

# Neural Data Analysis

Tutorial 2: Linear Model. Direct Fit

# Rev-Correlations for Nat Stats

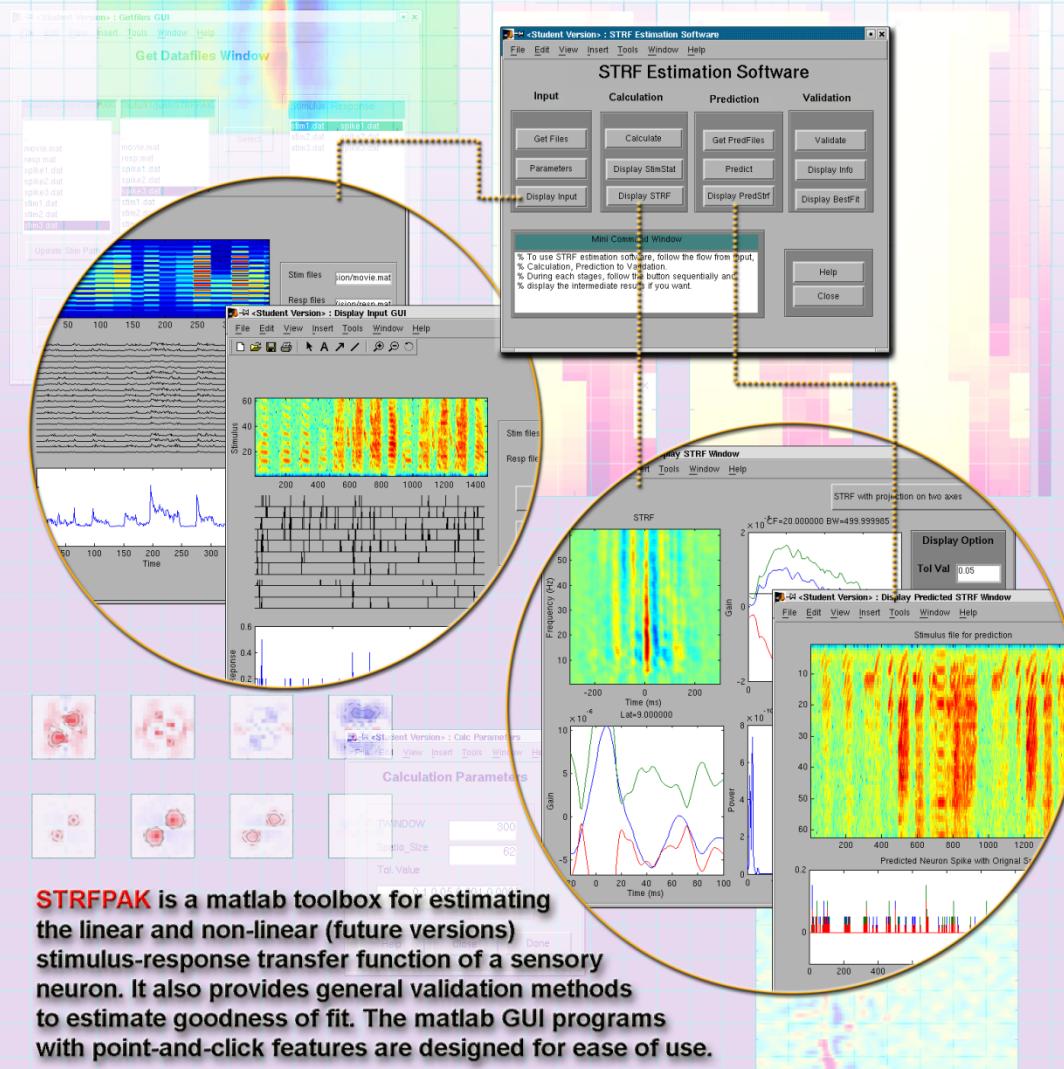
- STRFPAK.
  - Non stationary spatial stimulus correlations
  - Regularization in eigen-space
  - Regularization in joint eigen/pixel space
  - Prediction Validation
- Preprocessing for auditory neurons.
  - Compression
  - Spectrograms vs Wavelets and Time-frequency scale
  - Adaptive gain control

# STRFPAK

Spatio-Temporal Receptive Field Estimation Software



<http://www.nimh.nih.gov/euroinformatics/index.cfm>



STRF  
UCBSTRF



<http://strfpak.berkeley.edu>

# Reducing the dimensions: The Classical STRF Model

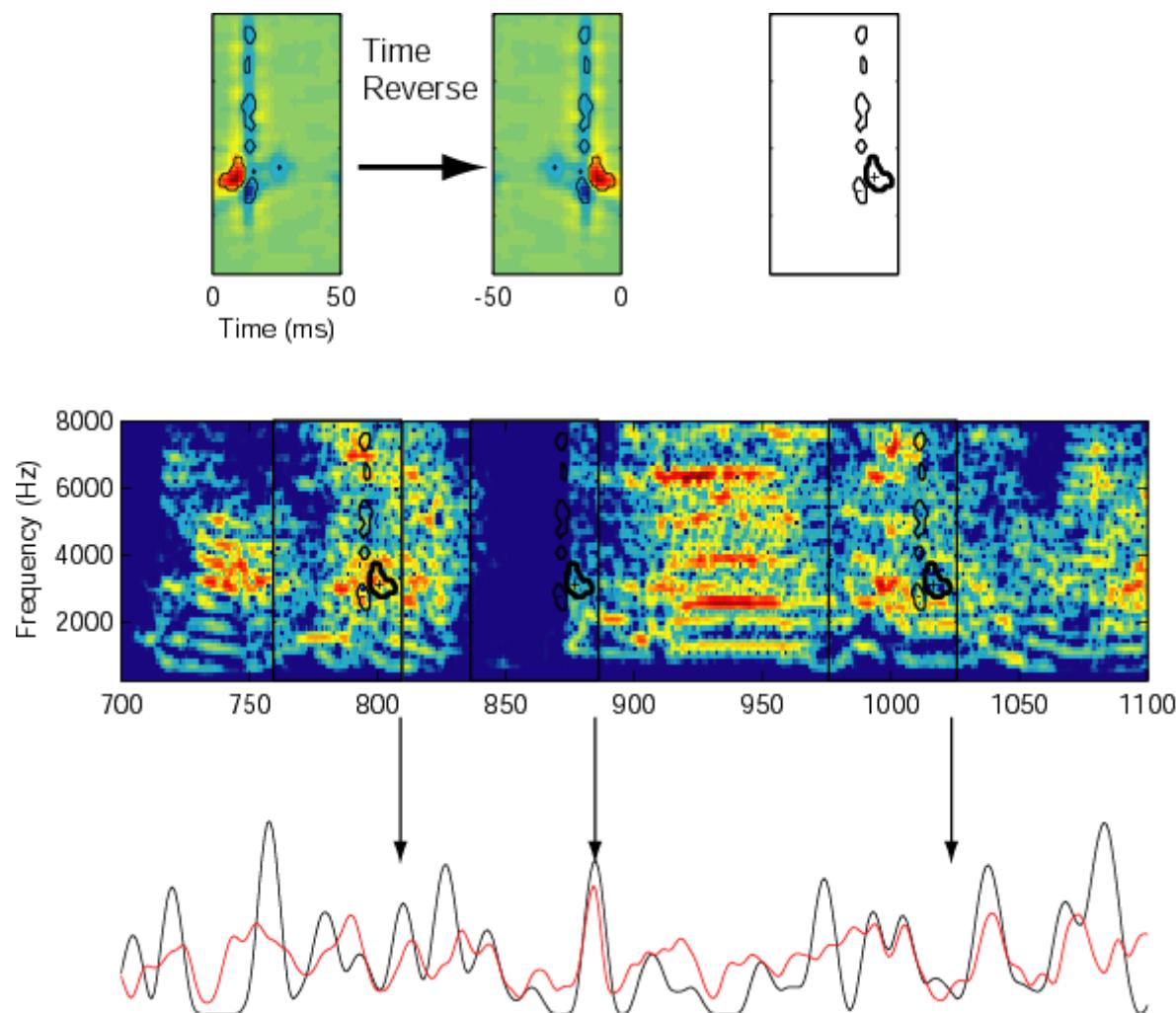
- Encoding Analysis: Linear Model

$$\overbrace{\vec{r}(t)}^{Est} = f(\vec{s}(t)) \Rightarrow \overbrace{\vec{r}(t)}^{Est} = \vec{h} \cdot \vec{\phi}(\vec{s}(t))$$

- Mutual information: Gaussian Noise

$$I(s, r) = H(r) - H(r | s) \quad \rightarrow \quad p(r(t)) = \frac{1}{\sqrt{2\pi n}} e^{-\frac{1}{2} \frac{(r(t) - \bar{r}(t))^2}{n^2}}$$

# Spectro-temporal Receptive Fields of Auditory Neurons



# Receptive Fields and Linear Filters in Sensory Neuroscience

- Vision: Spatio-Temporal
  - Hubel & Wiesel
  - deValois
  - Shapley, Ringach, Furster
  - Freeman
  - Gallant, Dan.
  - Pillow
- Audition: Spectro-Temporal
  - De Boer, Eggermont, Aertsen, Young
  - Shamma, Schreiner
  - Linden, Sahani
  - Theunissen

# Mathematics of linear STRF Estimation – analytical solution

- White-noise analysis.
  - Revcor. Spike-triggered average (STA).
- Non-white analysis.
  - Linear algebra problem.
  - Stationary. Fourier Transform.
  - LTI

# Mathematics of STRF Estimation

- Maximum Likelihood and LMSE (Least Mean Square Error)
- 1-d
- N-d
- Time
- Time/space
- Maximum a posterior (MAP) estimates and Regularization. Ridge Regression.
- Validation

# Likelihood Function: Probability of observing data given model

$$L = \prod_i p(\vec{r}_i | f(\vec{s}_i))$$

*i trials/time=data points  
f() encoding model*

Maximizing the likelihood = Minimizing the negative log likelihood

$$-\log(L) = -\sum_i \log(p(\vec{r}_i | f(\vec{s}_i)))$$

Likelihood between 0 and 1 but has a ceiling value  $\leq 1$  for a saturated model

Negative log Likelihood  $\geq 0$  but has a minimum value

$$p(\vec{r}_i \mid f(\vec{s}_i)) = p(\vec{r}_i \mid \vec{h}, \vec{s}_i)$$

$$\hat{\vec{r}}_i = \vec{h} \cdot \vec{s}_i \quad \text{and} \quad \vec{r}_i = \vec{h} \cdot \vec{s}_i + \vec{n}_i$$

$$p(\vec{r}_i \mid \vec{h}, \vec{s}_i) = N(\vec{h} \cdot \vec{s}_i, n) = \frac{1}{\sqrt{2\pi n}} e^{-\frac{1}{2n^2}(\vec{r}_i - \vec{h} \cdot \vec{s}_i)^2}$$

$$-\log(L) = \sum_i \left( \log(\sqrt{2\pi n}) + \frac{1}{2n^2} (\vec{r}_i - \vec{h} \cdot \vec{s}_i)^2 \right)$$

Minimizing  $-\log(L)$   Minimizing  $\sum_i ((\vec{r}_i - \vec{h} \cdot \vec{s}_i)^2)$

Maximizing Likelihood  Minimizing Mean Square Error

# 1-D

# 1-D

# 1-D

$s$  = stimulus

$r$  = response

$\hat{r}$  = Predicted Response

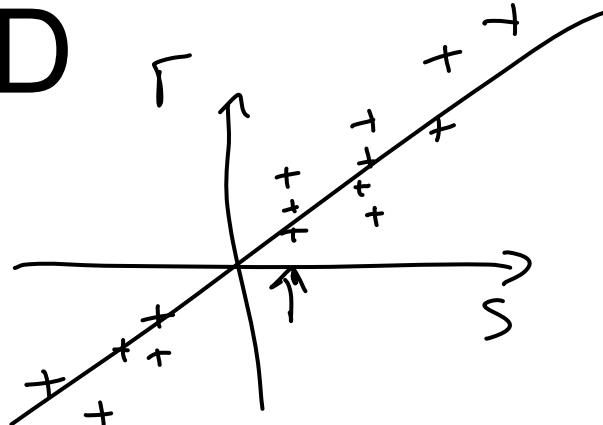
$\hat{r} = h s$      $h$  = parameters of model  $l$  = linear filter

$$\langle \cdot \rangle = \langle (\hat{r} - r)^2 \rangle \quad \langle \cdot \rangle = \text{average } r_i, s_i$$

↳ minimum

$$\langle r \rangle = \frac{1}{N} \sum_{i=1}^N r_i \quad i = 1, \dots, N$$

$$\text{Noise} = p(r|s) = \mathcal{N}(\bar{r}_s, \sigma_s) = \frac{1}{\sqrt{2\pi\sigma_s^2}} e^{-\frac{1}{2} \frac{(r - \bar{r}_s)^2}{\sigma_s^2}}$$



