

# Neural Signal and Neural Noise in Primary Auditory Cortex

David J. Klein  
Jonathan Z. Simon  
Didier A. Depireux  
Shihab A. Shamma

Institute for Systems Research  
and Dept. of Electrical & Computer Engineering  
University of Maryland

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# Introduction

- Information is represented in neurons by sequences of action potentials (spikes).
- The response of a neuron to a given stimulus exhibits variability.
- Standard model: an underlying time-varying *probability function* governs the firing of spikes, usually modeled as a non-stationary point process.
- We measure the response of cell to broadband sounds and derived Spectro-Temporal Receptive Fields (STRF), a linear, quantitative descriptor of how a cell responds to dynamic sounds.
- When predicting responses to a new sound, there is a difference between the response predicted by the STRF and the actual response. How much difference is due to non-linearity, and how much is expected from neural variability, such as a Poisson processes?

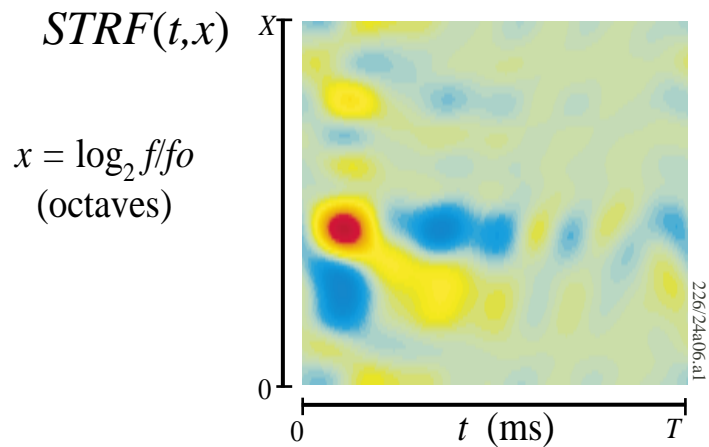
# Summary

- We previously modeled cells in Primary Auditory Cortex (AI) of ferrets as responding linearly to the low-passed envelope of incoming sounds.
- We model the response of a cell by a linear convolution between an STRF and the envelope of the sound.
- There is typically a difference between the predicted response and the actual response. How much can be attributed to intrinsic variability in the neural firings, and how much to non-linear effects?
- We conclude that most of the difference is attributable to the intrinsic variability (“noise”) of the neurons, as manifested by the (non-homogeneous) Poisson statistics of the firings

# STRFs in AI

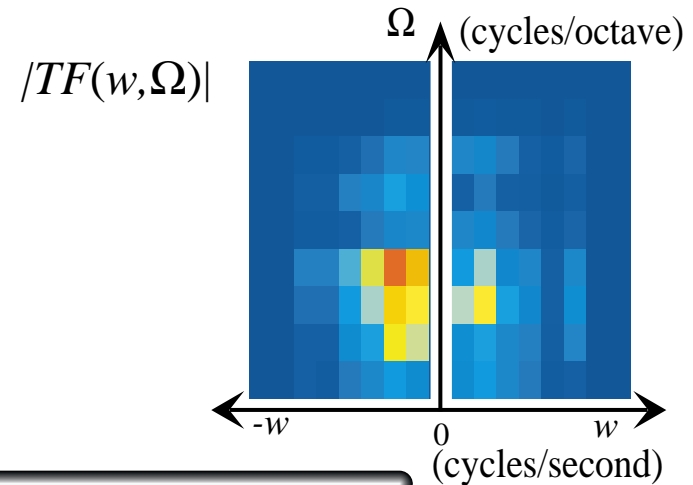
Cells are characterized their Spectro-Temporal Response Field (STRF)...

... or by the (Fourier domain) ripple transfer function (TF).

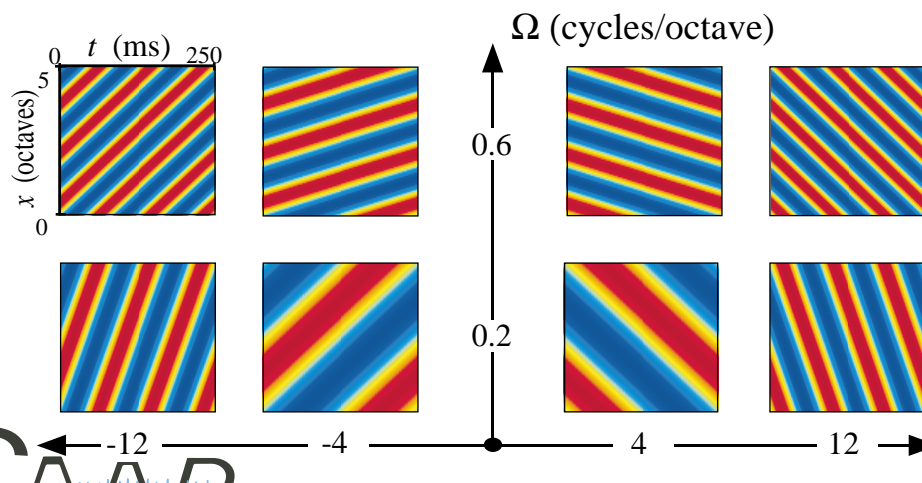


$$|\mathcal{F}\{\cdot\}|$$

$$\longleftrightarrow$$



**Moving ripples** form the basis for the Fourier domain description of dynamic spectra. At time  $t$  and frequency  $x$ , the amplitude  $S(t,x)$  is given by:



