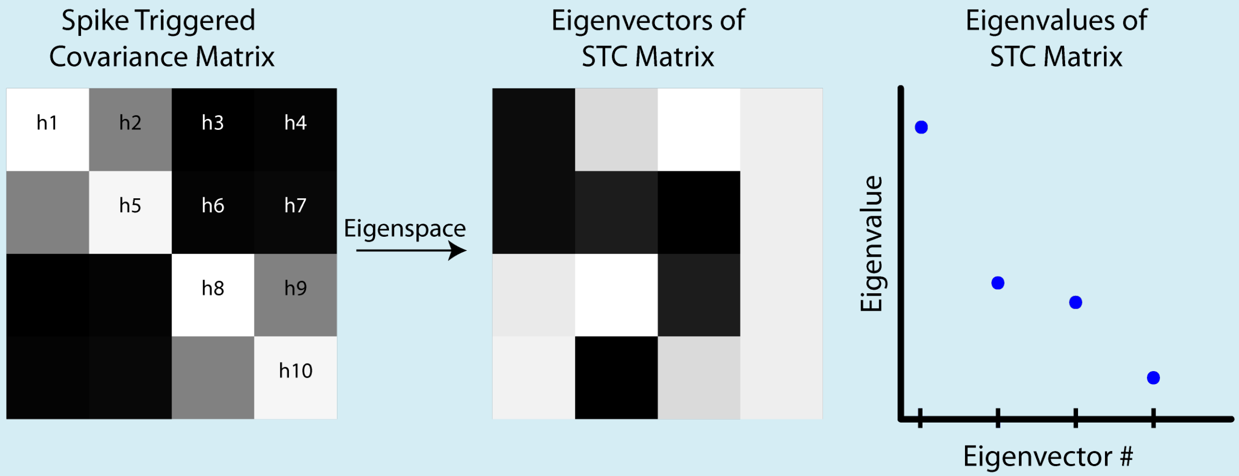
Spike Triggered
Covariance Matrix



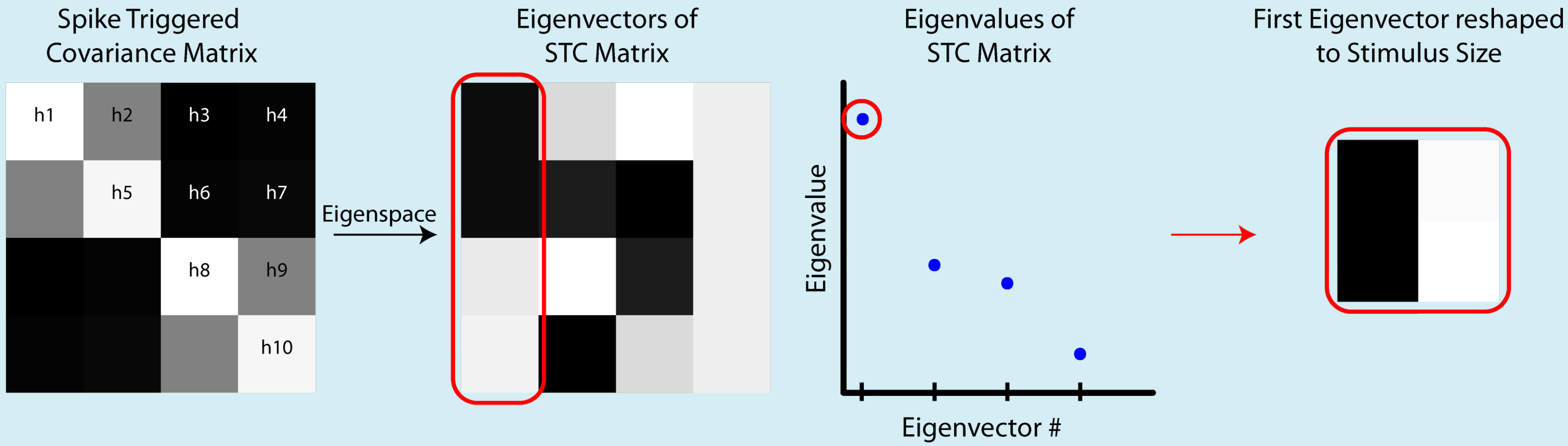
$$C(t) = (S(t) - \overline{S})^{\mathsf{T}} (S(t) - \overline{S})$$

$$\hat{\mathbf{h}}_{cSTC} = \left(\mathbf{C}^{\mathbf{T}}\mathbf{C}\right)^{-1}\mathbf{C}^{\mathbf{T}}\mathbf{r}$$