# 1-D

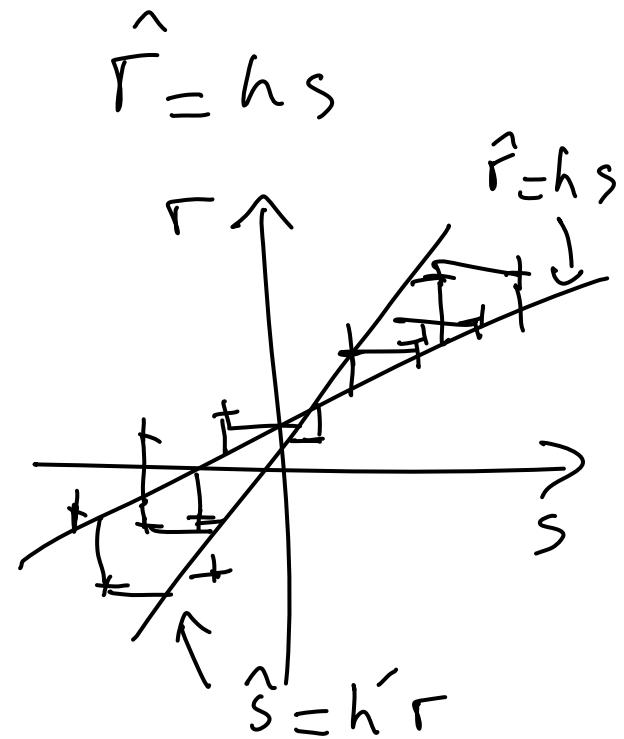
$$\langle (\hat{r} - r)^2 \rangle \rightarrow \min$$

$$\frac{d}{dh} \langle (hs - r)^2 \rangle = 0$$

$$\langle 2(hs - r)s \rangle = 0$$

$$h \langle s^2 \rangle = \langle rs \rangle$$

$$h = \frac{\langle rs \rangle}{\langle s^2 \rangle}$$



$$h' = \frac{\langle rs \rangle}{\langle rr \rangle}$$

$$h \neq \frac{1}{h'}$$

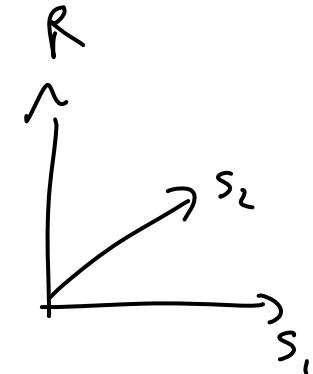
**2-D**

**2-D**

## 2-D

$$\begin{aligned} \vec{r} &= (s_1, s_2) = \vec{s} \\ (\vec{h}_1, \vec{h}_2) &= \vec{h} \end{aligned}$$

$$\hat{r} = h_1 s_1 + h_2 s_2$$



$$\langle (\hat{r} - r)^2 \rangle \text{ min}$$

$$\left\{ \begin{array}{l} \frac{d}{dh_1} \langle (\hat{r} - r)^2 \rangle = 0 \\ \frac{d}{dh_2} \langle (\hat{r} - r)^2 \rangle = 0 \end{array} \right. \iff \left\{ \begin{array}{l} h_1 \langle s_1 s_1 \rangle + h_2 \langle s_1 s_2 \rangle = \langle r s_1 \rangle \\ h_1 \langle s_2 s_1 \rangle + h_2 \langle s_2 s_2 \rangle = \langle r s_2 \rangle \end{array} \right.$$

$$C_{ss} = \begin{pmatrix} \langle s_1 s_1 \rangle & \langle s_1 s_2 \rangle \\ \langle s_2 s_1 \rangle & \langle s_2 s_2 \rangle \end{pmatrix}$$

$$C_{ss} \vec{h} = C_{sr}$$

$$\vec{C}_{sr} = \begin{pmatrix} \langle r s_1 \rangle \\ \langle r s_2 \rangle \end{pmatrix}$$

$\vec{h} = \frac{\vec{C}_{sr}}{C_{ss}}$

## 2-D

$$C_{ss} \vec{h} = \vec{C}_{sr}$$

$$\vec{h} = C_{ss}^{-1} \vec{C}_{sr}$$

$$C_{ss} = Q_{ss}^{-1} \begin{matrix} \nearrow \\ \nwarrow \end{matrix} Q_{ss}$$

Eigenvalues

Eigenvectors

$$= \begin{pmatrix} \lambda_1 & & & & \\ & \ddots & & & \\ & & \lambda_2 & & \\ & & & \ddots & \\ & & & & \lambda_n \end{pmatrix}$$

$$Q_{ss} \vec{h} = \underbrace{Q_{ss} \vec{C}_{sr}}_{\text{ss}}$$

# The Normal Equation

$$\vec{h} = \frac{\vec{C}_{sr}}{\mathbf{C}_{ss}} = \frac{\langle \vec{s}r \rangle}{\langle \vec{s}\vec{s} \rangle}$$

n = number of data points  
k = number of parameters

$$\begin{aligned}\langle \vec{s}r \rangle &= \frac{1}{n} \left( \begin{array}{c} \sum_{i=1}^n s_{i,1} r \\ \sum_{i=1}^n s_{i,2} r \\ \vdots \\ \sum_{i=1}^n s_{i,k} r \end{array} \right) \\ \langle \vec{s}\vec{s} \rangle &= \frac{1}{n} \left( \begin{array}{ccc} \sum_{i=1}^n s_{i,1}s_{i,1} & \cdots & \sum_{i=1}^n s_{i,1}s_{i,k} \\ \vdots & \ddots & \vdots \\ \sum_{i=1}^n s_{i,k}s_{i,1} & & \sum_{i=1}^n s_{i,k}s_{i,k} \end{array} \right)\end{aligned}$$

# The Normal Equation

If we write the stimulus as a Matrix, where rows are data points (from 1 to n) and columns are the stimulus dimensions (from 1 to k):

$$\mathbf{S} = \begin{pmatrix} s_{1,1} & s_{1,2} & & s_{1,k} \\ s_{2,1} & s_{2,2} & & s_{2,k} \\ \vdots & \ddots & & \vdots \\ s_{n,1} & s_{n,2} & \dots & s_{n,k} \end{pmatrix} \quad \text{and} \quad \mathbf{r} = \begin{pmatrix} r_1 \\ r_2 \\ \vdots \\ r_n \end{pmatrix} \quad \text{then:}$$

$$\langle \vec{s}\vec{s} \rangle = \frac{1}{n} \begin{pmatrix} \sum_{i=1}^n s_{i,1}s_{i,1} & \dots & \sum_{i=1}^n s_{i,1}s_{i,k} \\ \vdots & \ddots & \vdots \\ \sum_{i=1}^n s_{i,k}s_{i,1} & \dots & \sum_{i=1}^n s_{i,k}s_{i,k} \end{pmatrix} = \frac{1}{n} \mathbf{S}^T \mathbf{S} \quad \langle \vec{s}r \rangle = \frac{1}{n} \begin{pmatrix} \sum_{i=1}^n s_{i,1}r_i \\ \vdots \\ \sum_{i=1}^n s_{i,k}r_i \end{pmatrix} = \frac{1}{n} \mathbf{S}^T \mathbf{r}$$

# The Normal Equation

The normal equation in Matrix notation (think Matlab/Python) is then:

$$\vec{h} = \frac{\vec{C}_{sr}}{\mathbf{C}_{ss}} = \frac{\langle \vec{s}r \rangle}{\langle \vec{s}\vec{s} \rangle} = \frac{1/n \mathbf{S}^T \mathbf{r}}{1/n \mathbf{S}^T \mathbf{S}} = \frac{\mathbf{S}^T \mathbf{r}}{\mathbf{S}^T \mathbf{S}}$$

$$\vec{h} = (\mathbf{S}^T \mathbf{S})^{-1} \mathbf{S}^T \mathbf{r}$$

# Normal Equation in EigenSpace

$$(S^T S) = Q \cdot \Lambda \cdot Q^T$$

$Q$  is a  $k$  by  $k$  matrix of eigenvectors in columns

Or from an Singular Value Decomposition of  $S$ :

$$S = U \cdot W \cdot V^T$$

$V$  =  $k$  by  $k$  input vectors

$U$  =  $n$  by  $k$  output vectors

$W$  =  $k$  by  $k$  diagonal singular values (called  $S$  in Matlab)

$$(S^T S) = V \cdot W^2 \cdot V^T$$

$$\begin{aligned}V &= Q \\W^2 &= \Lambda\end{aligned}$$

# The Normal Equation in Eigen Space

$$\vec{h} = (\mathbf{S}^T \mathbf{S})^{-1} \mathbf{S}^T \mathbf{r}$$

$$\vec{h} = \mathbf{V}^T (\Lambda)^{-1} \mathbf{V} \mathbf{S}^T \mathbf{r}$$

$$\mathbf{V} \vec{h} = (\Lambda)^{-1} \mathbf{V} \mathbf{S}^T \mathbf{r}$$

Uncorrelate

Whiten

# The Normal Equation directly from SVD

$$\vec{h} = (\mathbf{S}^T \mathbf{S})^{-1} \mathbf{S}^T \mathbf{r}$$

$$\vec{h} = \mathbf{V}^T (\mathbf{W}^2)^{-1} \mathbf{V} \mathbf{S}^T \mathbf{r}$$

# Time is special

- Causal
- Wide sense stationarity
- Linear algebra can be written in terms of correlations and convolutions.
- The eigenvectors of the correlation function is the discrete Fourier Transform basis.

# Time is special

$$r(t)$$

$$s(t-0), s(t-1), s(t-2) \dots$$

$$\hat{r}(t) = h(0) s(t-0) + h(1) s(t-1) + h(2) s(t-2) + \dots$$

$$\hat{r}(t) = \int_0^{\infty} h(\tau) s(t-\tau) d\tau$$

$$C_{ss} \tilde{h} = C_{sr}$$

$$C_{ss} = \begin{pmatrix} \langle s(t-0)s(t-0) \rangle & \langle s(t-0)s(t-1) \rangle \\ \langle s(t-1)s(t-0) \rangle & \langle s(t-1)s(t-1) \rangle \dots \end{pmatrix}$$

$$C_{ss} = \begin{pmatrix} a & b & c & d \\ b & a & b & c \\ c & b & a & b \\ d & c & b & a \end{pmatrix}$$

symmetric Toeplitz matrix

# Time is special

$$Q_{ss} \vec{h}_t = \tilde{\Lambda}_{ss}^{-1} Q_{ss} \vec{C}_{sr_t}$$

$$\vec{h}(w_t) = \tilde{\Lambda}_{ss}^{-1} \vec{C}_{sr}(w_t)$$

# Time-Space

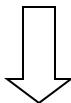
- If space is WSS as well – Fourier domain
- If second order statistics in space are not stationary then mixed: Fourier domain for time and linear algebra in space

# Estimating STRFs – Modified Reverse Correlation

## Linear Time Invariant Transfer Functions

### for Non Stationary Spatial Statistics

$$\hat{r}[t] = \sum_{i=0}^{N-1} \sum_{j=0}^{M-1} h[i, j] s[t - i; j] + r_0$$



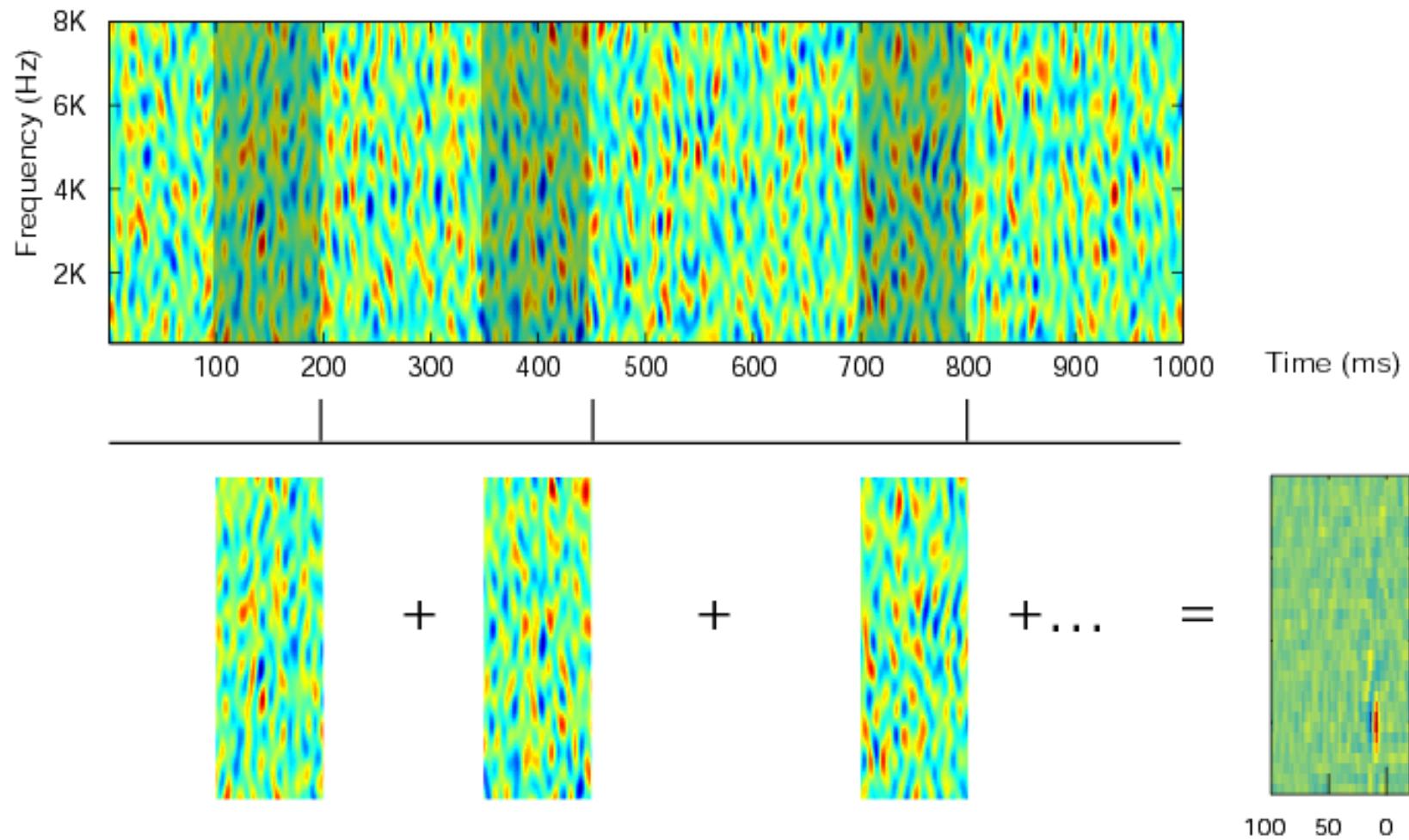
$$\mathbf{k} = \mathbf{C}_{ss}^{-1} \mathbf{C}_{sr} \quad C_{ss} = \begin{pmatrix} \mathbf{r}_{0,0} & \cdots & \mathbf{r}_{0,M-1} \\ \vdots & \ddots & \vdots \\ \mathbf{r}_{M-1,0} & \cdots & \mathbf{r}_{M-1,M-1} \end{pmatrix}$$

$$\mathbf{r}_{i,j} = \begin{pmatrix} \langle s[t,i]s[t,j] \rangle & \langle s[t,i]s[t-1,j] \rangle & \cdots & \langle s[t,i]s[t-(N-1),j] \rangle \\ \langle s[t-1,i]s[t,j] \rangle & \langle s[t-1,i]s[t-1,j] \rangle & & \vdots \\ \vdots & & \ddots & \\ \langle s[t-(N-1),i]s[t,j] \rangle & \cdots & & \langle s[t-(N-1),i]s[t-(N-1),j] \rangle \end{pmatrix}$$

$$\mathbf{H}(\omega_t[i]) = \Lambda(\omega_t[i])^{-1} \mathbf{C}_{SR}(\omega_t[i])$$