$$S(t,x) = \sin(2\pi w t + 2\pi \Omega x + \Phi)$$

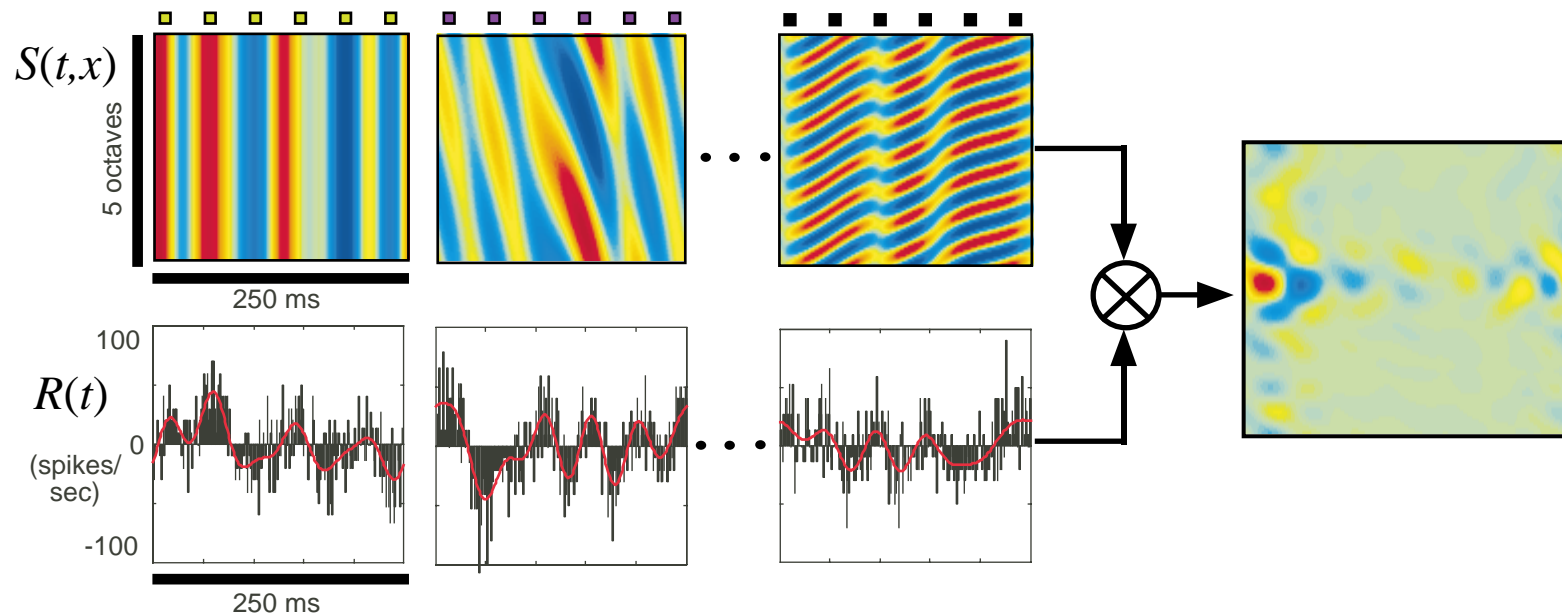
$$x = \log_2[f/f_0]$$

$w$  = ripple velocity, modulation rate

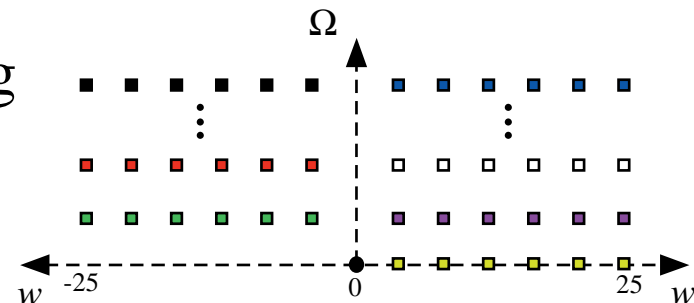
$\Omega$  = ripple frequency, spectral density

# Temporally Orthogonal Ripple Combinations

- STRF measured by reverse-correlating with dynamic spectrum of a broad-band stimulus.
- Temporally Orthogonal Ripple Combinations composed of ripples with different modulation rates.
- Allow clean STRF estimates in relatively short time.



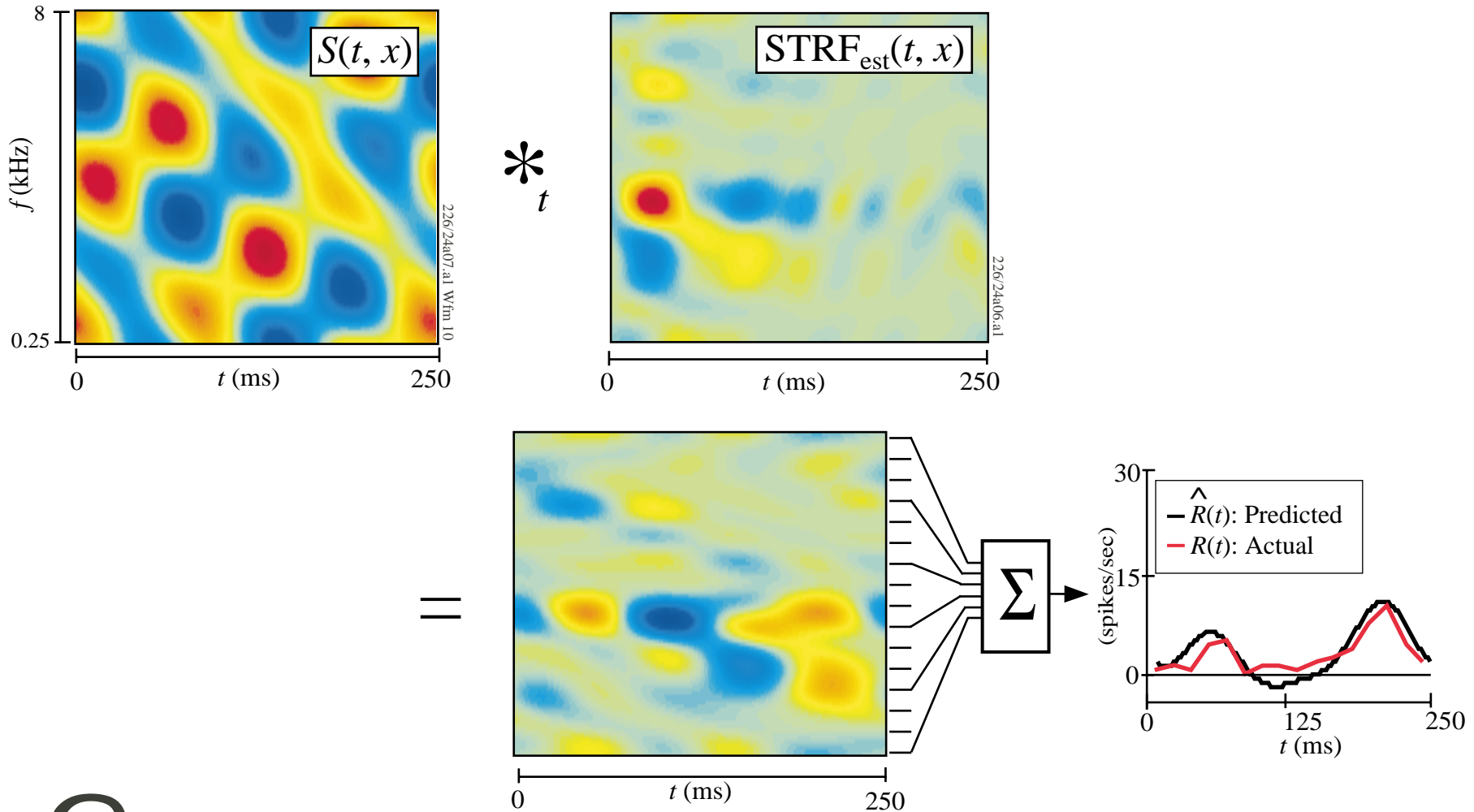
The stimuli shown contain ripples covering the same range of ripple velocities, but at different ripple frequencies.