Spike Triggered Covariance Analysis



Spike Triggered Covariance Analysis



“Curse of dimensionality”

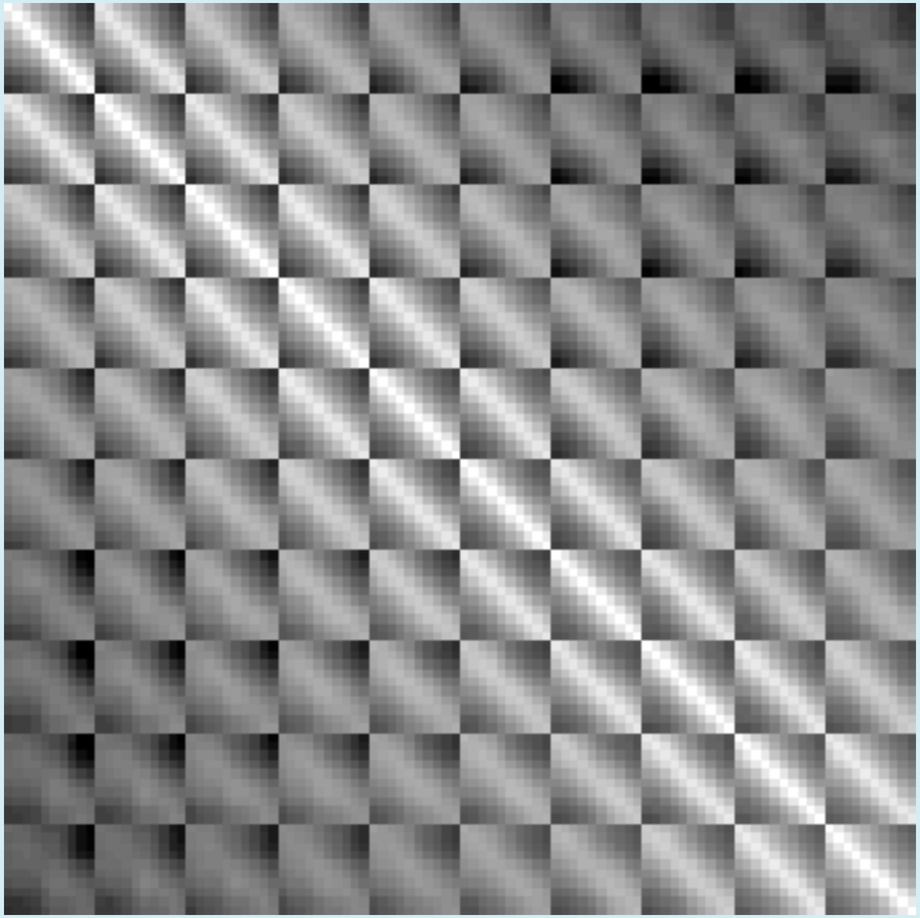
Stimulus

1	2	3
3	4	6
7	8	9

Covariance Matrix

	1	2	3	4	5	6	7	8	9
1									
2									
3									
4									
5									
6									
7									
8									
9									

2D Covariance Matrix



Spike Triggered Covariance in V1

Filter 1

Filter 2

Touryan et al., 2005

What about motion?

STC and Volterra Expansion

$$\hat{y}(t) = h_0 + \sum_{\tau=0}^{T-1} h_1(\tau)s(t-\tau) + \sum_{\tau_1=0}^{T-1}\sum_{\tau_2=0}^{T-1} h_2(\tau_1,\tau_2)s(t-\tau_1)s(t-\tau_2) + \cdots$$

Bias

Linear Filter (cSTA)

2nd order Filter (cSTC)

STC and Volterra Expansion

$$\hat{y}(t) = h_0 + \sum_{\tau=0}^{T-1} h_1(\tau)s(t-\tau) + \sum_{\tau_1=0}^{T-1}\sum_{\tau_2=0}^{T-1} h_2(\tau_1,\tau_2)s(t-\tau_1)s(t-\tau_2) + \cdots$$

$$h_{1,1}^{2}s_1s_1 + h_{1,2}^{2}s_1s_2 + \ldots + h_{2,1}^{2}s_2s_1 + h_{2,2}^{2}s_2s_2 + \ldots$$

That's just a linear regression problem with additional regressors....