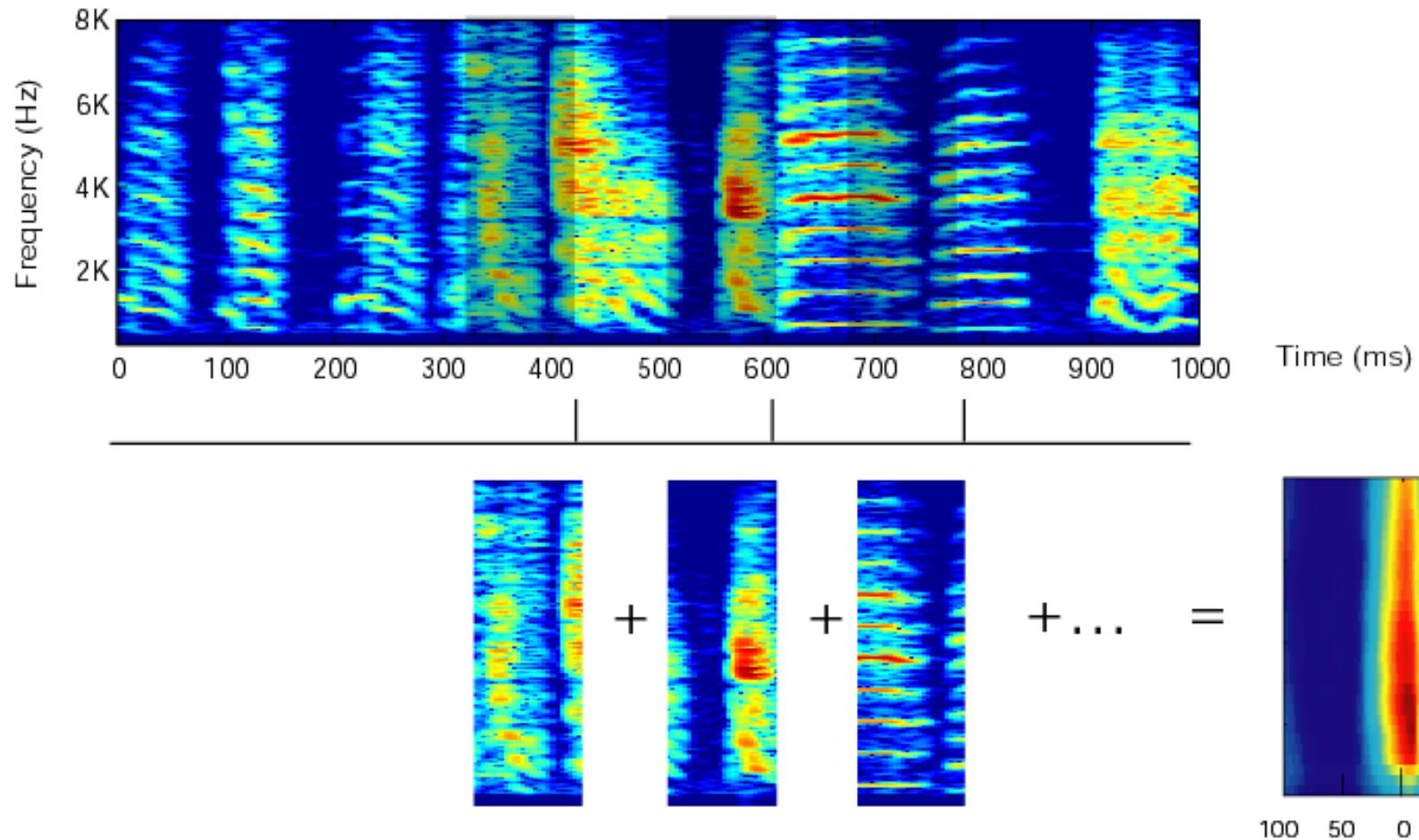
# Estimating the STRF

A. Reverse correlation: Spike-triggered average with ripple-noise yields the STRF

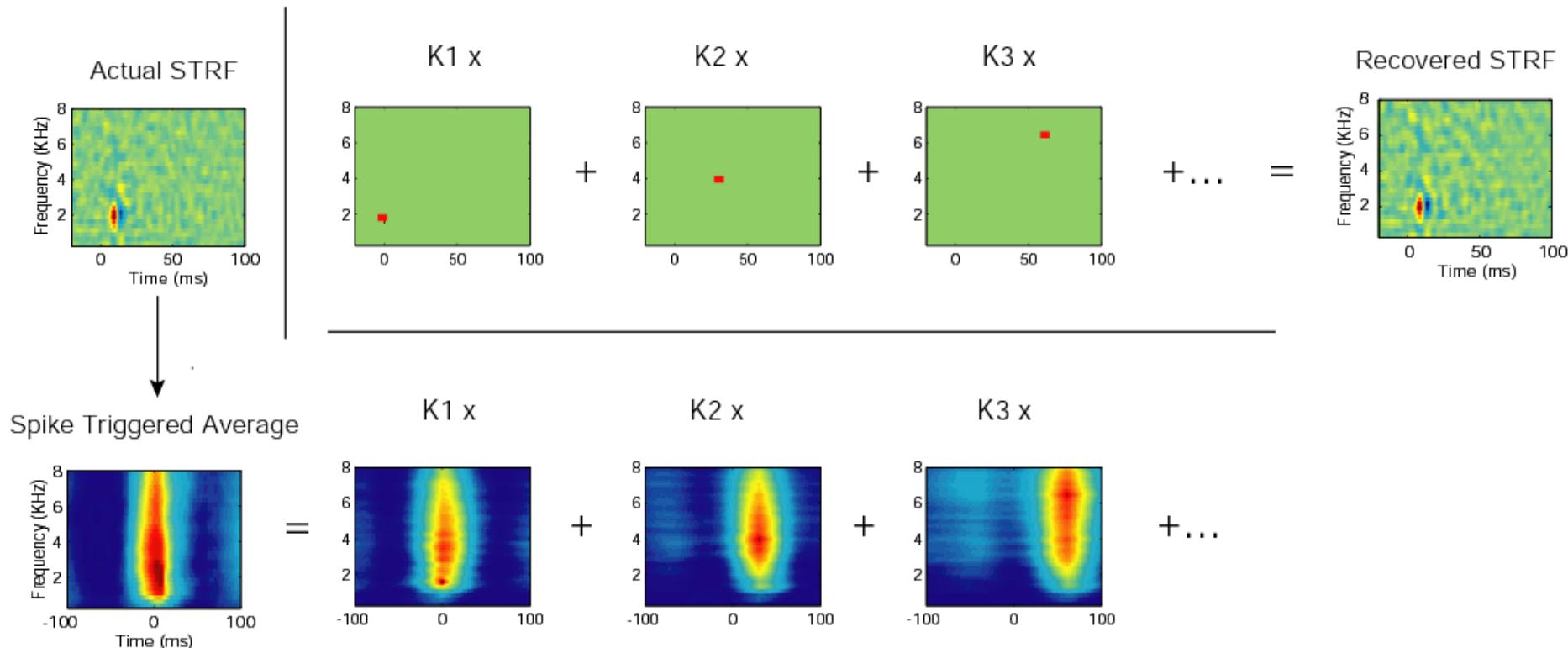


# Estimating the STRF

B. Spike-triggered average with song does not recover the STRF



# Estimating the STRF



$$\vec{h} \cdot \text{AutoCorrelation} = \text{SpikeTriggeredAverage}$$

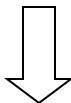
Two point correlation function is translation invariant in time but not in space, Here  $h=(k_1, k_2, k_3\dots)$

# Estimating STRFs – Modified Reverse Correlation

## Linear Time Invariant Transfer Functions

### for Non Stationary Spatial Statistics

$$\hat{r}[t] = \sum_{i=0}^{N-1} \sum_{j=0}^{M-1} h[i, j] s[t - i; j] + r_0$$



$$\mathbf{k} = \mathbf{C}_{ss}^{-1} \mathbf{C}_{sr} \quad C_{ss} = \begin{pmatrix} \mathbf{r}_{0,0} & \cdots & \mathbf{r}_{0,M-1} \\ \vdots & \ddots & \vdots \\ \mathbf{r}_{M-1,0} & \cdots & \mathbf{r}_{M-1,M-1} \end{pmatrix}$$

$$\mathbf{r}_{i,j} = \begin{pmatrix} \langle s[t,i]s[t,j] \rangle & \langle s[t,i]s[t-1,j] \rangle & \cdots & \langle s[t,i]s[t-(N-1),j] \rangle \\ \langle s[t-1,i]s[t,j] \rangle & \langle s[t-1,i]s[t-1,j] \rangle & & \vdots \\ \vdots & & \ddots & \\ \langle s[t-(N-1),i]s[t,j] \rangle & \cdots & & \langle s[t-(N-1),i]s[t-(N-1),j] \rangle \end{pmatrix}$$

$$\mathbf{H}(\omega_t[i]) = \Lambda(\omega_t[i])^{-1} \mathbf{C}_{SR}(\omega_t[i])$$

# STRF Estimation

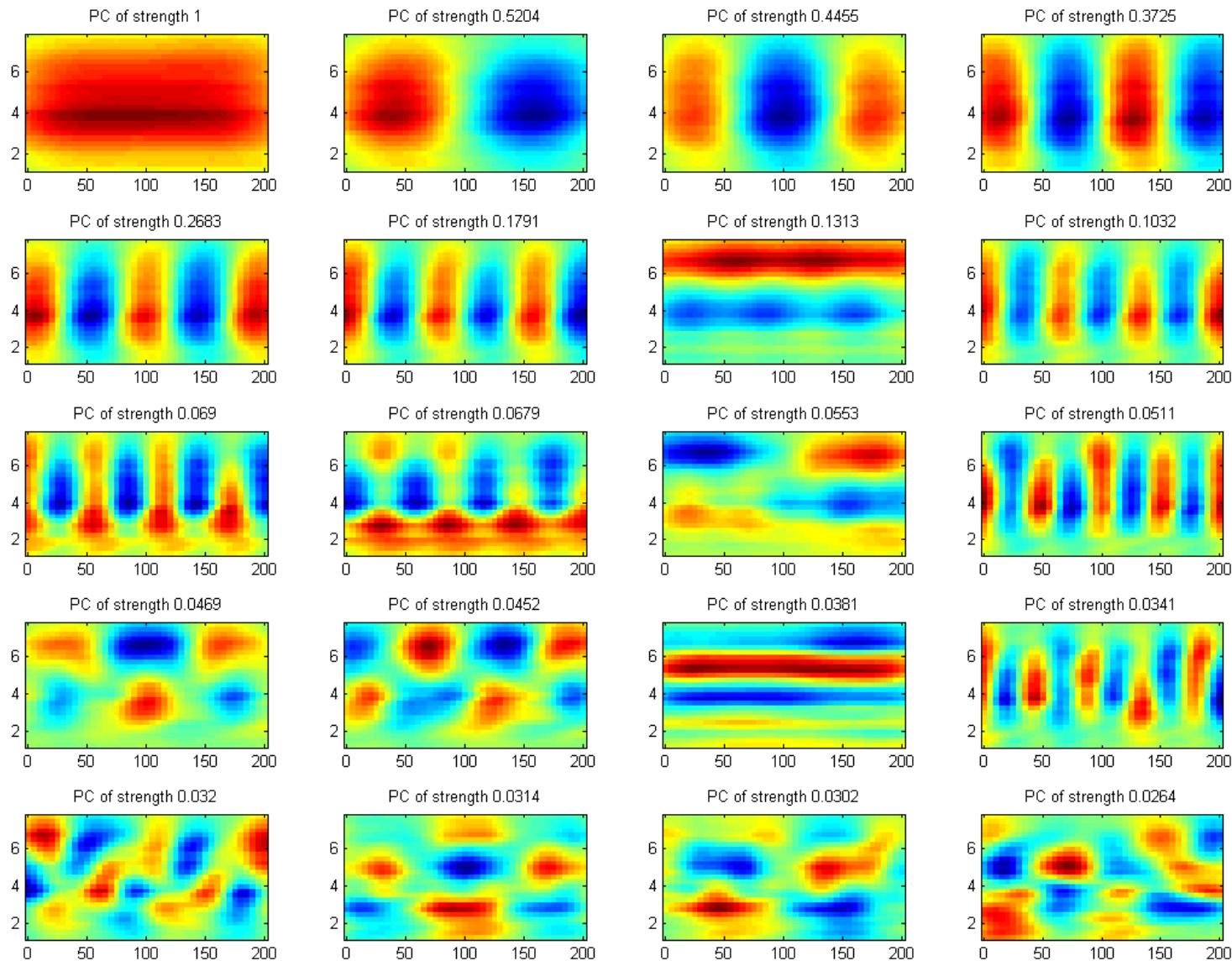
- Calculate STA and Stimulus Covariance Matrix as a function of spatial dimension and time delays.
- Take Fourier Transform of temporal dimension of STA and Stim Cov
- For each temporal frequency solve a set of  $M$  linear equations where  $M$  is the number of spatial dimensions.
- $M$  equations are not necessarily independent. Perform the inverse in a subspace. Use this step for regularization.
- Take the inverse Fourier Transform of  $K(\omega_t)$ .