# Predicting Responses from STRF

The response to an arbitrary sound is predicted by the convolution of the STRF with the stimulus' spectro-temporal envelope (plus a constant).

$$\hat{R}(t) = \frac{1}{X} \sum_x \{ \text{STRF}_{\text{est}}(t, x) *_t S(t, x) \} + E\{R(t)\}$$

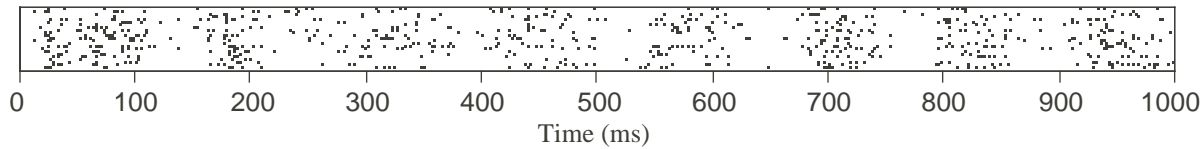


# Bootstrap Technique

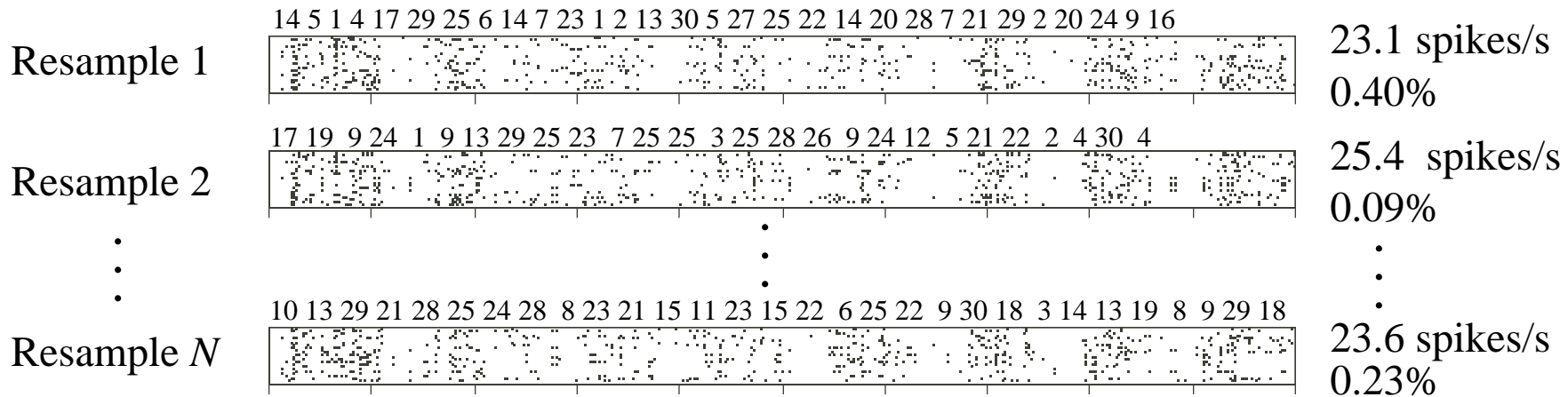
- From presentation to presentation, there is **variability** or “noise”.
- We use **resamples** of data to estimate variability.
- Resamples are of same size as original samples:  $N$  samples of bootstrap data are drawn *with replacement* from the  $N$  original samples.
- Repeat procedure many times to create a population of bootstrap resamples whose probability distribution is a good estimator of the probability distribution from which the original data was drawn.
- Mean, variance, and higher order moments of bootstrap population are good, unbiased, estimators of those same moments of the true distribution.
- Related to “Jackknife” technique.

# Bootstrap Example

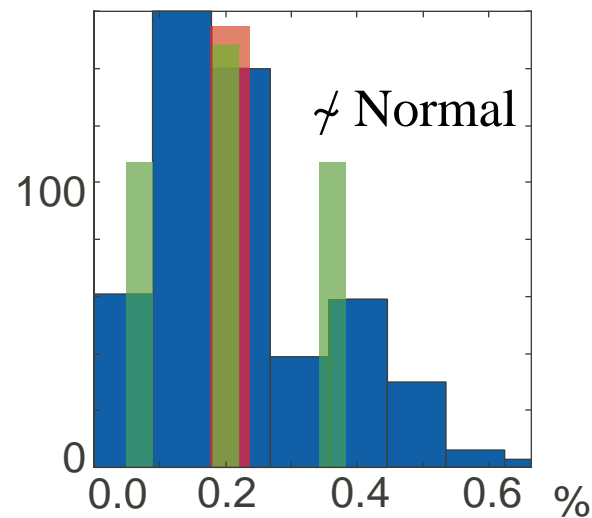
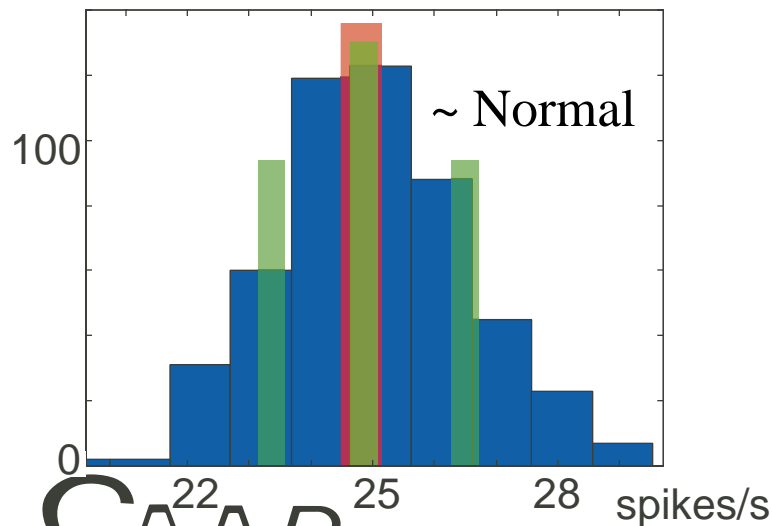
## Raster Data 30 sweeps