The second order regressors can be written as a vector or a matrix

$$N^2 \cdot 1 \qquad\qquad N \cdot N$$

$$\begin{matrix} s_1 s_1 \\ s_1 s_2 \\ \vdots \\ s_2 s_1 \\ \vdots \end{matrix} \qquad \text{or} \qquad \begin{matrix} s_1 s_1 & s_1 s_2 & \cdots & s_1 s_N \\ s_2 s_1 & s_2 s_2 & \cdots & s_2 s_N \\ \vdots & & \ddots & \vdots \\ s_N s_1 & \cdots & & s_N s_N \end{matrix}$$

Note that $s_1 s_2 = s_2 s_1$ → there are only $(N^2-N)+1$ independent regressors
→ The regressor matrix is symmetric.

Solving only for the second order regressors

$$\boxed{\vec{h}^2 = \frac{\langle rs_{i,j} \rangle}{\langle s_{i,j} s_{i,j} \rangle}}$$

$N^2 \cdot 1$

$$\begin{matrix} \langle rs_1 s_1 \rangle \\ \langle rs_1 s_2 \rangle \\ \vdots \\ \langle rs_2 s_1 \rangle \\ \vdots \\ \langle rs_N s_N \rangle \end{matrix}$$

Cross-correlation

This is the STC!

Auto-correlation

$N^2 \cdot N^2$

$$\begin{matrix} \langle (s_1 s_1)(s_1 s_1) \rangle & \langle (s_1 s_1)(s_1 s_2) \rangle & \cdots & \langle (s_1 s_1)(s_N s_N) \rangle \\ \langle (s_1 s_2)(s_1 s_1) \rangle & \langle (s_1 s_2)(s_1 s_2) \rangle & \cdots & \langle (s_1 s_2)(s_N s_N) \rangle \\ \vdots & & \ddots & \vdots \\ \langle (s_N s_N)(s_1 s_1) \rangle & \cdots & & \langle (s_N s_N)(s_N s_N) \rangle \end{matrix}$$

The linear filter in STC:

- In STC, the spike-triggered average is firstsubtracted from the stimulus at each spike event. Since the STA is the reverse filter (as long as there is little structure in the spike auto-correlation function), this effectively allows one to estimate the second order filter.
- This approach involves solving for the first and second order filter sequentially.
- A better solution would be to solve for the two simultaneously. Using gradient descent methods, one could first initialize the parameters for the first order filter. These parameter would then get adjusted when the second order filter is fitted as needed.

Visualizing the second order filter

- The second order filter is visualized by writing it as a matrix and finding the eigenvectors of this symmetric matrix.
- The projection of the stimulus features into these eigenspace yield simple quadratic predictions for the responses.

Step 1. Write the second order filter as a symmetric matrix

$$\vec{h}^2 = \begin{bmatrix} h_{1,1}^2 \\ h_{1,2}^2 \\ \vdots \\ h_{2,1}^2 \\ \vdots \\ h_{N,N}^2 \end{bmatrix} = \begin{bmatrix} h_{1,1}^2 & h_{1,2}^2 & \cdots & h_{1,N}^2 \\ h_{2,1}^2 & h_{2,2}^2 & & \vdots \\ \vdots & & \ddots & \\ h_{N,1}^2 & \cdots & & h_{N,N}^2 \end{bmatrix} = \mathbf{H}^2$$

Step 2. The second order term is then:

$$\vec{s}^{\,T}\mathbf{H}^2\vec{s}$$

Step 3. Find the eigenvectors of H^2

$$\mathbf{H}^2 = \mathbf{S}_e \Lambda \mathbf{S}_e^T$$

Where S_e is the matrix of column eigenvectors and lambda is the diagonal matrix of eigenvalues.

Step 4. Examine the eigenvectors and the contribution of each projection of the stimulus on that eigenvector to the second order term

If $\vec{S}_{ei}$ are eigenvectors and S is the stimulus and the projection of S on the eigenspace is given by k_i:

$$\vec{S} = k_1\vec{S}_{e1} + k_2\vec{S}_{e2} + \cdots + k_N\vec{S}_{eN}$$

The second order term is then:

$$\vec{s}^T H^2 \vec{s} = k_1^2\lambda_1 + k_2^2\lambda_2 + k_3^2\lambda_3 + \cdots + k_N^2\lambda_N$$