*Theunissen, David et al. Network: Comput. Neural Syst. 12 (2001) 289–316*

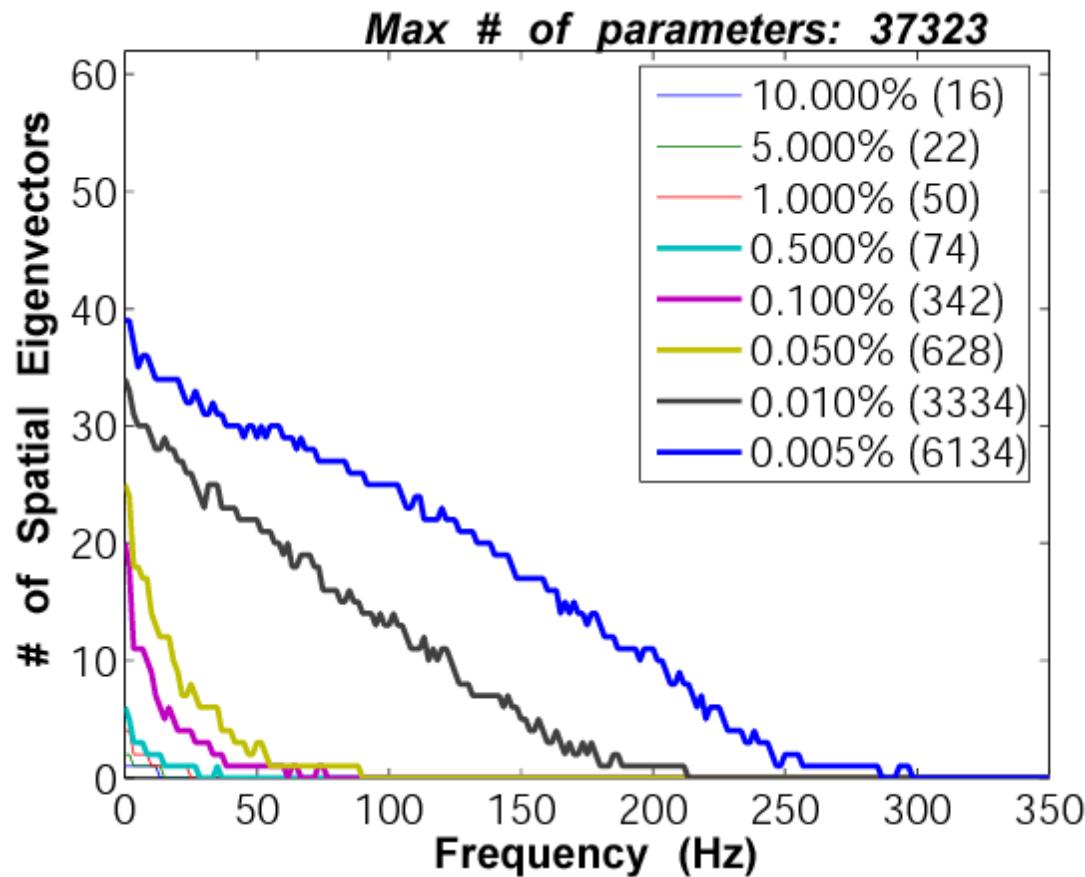
# Regularization

- Too many parameters – too little data
- Priors on what the parameters should look like
- Normal Priors give L2 regularization or ridge regression.
- L2 solves the problem into the subspace of the stimulus Principal Components with the largest eigenvalues

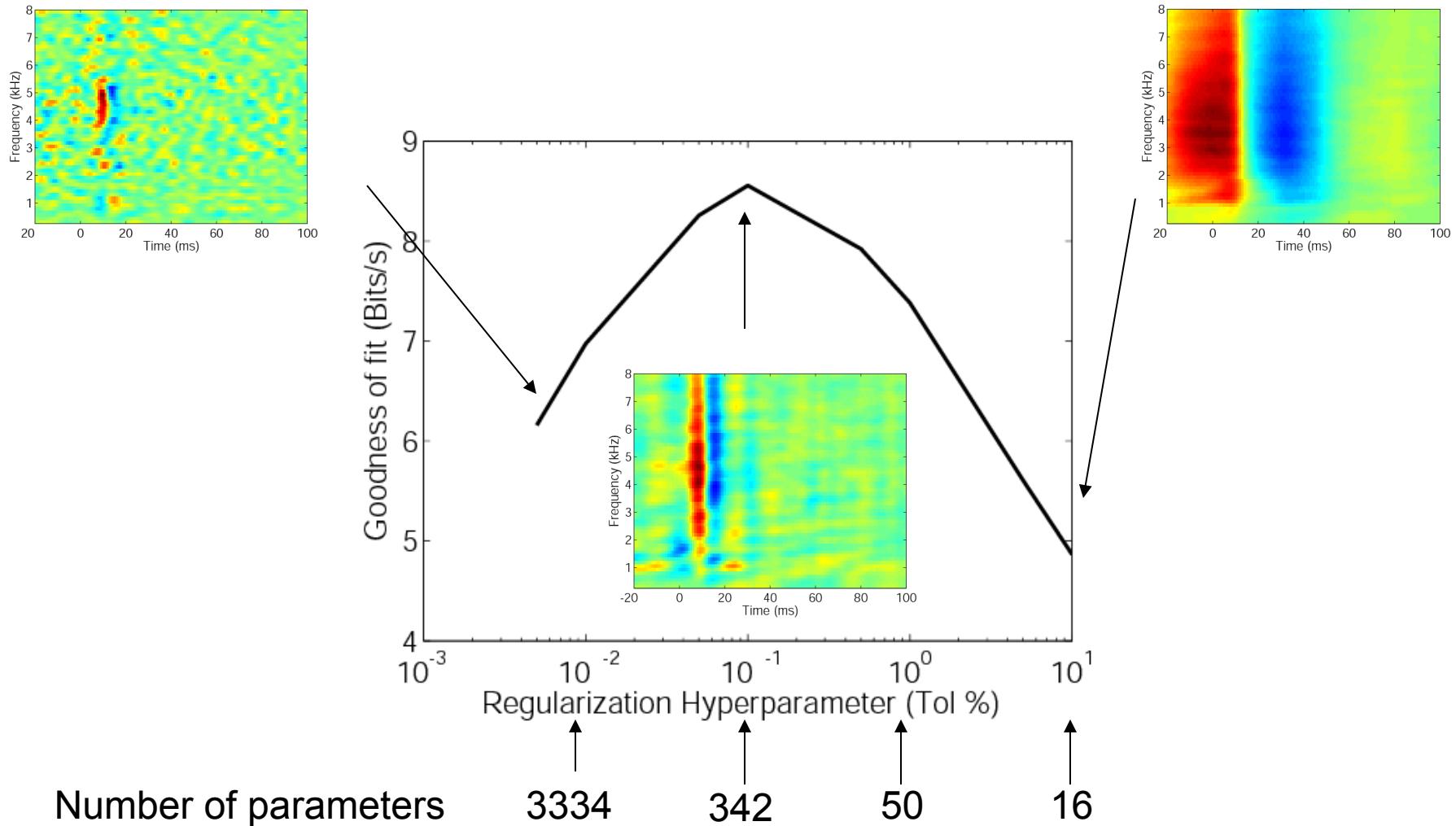
# PCAs of Zebra Finch Song



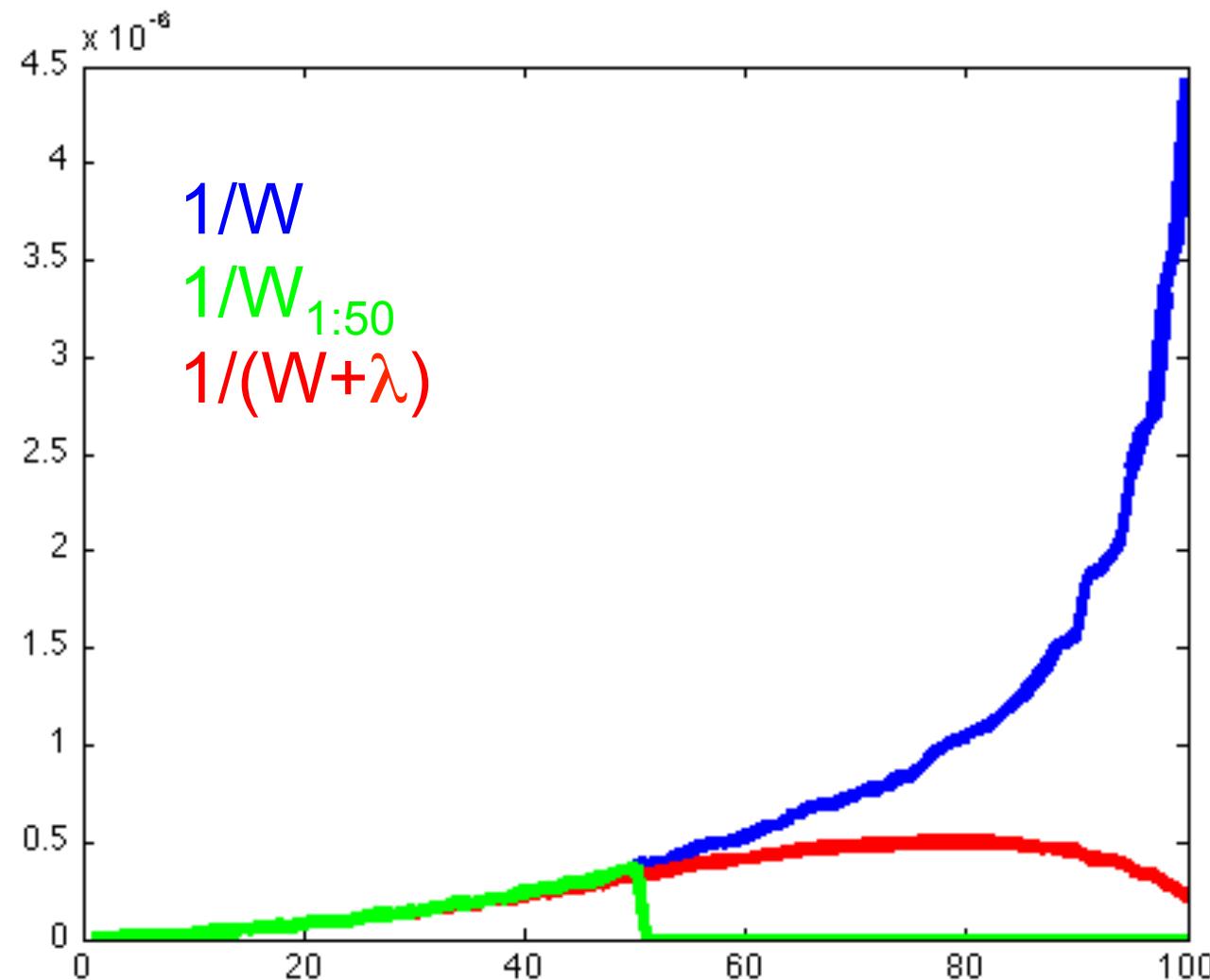
# Regularization in Eigen-Space of Stimulus Autocorrelation



# Regularization in Eigen-Space of Stimulus Autocorrelation



# Ridge vs Subspace Regression



# Bayesian Formulation

MAP estimates  
Ridge Regression

# Neural Response Model

- Model response as a function of stimulus plus noise

$$r = y(S, h) + \varepsilon$$

- For simplicity let's assume a linear model with Gaussian noise

$$r = Sh + \varepsilon \quad \varepsilon = \mathcal{N}(0, \sigma^2)$$

$$p(r | S, h) = \mathcal{N}(r | Sh, \sigma^2)$$

# How do we find the parameters that determine response?

- We have a response distribution: the probability of response,  $r$ , given stimulus,  $S$ , and parameters,  $h$

$$p(r | S, h) = \mathcal{N}(r | Sh, \sigma^2)$$

- How do we determine  $h$ ? What is the probability of  $h$ , given the stimulus,  $S$ , and responses,  $r$

$$p(h | S, r)$$

# Bayes' Rule

$$p(a,b) = p(b,a)$$

$$p(a,b) = p(a \mid b)p(b)$$

$$p(b,a) = p(b \mid a)p(a)$$

$$p(a \mid b) = \frac{p(b \mid a)p(a)}{p(b)}$$

# Posterior and Likelihood

Likelihood: Probability of data given the model

Posterior: Probability of model given data

$$p(\vec{h} \mid \vec{s}_i, r_i) = \frac{p(r_i \mid \vec{s}_i, \vec{h}) p(\vec{h})}{p(r_i)}$$