Mean firing rate: 25.0 spikes/s  
 Percentage ISI = 40 ms: 0.23%



## Bootstrap distributions



Best Estimate

Bootstrap mean and standard deviations

*N* = 500

# Poisson Statistics

- The measured observable is the spike train, which we model as a Poisson random variable.
- Assume underlying, deterministic, probability density for firing,  $r(t)$
- # of measurements (stimulus presentations) =  $n$
- probability of measuring  $N$  spikes between  $t$  and  $\Delta t$ :  $p(N(t;\Delta t)) = r(t) \Delta t$
- Expectation values for mean,  $\eta$ , and variance,  $\sigma$ , of  $N$ :

$$\eta_N(t;\Delta t) := E\{N(t;\Delta t)\} = n r(t) \Delta t$$

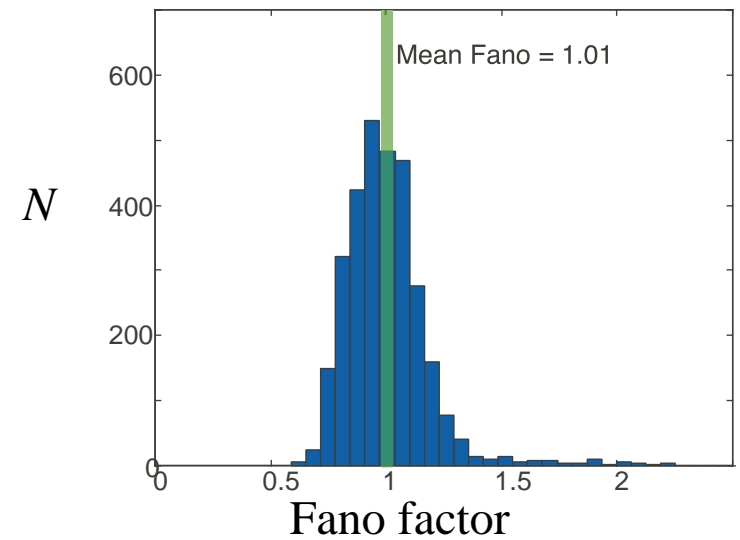
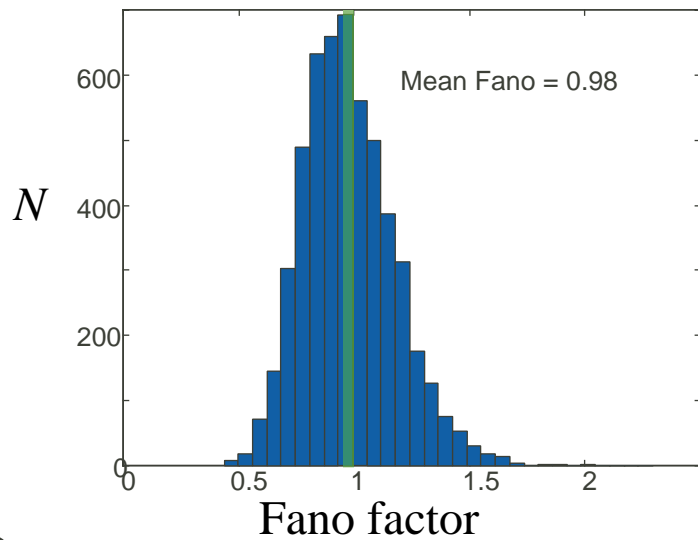
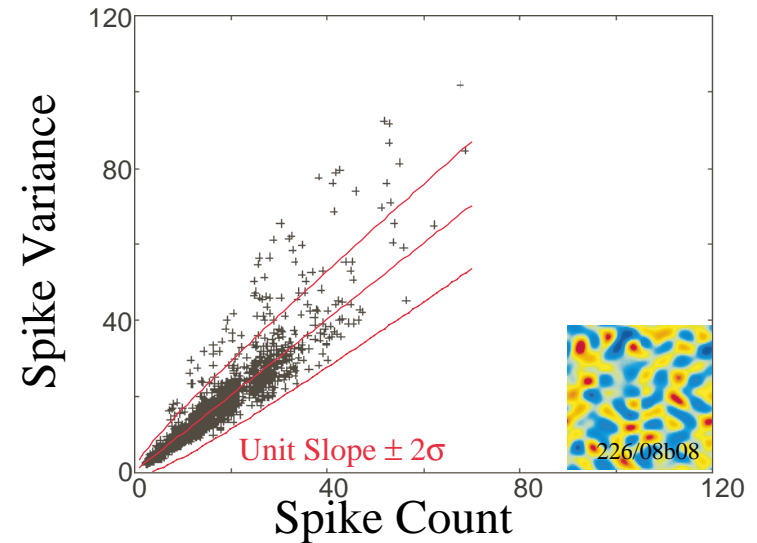
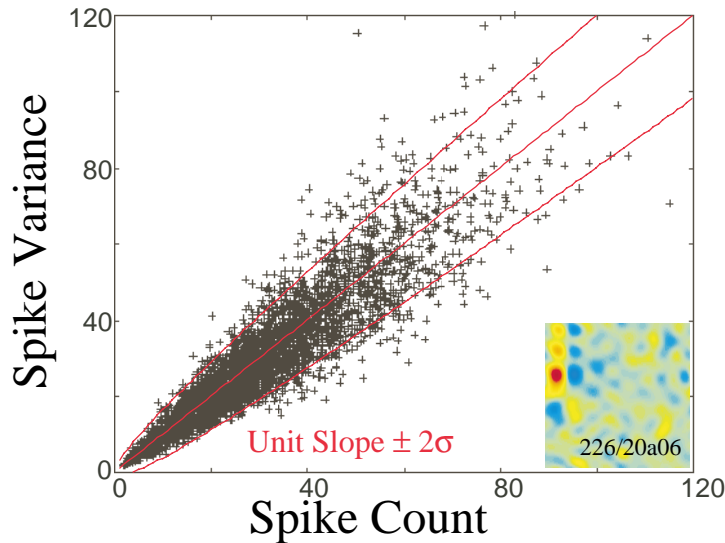
$$\sigma_N^2(t;\Delta t) := E\{(N[t;\Delta t])^2\} - [\eta_N(t;\Delta t)]^2 = \eta_N(t;\Delta t) = n r(t) \Delta t$$