We can drop  $p(r)$  and convert to a proportionality

$$p(\vec{h} \mid \vec{s}_i, r_i) \propto p(r_i \mid \vec{s}_i, \vec{h}) p(\vec{h})$$

Posterior                      Likelihood              Prior

# Case of flat prior

$$p(\vec{h} \mid \vec{s}_i, r_i) \propto p(r \mid \vec{s}_i, \vec{h})$$

Maximizing the  
Posterior



Maximizing the  
likelihood

# The Maximum a Posteriori (MAP) Estimate

$$p(\vec{h} \mid \vec{s}_i, r_i) \propto p(r \mid \vec{s}_i, \vec{h}) p(\vec{h})$$

Posterior                      Likelihood                      Prior

If we choose a Gaussian Prior to combine with the Gaussian Likelihood, the Posterior distribution will also be Gaussian,  
i.e. it is a conjugate prior

$$L = \prod_{i=1}^n \mathcal{N}(r_i \mid \vec{s}_i, \vec{h}, \sigma_n^2)$$

$$p(\vec{h} \mid \lambda) = \mathcal{N}(0, \lambda^{-1} I)$$

# Negative log of MAP Estimate

$$Posterior \propto \left( \prod_{i=1}^n \mathcal{N}(r_i | \vec{h}, \vec{s}_i, \sigma^2) \right) \mathcal{N}(0, \lambda^{-1} I)$$

$$-\ln(Posterior) \propto \frac{1}{2} \sum_{i=1}^n (r_i - \vec{h} \cdot \vec{s}_i)^2 + \frac{\lambda}{2} \|\vec{h}\|^2$$

Error/Cost

Penalty

A Gaussian prior is equivalent to an L2  
penalty on the Least Squares Solution

# Solving for the MAP Estimate

$$-\ln(Posterior) \propto \frac{1}{2} \sum_{i=1}^n (r_i - \vec{h} \cdot \vec{s}_i)^2 + \frac{\lambda}{2} \|\vec{h}\|^2$$

$$\frac{\partial}{\partial h} \left( \frac{1}{2} \sum_{i=1}^n (r_i - \vec{h} \cdot \vec{s}_i)^2 + \frac{\lambda}{2} \vec{h} \cdot \vec{h} \right) = 0$$

$$\mathbf{S}^T \mathbf{r} - \mathbf{S}^T \mathbf{S} \vec{h} + \lambda \mathbf{I} \vec{h} = 0 \quad \mathbf{S}^T \mathbf{r} = (\mathbf{S}^T \mathbf{S} + \lambda \mathbf{I}) \vec{h}$$

$$\vec{h} = (\mathbf{S}^T \mathbf{S} + \lambda \mathbf{I})^{-1} \mathbf{S}^T \mathbf{r}$$

# L2=Ridge Regression=Isotropic Gaussian Prior on model parameters Analytical Solution!

$$\vec{h} = (\mathbf{S}^T \mathbf{S} + \lambda \mathbf{I})^{-1} \mathbf{S}^T \mathbf{r}$$

$$(\mathbf{S}^T \mathbf{S}) = \mathbf{Q} \cdot \Lambda \cdot \mathbf{Q}^T$$

$$(\mathbf{S}^T \mathbf{S} + \lambda \mathbf{I})^{-1} = \mathbf{Q}^T \cdot (1 / (\Lambda + \lambda)) \cdot \mathbf{Q}$$

$$\vec{h} = \mathbf{Q}^T (\Lambda + \lambda \mathbf{I})^{-1} \mathbf{Q} \mathbf{S}^T \mathbf{r}$$

# Ridge vs Subspace Regression

$$\vec{h} = \mathbf{Q}^T \left( \frac{1}{\Lambda} \right) \mathbf{Q} \mathbf{S}^T \mathbf{r}$$

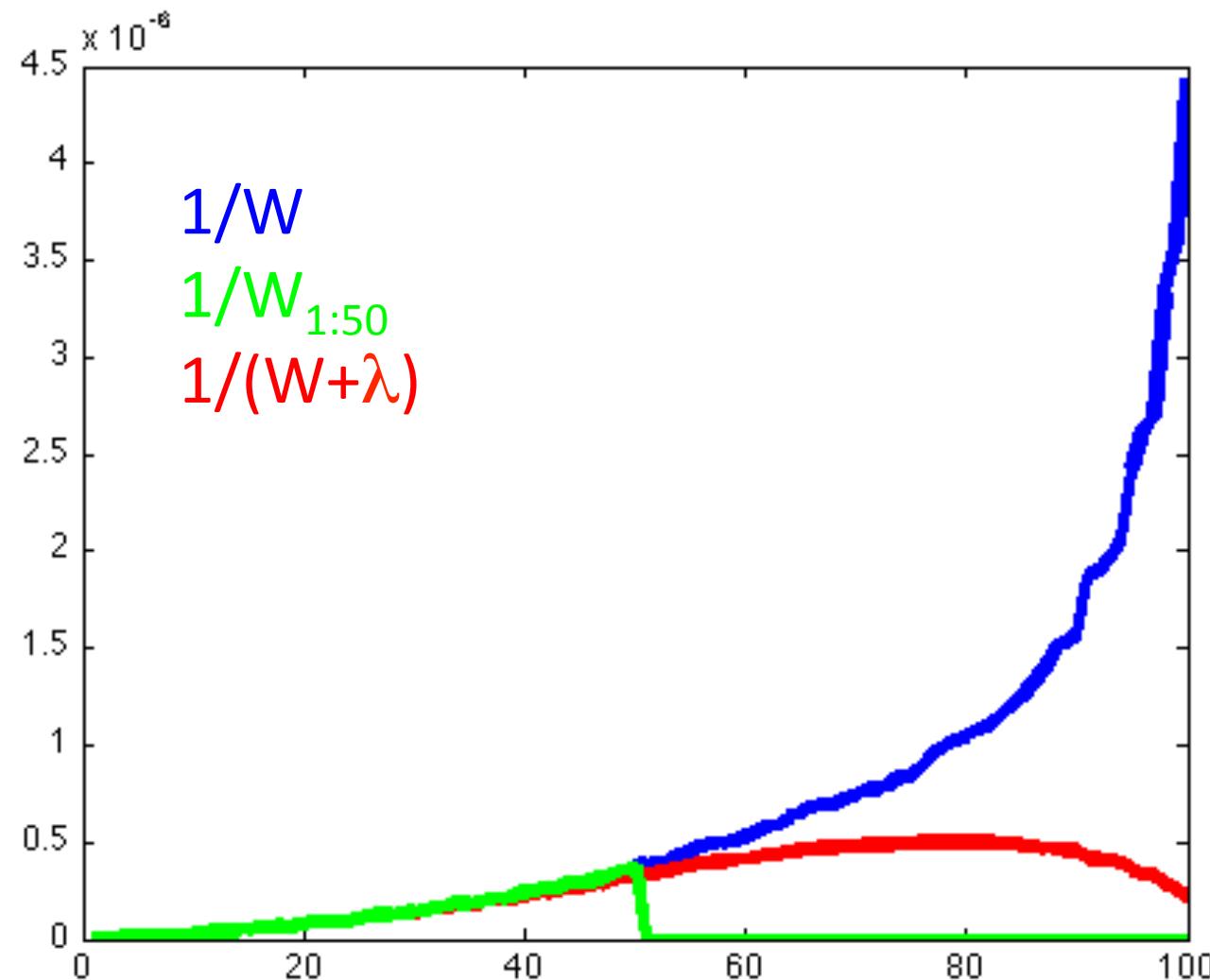
For subspace regression, a subset of the Eigenvalues are used:

$$\vec{h} = \mathbf{Q}^T \left( \frac{1}{\Lambda_{1:50}} \right) \mathbf{Q} \mathbf{S}^T \mathbf{r}$$

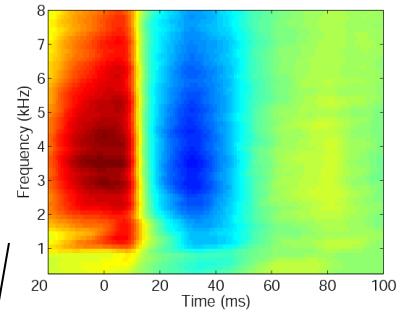
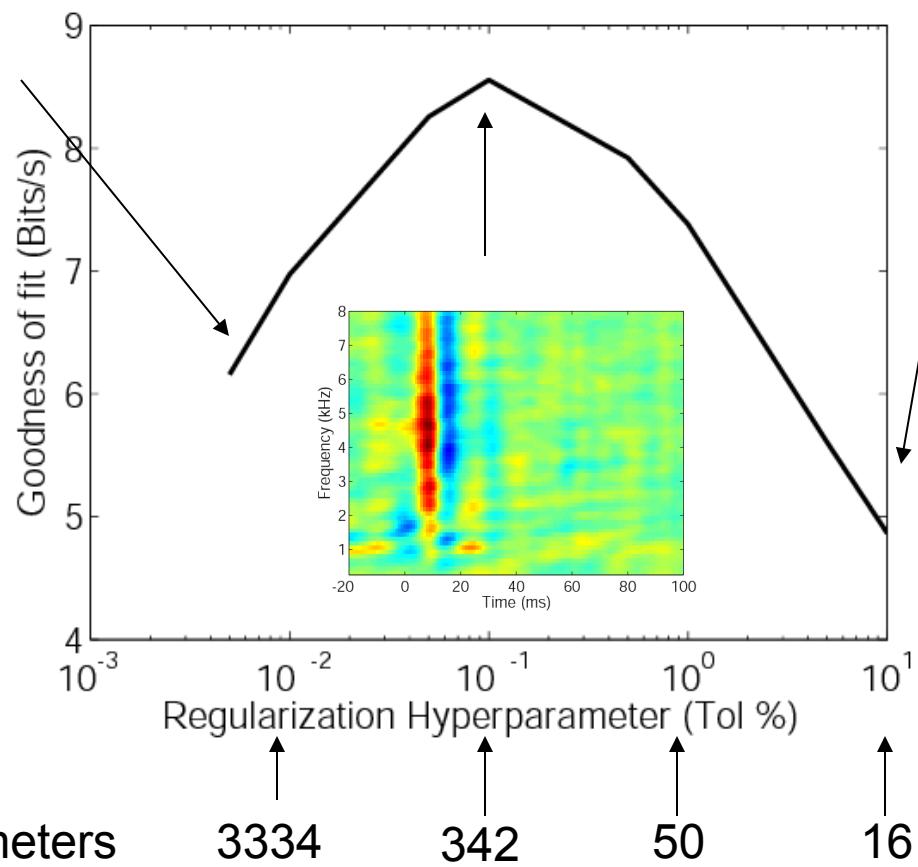
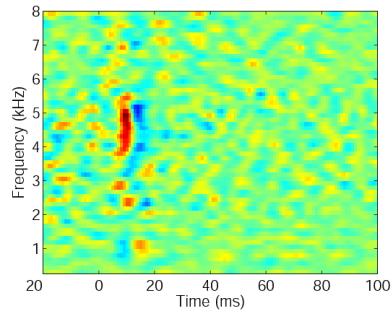
For Ridge regression, all eigenvalues are used, but reweighted:

$$\vec{h} = \mathbf{Q}^T \left( \frac{1}{(\Lambda + \lambda \mathbf{I})} \right) \mathbf{Q} \mathbf{S}^T \mathbf{r}$$

# Ridge vs Subspace Regression

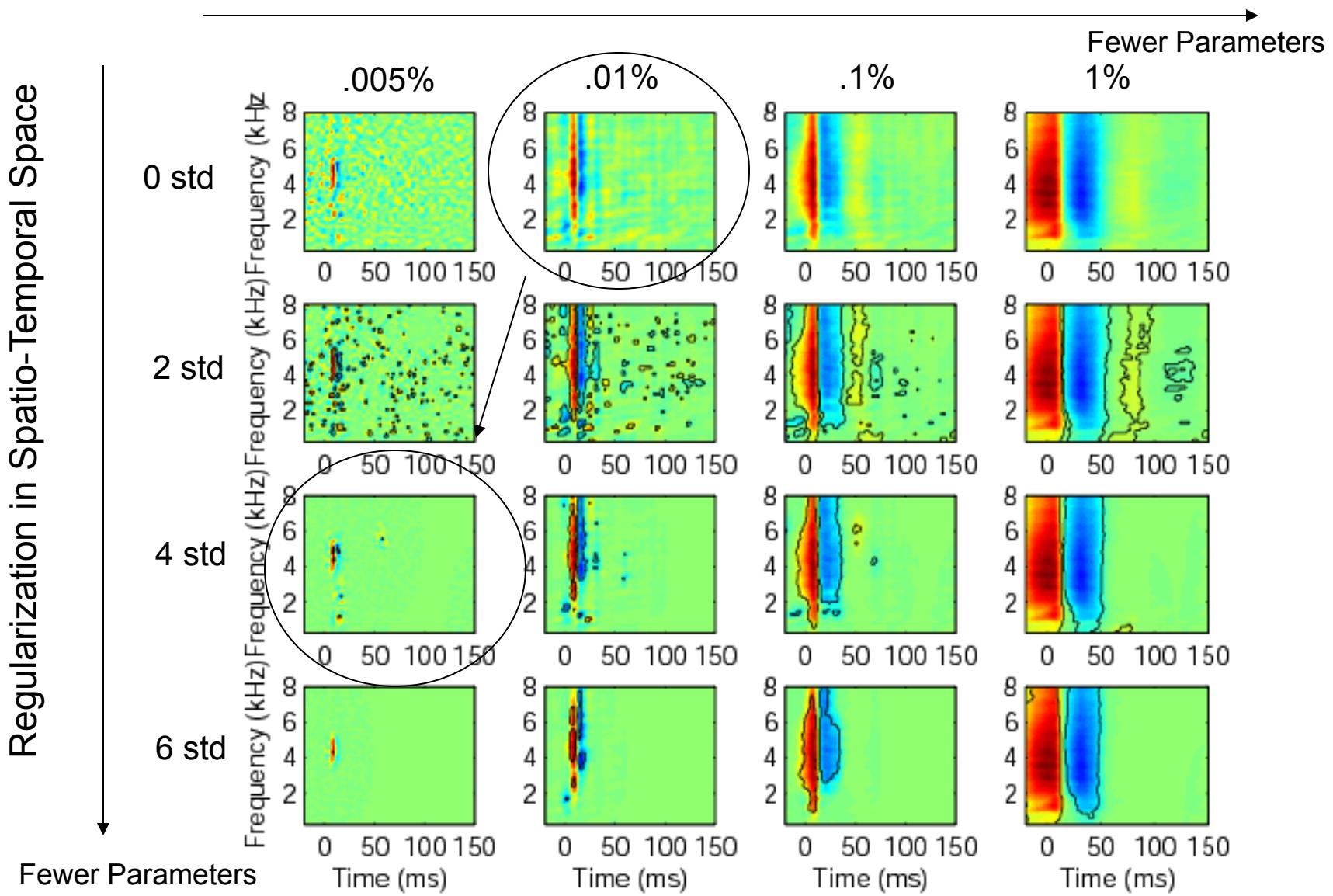


# Regularization in Eigen-Space of Stimulus Autocorrelation



# Regularization with Two Hyper Parameters

# Regularization in Stimulus Eigen Space



# Validation

Neural Responses are noisy

$$R^2(\omega) = A^2(\omega) + N^2(\omega)$$

PSTH is less noisy but still noisy

$$\bar{R}_M^2(\omega) = A^2(\omega) + N^2(\omega)/M$$

Actual Response A is unknown

# Validation

Solution: Compare the coherence function between a single spike train, R, and the actual rate, A, with the coherence function between a single spike train, R, and the predicted rate, B.

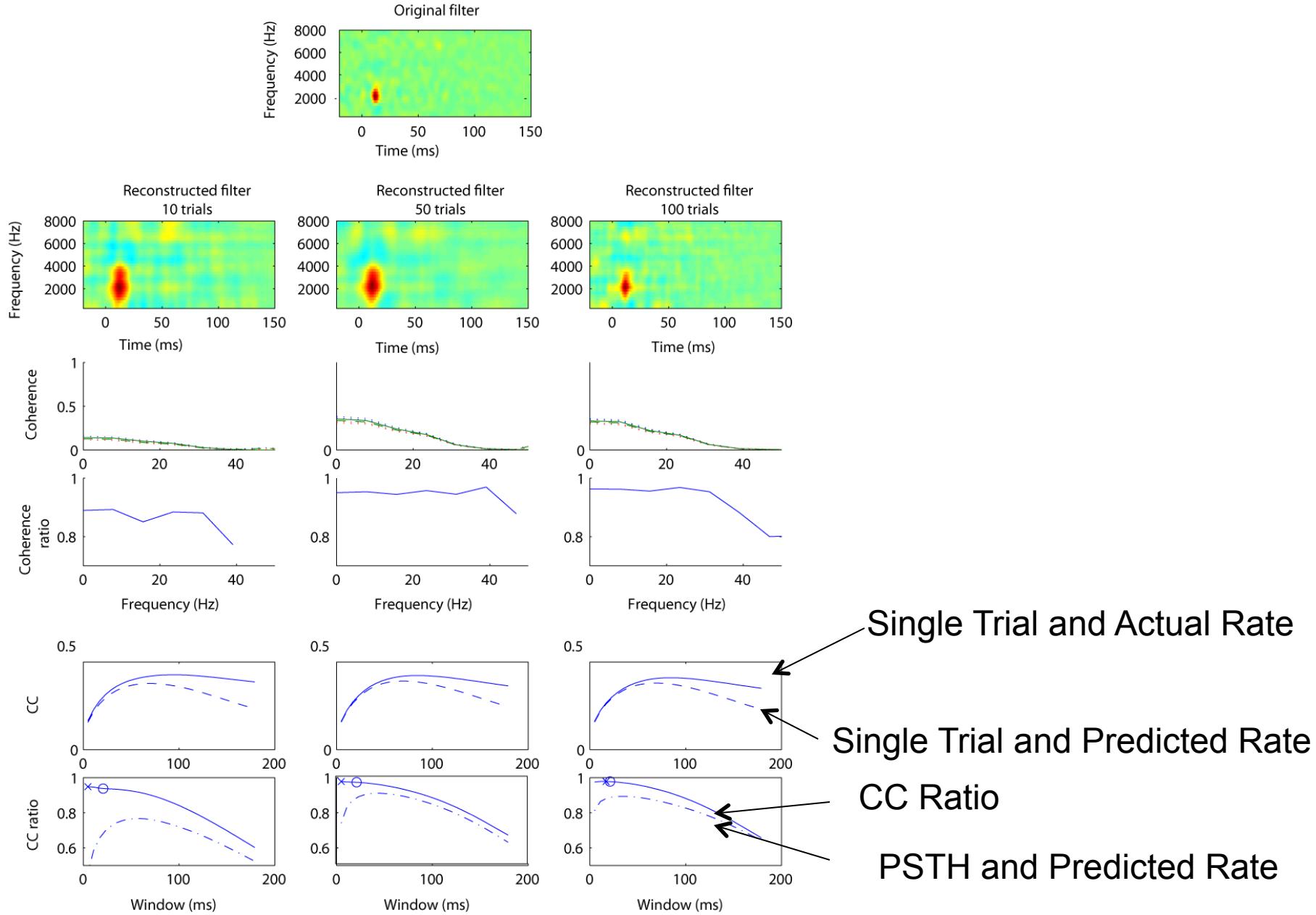
Coherence between R and A is estimated by resampling:

$$\frac{1}{\gamma_{AR}^2} - 1 = \frac{-M + M \sqrt{\left( \frac{1}{\gamma_{\bar{R}_{1,M/2} \bar{R}_{2,M/2}}^2} \right)}}{2}$$

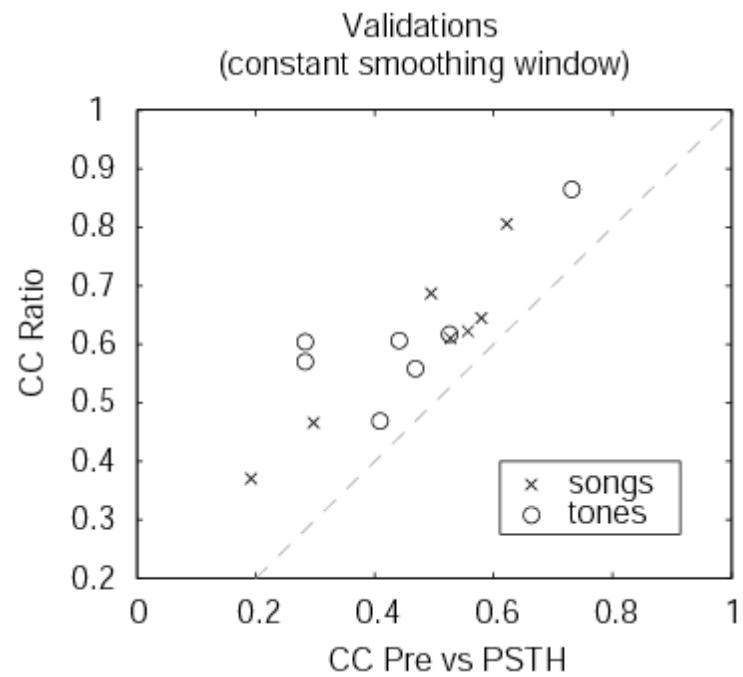
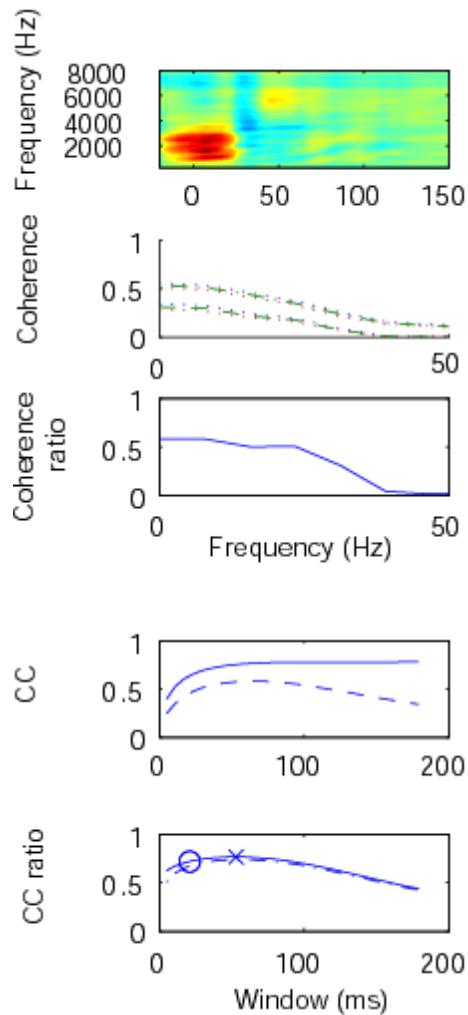
Coherence between R and B can be estimated from the coherence between the PSTH and B:

$$\frac{\gamma_{BR}^2}{\gamma_{B\bar{R}}^2} = \frac{1 + \sqrt{\left( \frac{1}{\gamma_{\bar{R}_{1,M/2} \bar{R}_{2,M/2}}^2} \right)}}{-M + M \sqrt{\left( \frac{1}{\gamma_{\bar{R}_{1,M/2} \bar{R}_{2,M/2}}^2} \right)} + 2}$$

# Validation: Model Linear Neuron



# Validation: Actual Data (Auditory Neurons)



# Validation: Summary Lessons

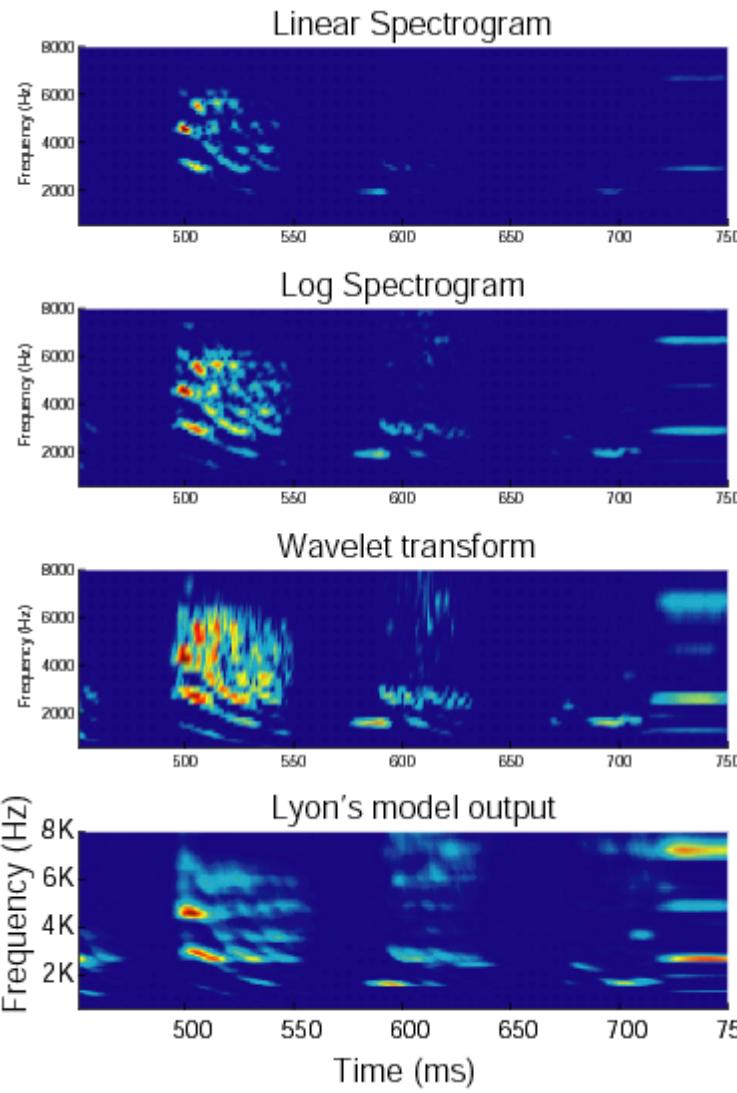
- Figure out your ceiling value
- Use coherence function
- If you use the correlation coefficient ( $r$ ) specify the time scale (smoothing window).