- Thus a prediction for the Fano factor:

$$\phi_N(t;\Delta t) := \eta_N(t;\Delta t)/\sigma_N^2(t;\Delta t) = 1$$

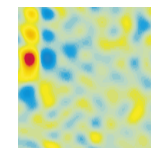
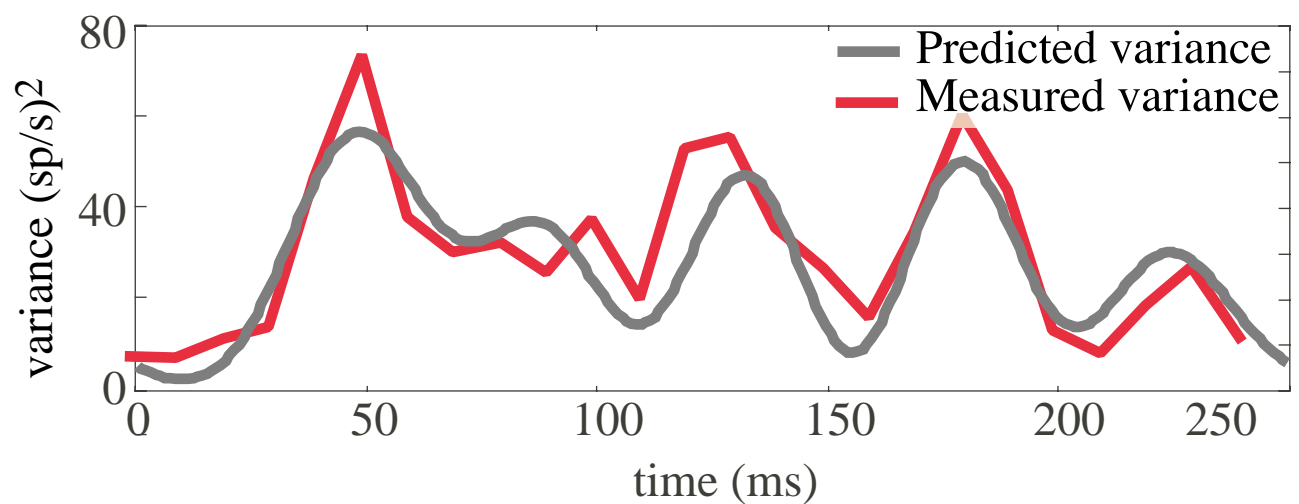
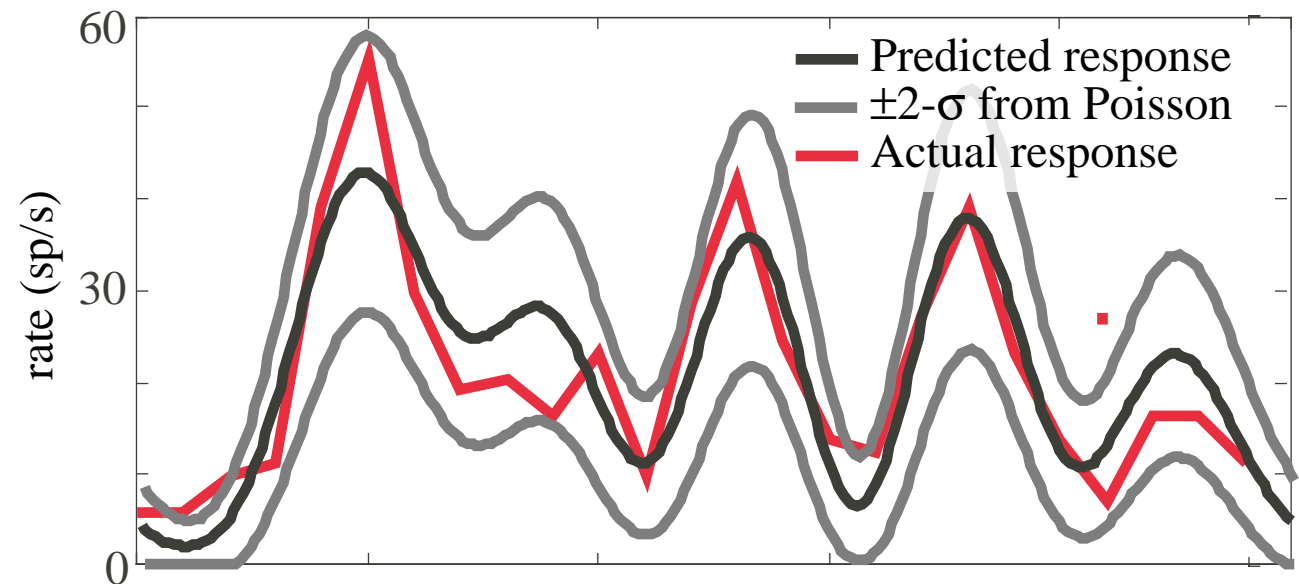
# Poisson Variance Examples

- Examples of the computation of the Fano factor for two cells, one “clean” and the other very noisy.