*Hsu, Borst and Theunissen. Network: Comput. Neural Syst. 15 (2004) 91–109*

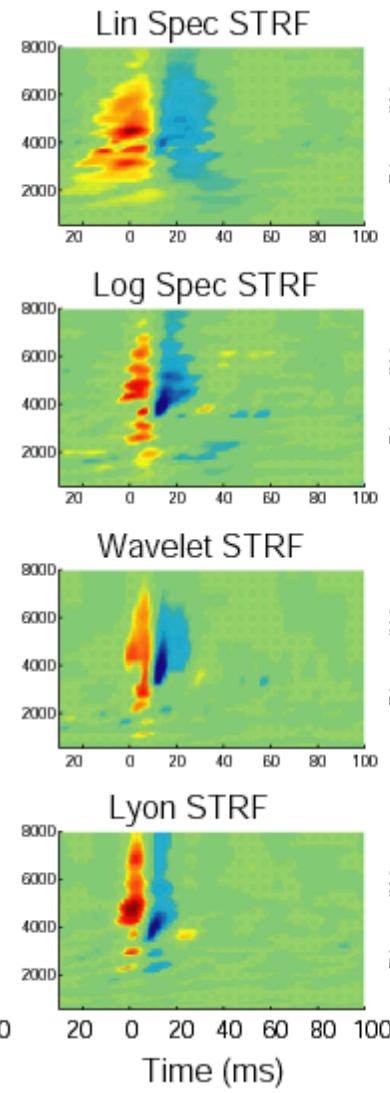
# Rev-Correlations for Nat Stats

- STRFPAK.
  - Non stationary spatial stimulus correlations
  - Regularization in eigen-space
  - Regularization in joint eigen/pixel space
  - Prediction Validation
- Non-linear Preprocessing for auditory neurons.
  - Compression
  - Spectrograms vs Wavelets and Time-frequency scale
  - Adaptive gain control

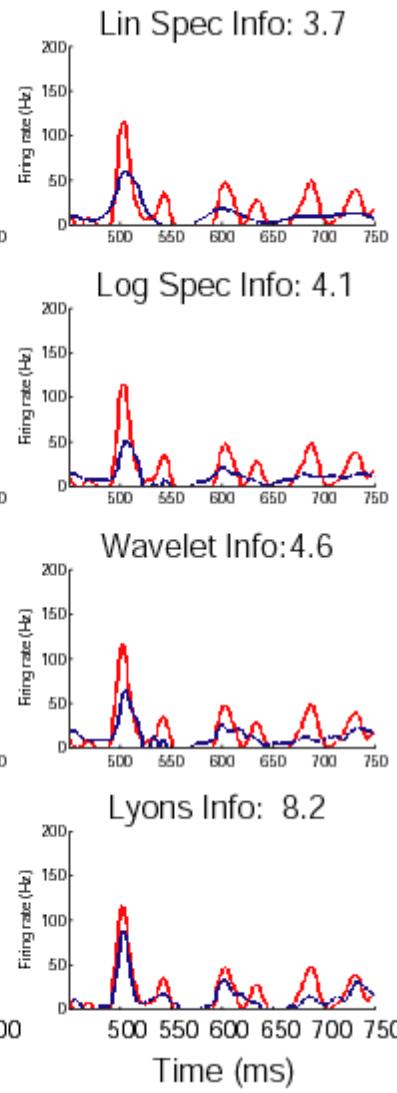
Pre-processed Stimulus



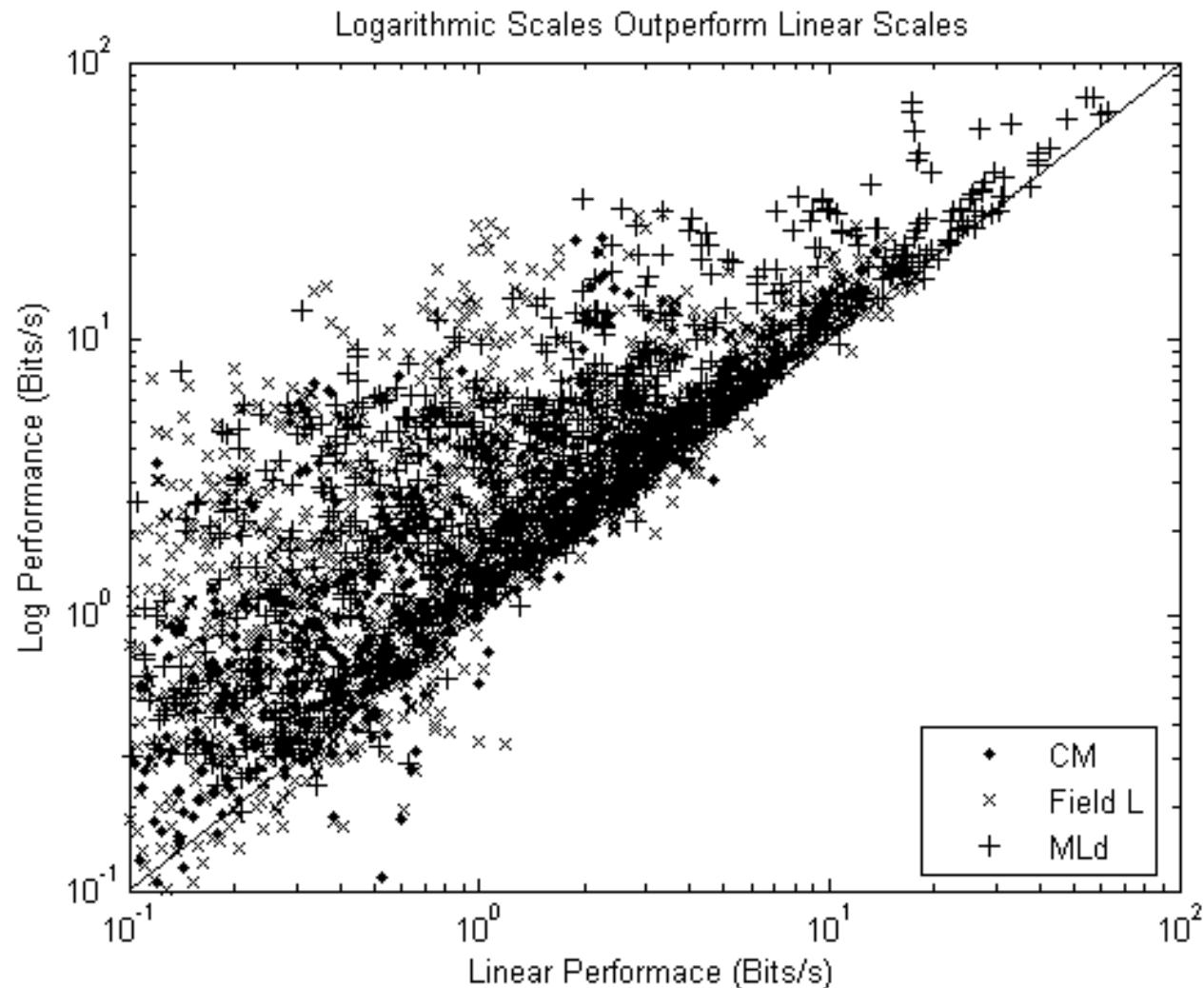
STRF



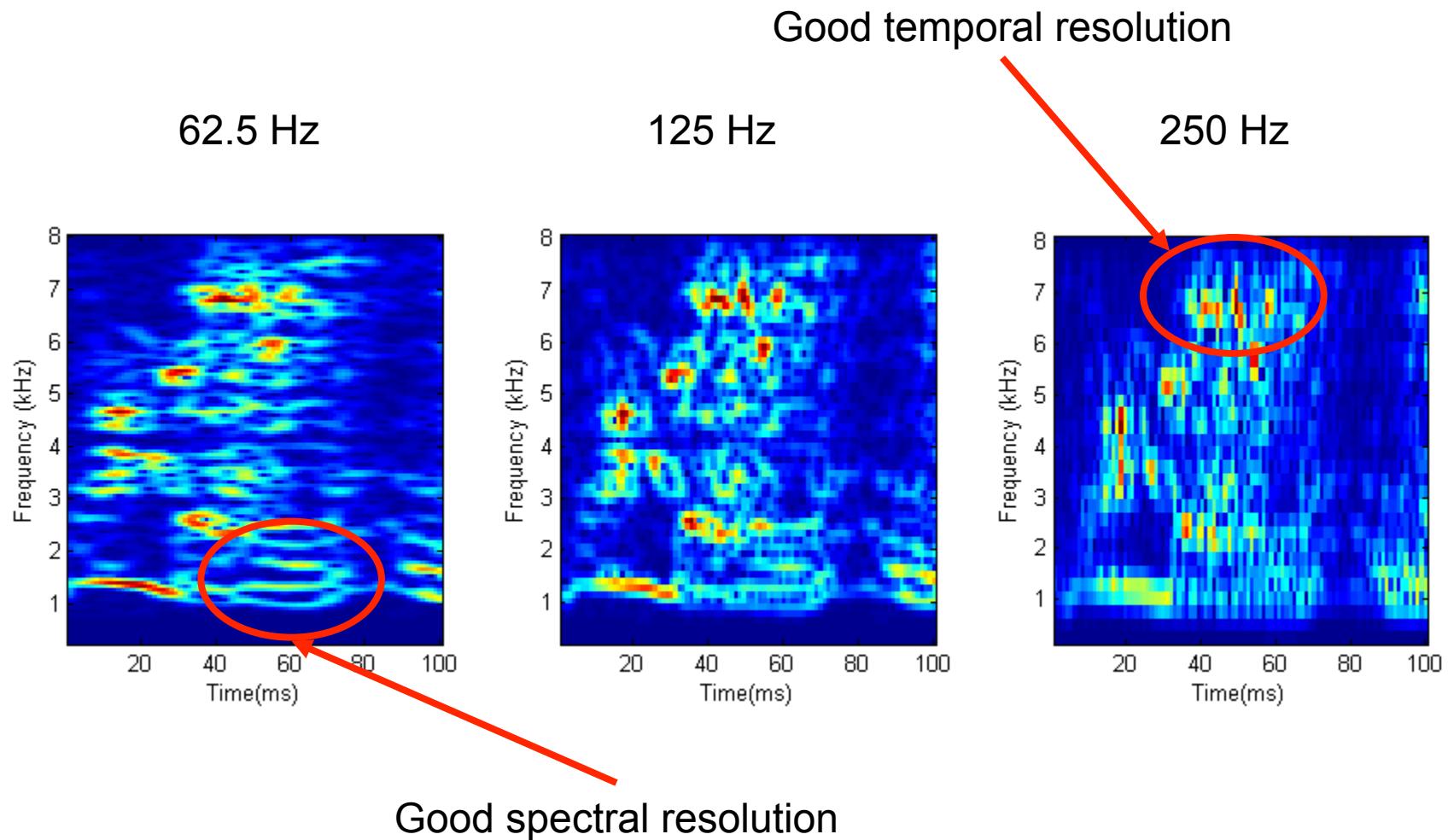
Predictions



# Compression is a must!

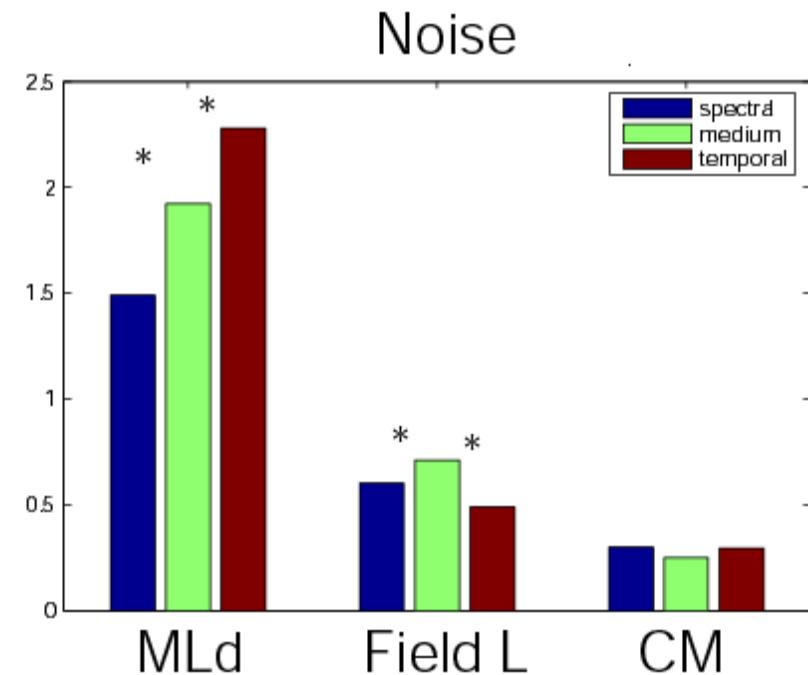
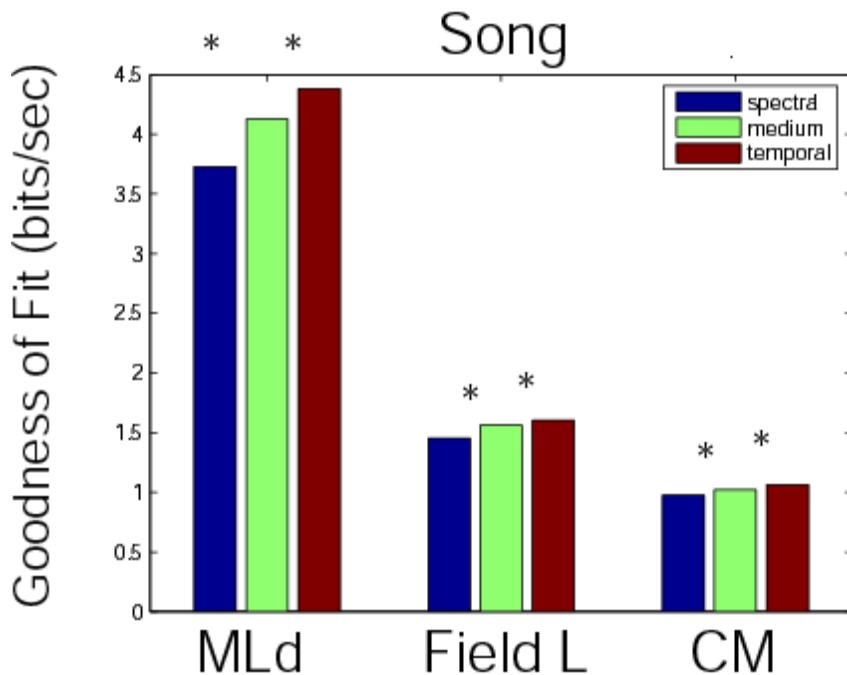


# Three Time-Frequency Scales



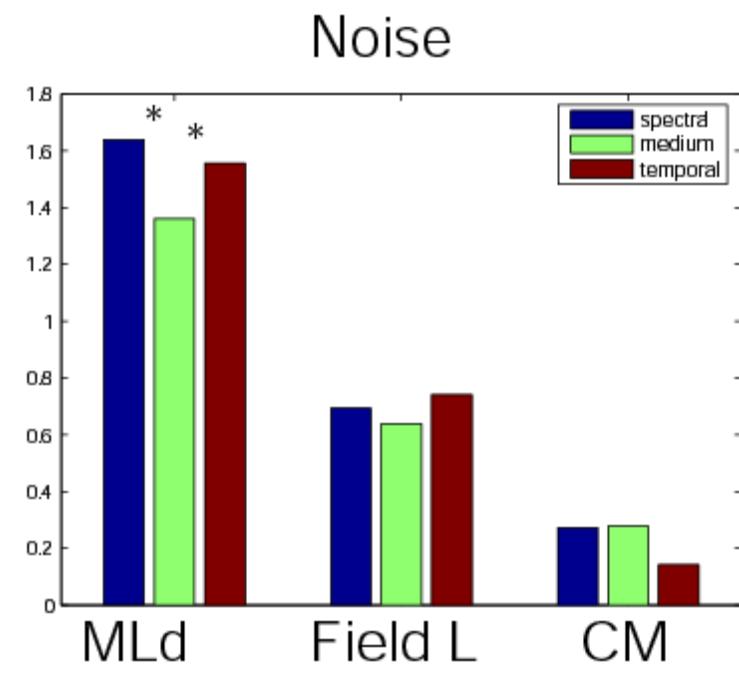
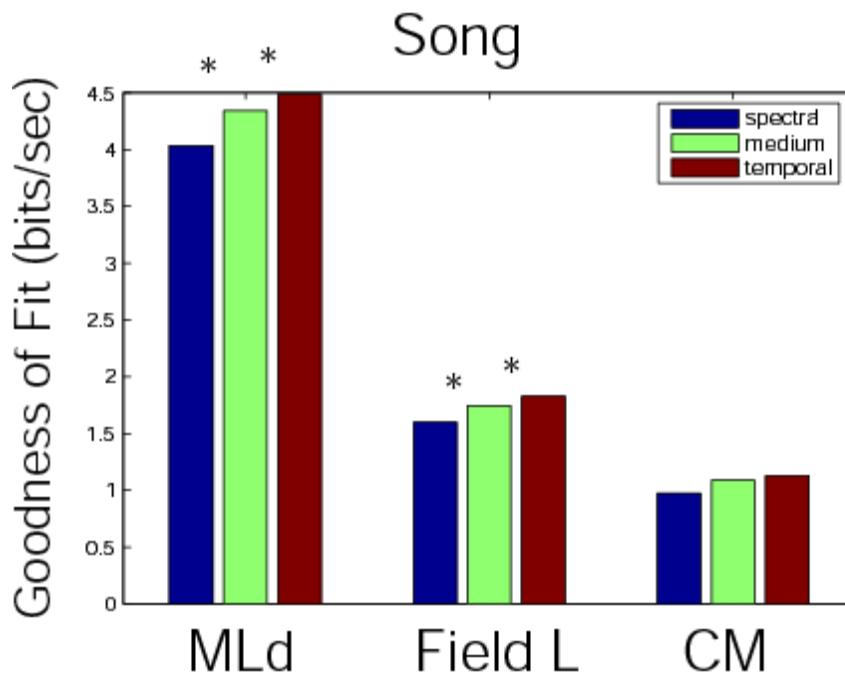
# Temporal Representations are favored for song

## Spectrograms

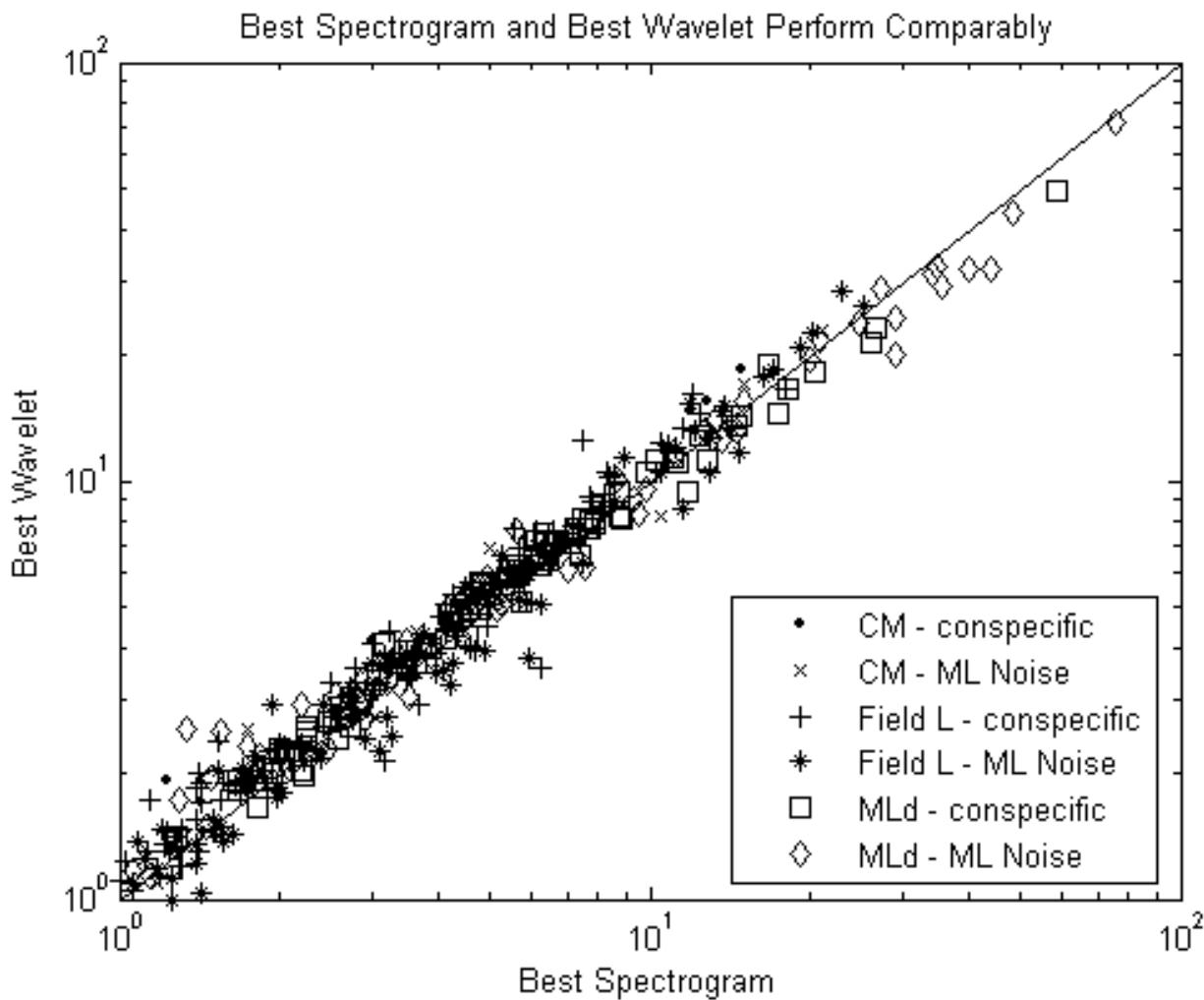


# Temporal Representations are favored for song

## Wavelets



# Spectrogram and Wavelet yield similar results



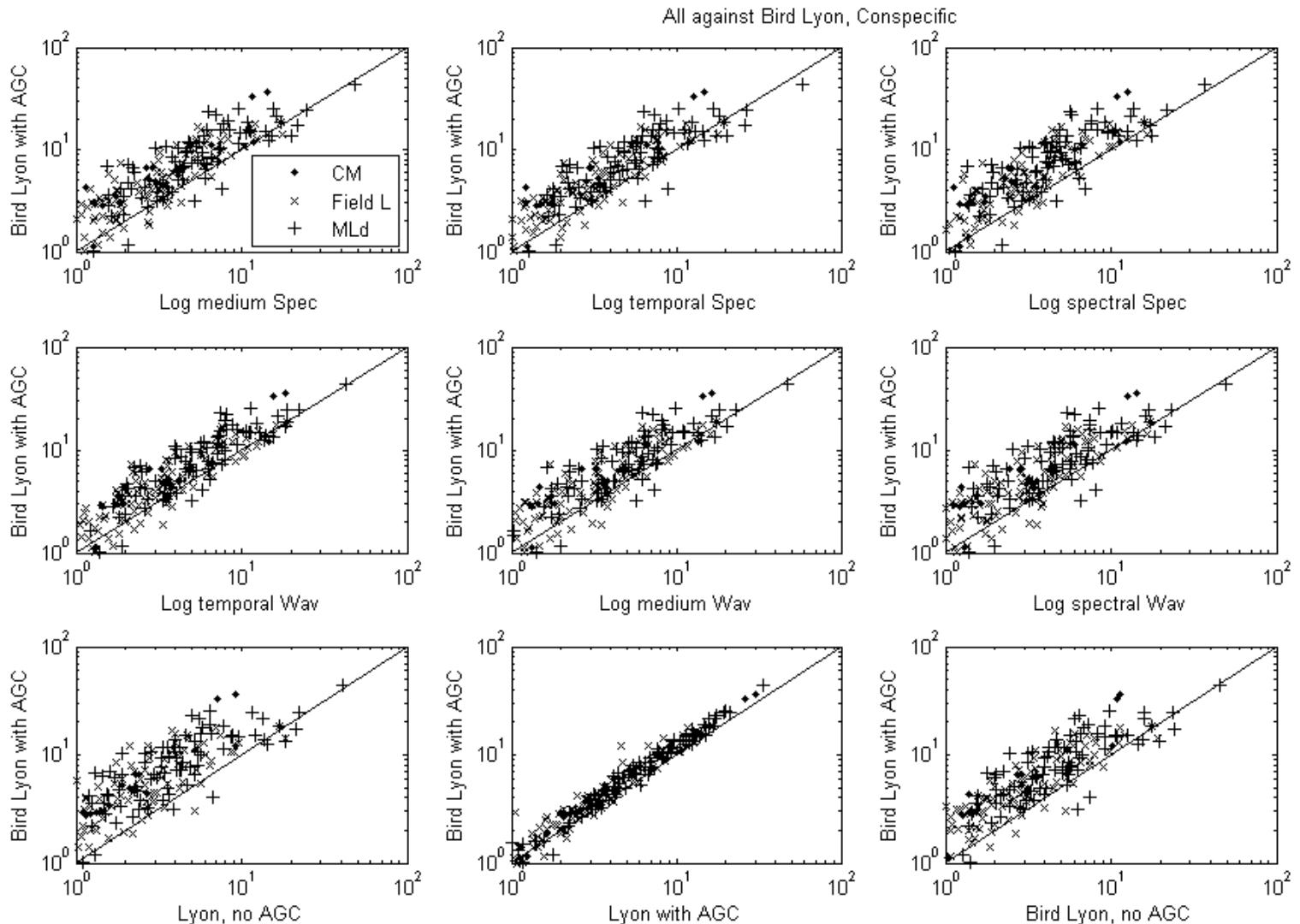
# Dynamic Gain Control in Lyon/ Slaney's cochlear model

The model generates a cochleogram. It incorporates:

- Wavelet like filter bank
- Rectification, Low Pass filter, Compression
- Adaptive Gain Control with 4 stages with time constants of 640, 160, 40 and 10 ms.
- We modified Lyon's model to use the time-frequency that gave us the best predictions for the wavelets.

## Bird Lyon's Model

# Adaptive gain control is a winner!



Other Models

# Pre-processing for auditory system

- Does NOT affect goodness of fit:
  - Spectrograms vs Wavelets.
- Has small effect on goodness of fit:
  - Time-frequency scale. Stimulus dependant.
- Increases goodness of fit:
  - Input compressive non-linearity
  - Dynamic gain control

# References

- Theunissen, F. E., S. V. David, N. C. Singh, A. Hsu, W. Vinje and J. L. Gallant (2001). "Estimating spatio-temporal receptive fields of auditory and visual neurons from their responses to natural stimuli." Network: Comp. Neural Syst. **12**: 1-28.
- Hsu, A., A. Borst and F. E. Theunissen (2004). "Quantifying variability in neural responses and its application for the validation of model predictions." Network **15**(2): 91-109.
- Gill, P., J. Zhang, S. M. Woolley, T. Fremouw and F. E. Theunissen (2006). "Sound representation methods for spectro-temporal receptive field estimation." J Comput Neurosci **22**: 22.
- Wu, M. C. K., S. V. David and J. L. Gallant (2006). Complete functional characterization of sensory neurons by system identification. Annual Review of Neuroscience. **29**: 477-505.

# Assignment

- `directfit_exercise.m`
- Finish the day by running:  
`direcfit_tutorial.m`