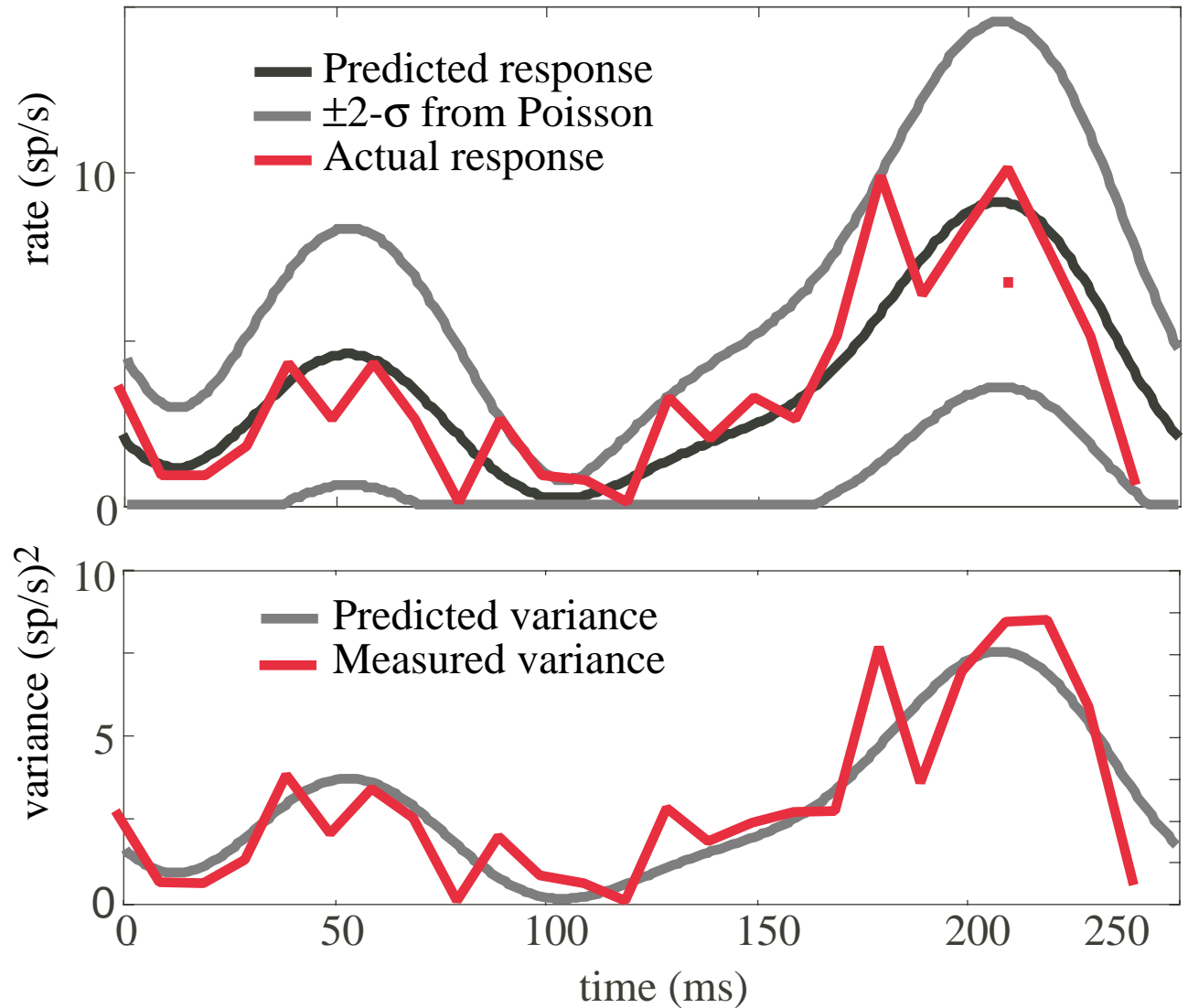
# Examples Continued

- The actual response lies nicely within the variability predicted by Poisson noise.
- The variance in the measured response corresponds nicely to the predicted variance.

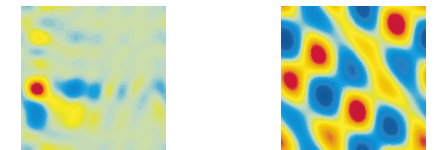


# Predictions with Variability

- The actual response lies nicely within the variability predicted by Poisson noise.
- The variance in the measured response corresponds nicely to the predicted variance.



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# Signal to Noise Theory

- Define observed firing rate:  $R(t;\Delta t) = (1/n) N(t,\Delta t)/\Delta t$

- $\eta_R(t,\Delta t) := E\{R(t;\Delta t)\} = r(t)$

$$\sigma_R^2(t;\Delta t) := E\{[R(t;\Delta t)]^2\} - [\eta_R(t;\Delta t)]^2 = r(t)/(n \Delta t)$$

- Signal & Variance (“Noise”) Power:

$$P := \sum_t [r(t)]^2 \qquad P_\sigma := \sum_t \sigma_R^2(t;\Delta t)$$

- Signal to Noise Ratio:

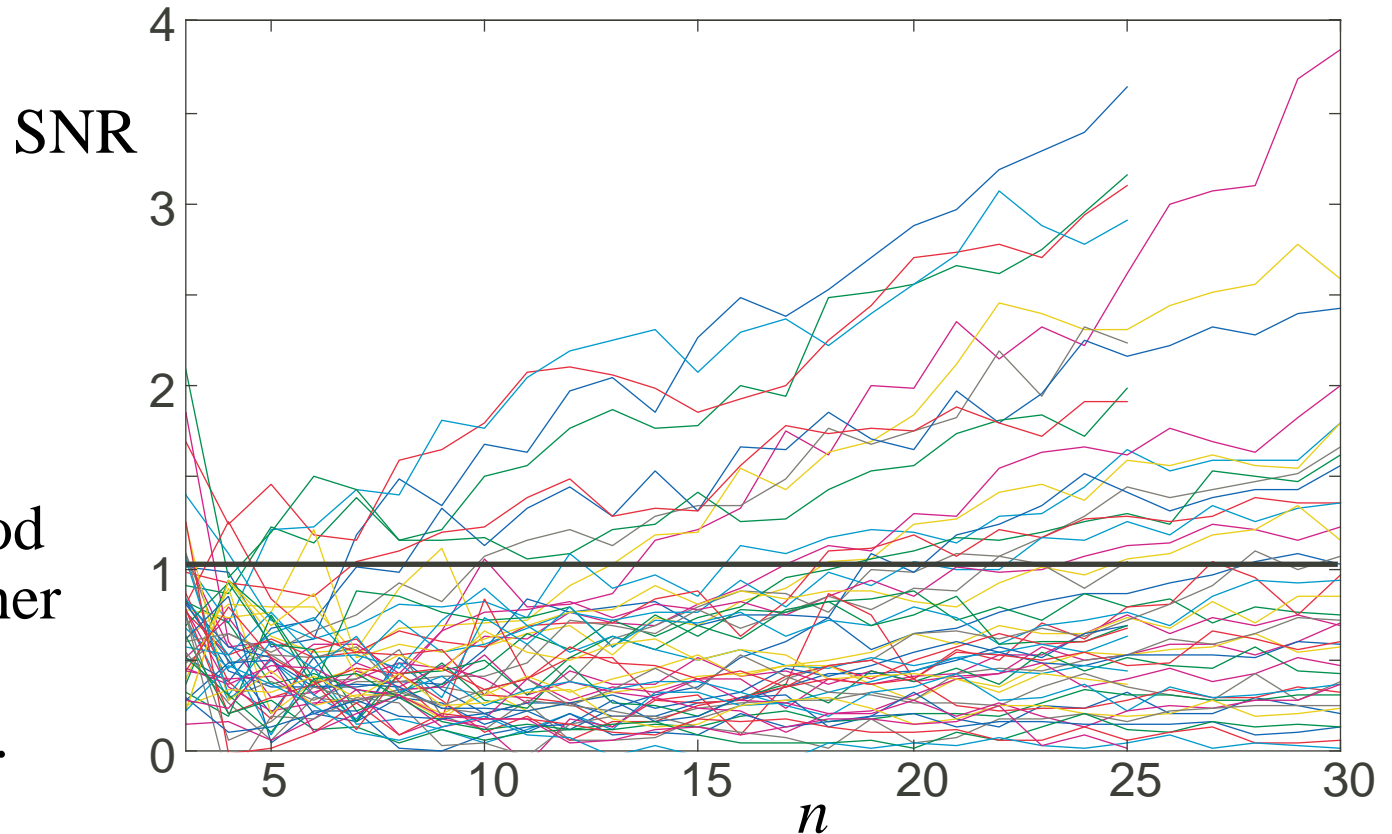
$$\text{SNR} := P/P_\sigma = n \Delta t \left( \sum_t [r(t)]^2 \right) / \left( \sum_t r(t) \right)$$

- SNR grows with rate
- SNR proportional to number of repetitions (more general than Poisson).

# Signal to Noise in Practice

- Variability analysis distinguishes high SNR ( $> 1$ ) from low SNR
- SNR for good cells increased (linear with steep slope) with # of sweeps  $n$ .

- SNR for linear component of good cells is much higher than that for non-linear component.



# Increasing the SNR

- Frequency domain:

- $\Pi_{\sigma}(\omega) = \mathcal{F}\{P_{\sigma}(t)\}$  is constant for all  $\omega$ .

- In practice,  $\Pi(\omega) = \mathcal{F}\{P(t)\}$  is band-limited, so

$$\sum_{-\infty}^{\infty} \Pi(\omega) = \sum_{-\omega^{crit}}^{\omega^{crit}} \Pi(\omega).$$

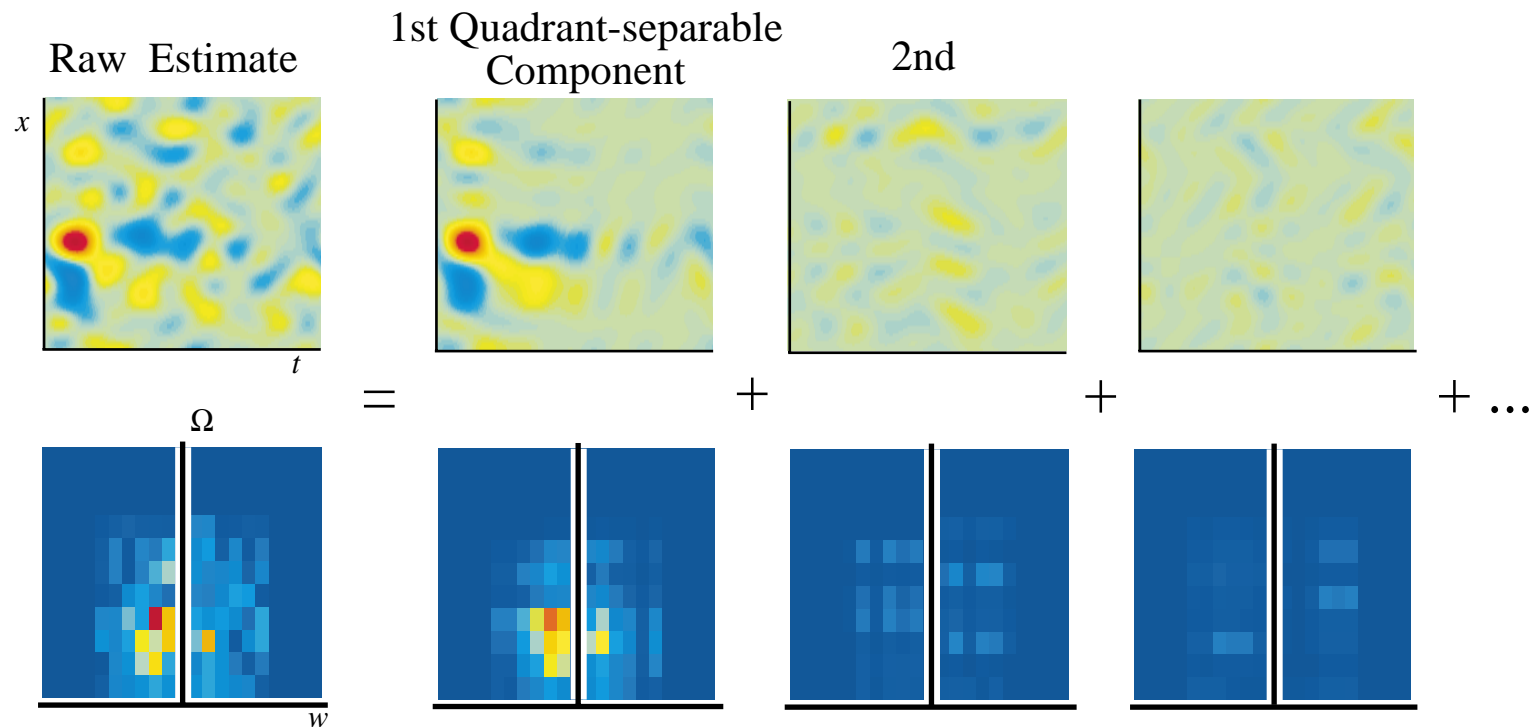
- We can increase the SNR by using

$$\text{SNR}^{incr} := P^{incr} / P_{\sigma}^{incr} = \left( \sum_{-\omega^{crit}}^{\omega^{crit}} \Pi(\omega) \right) / \left( \sum_{-\omega^{crit}}^{\omega^{crit}} \Pi_{\sigma}(\omega) \right)$$

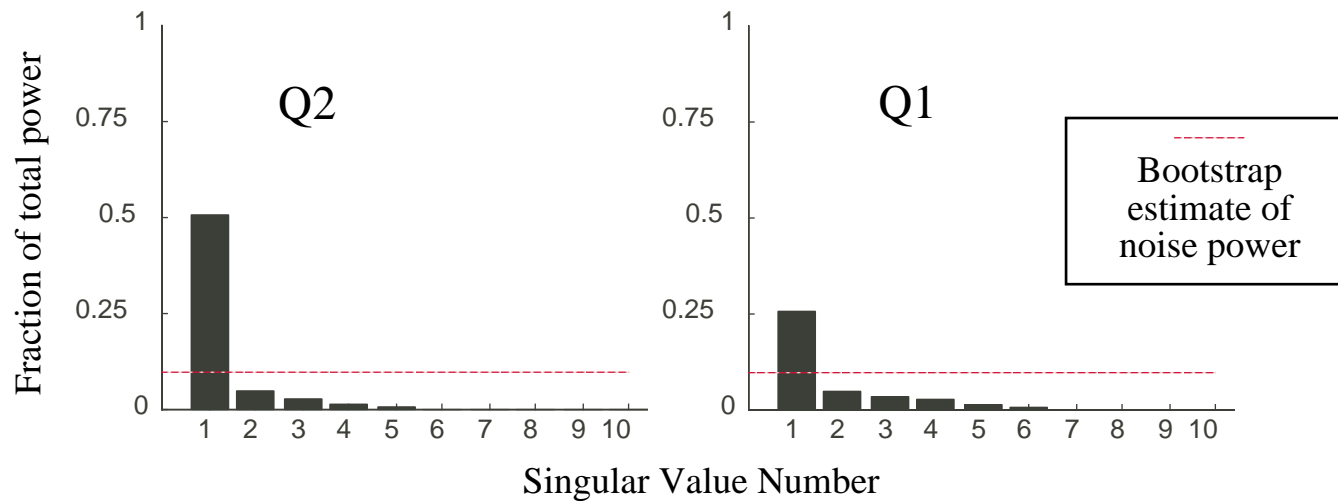
- This is done implicitly by binning or, when deriving the STRF, using low-passed frequency envelopes.

# Singular Value Decomposition

- Singular Value Decomposition (SVD) can be used to estimate the rank of a matrix corrupted by noise. It decomposes the matrix into a sum of rank one matrices, ordered by magnitude. The first  $k$  components sum to a matrix of rank  $k$  which minimizes the power of the remaining components.
- We apply SVD to each quadrant of the transfer function. Below, an STRF and the three most significant quadrant-separable components, derived from SVD, are shown.



# Singular Value Decomposition Example



- SVD naturally picks out high SNR components of a matrix.
- Large jumps in the singular values.
- Jumps straddle bootstrap estimate of noise.
- Noise can be removed by discarding lower-magnitude components.

# Selected References

## Spectro-Temporal Correlation Methods

- Klein DJ, Depireux DA, Simon JZ and Shamma SA, Robust spectro-temporal reverse correlation for the auditory system: Optimizing stimulus design, *J Computational Neurosci.* 1999.
- Eggermont JJ, *Hearing Research* 66 (1993) 177-201.

## Bootstrap method and Singular Value Decomposition

- Politis DN, Computer-intensive methods in statistical analysis, *IEEE signal processing*, 15(1) 39-54 (1998). Zoubir AM and Boashash B, The Bootstrap and its application, *ibid.* 56-77.
- Efron B and Tibshirano RJ, *An introduction to the bootstrap*, Chapman & Hall, New-York, 1993.
- Pilgram B, Schappacher W, Estimation of the dominant singular values for SVD based noise reduction methods, *Int. J. Bifurcation and Chaos* 8 (1999) 571-580.

## Poisson models, Fano factors, information theory and all that

- Oram, MW, Wiener, MC, Lestienne, R and Richmond, BJ, Stochastic nature of precisely timed spike patterns in visual system neuronal responses, *J Neurophysiol.* 81(6):3021-33 (1999).
- Johnson, DH, CM Gruner, K Baggerley, and C Seshagiri. Information-theoretic analysis of the neural code. Submitted to *J. Computational Neuroscience*, 1999.
- Rieke F, Warland D, de Ruyter R, Bialek W, *Spikes : Exploring the Neural Code*, MIT press, 1997.

## Related techniques and models

- Kowalski N, Depireux D and Shamma S, *J. Neurophysiol.* 76 (5) (1996) 3503-3523, & 3524-3534.
- Depireux DA, Simon JZ and Shamma SA, *Comments in Theoretical Biology* (1998).
- Wang K and Shamma SA, *IEEE Trans. on Speech and Audio* 2(3) (1994) 421-435, and 3(2) (1995) 382-395.