# Linearity and Temporal Symmetry in Primary Auditory Cortex

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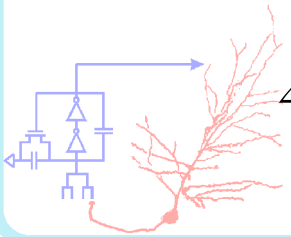

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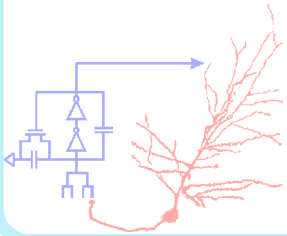
Computational Sensorimotor Systems Laboratory

# Topics

- The Spectro-Temporal Response Field (STRF) characterizes neuronal responses in Primary Auditory Cortex in ferret.
- STRF can be measured independently by different stimulus types
- STRF = Linear Statistic = Linearity in neuron?
- Application of Singular Value Decomposition
- Temporal Symmetry
- Neural Connectivity vs. Temporal Symmetry



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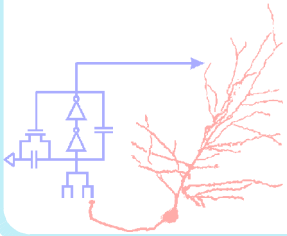
# Results

- Three Different Stimuli give strongly similar STRFs: *Linearity is strong* across varied stimuli
- Singular Value Decomposition optimally estimates STRFs with *Low Rank* approximation
- Temporal Symmetry predominates
- Simple models of neural connectivity inconsistent with temporal symmetry
- Models of neural connectivity consistent with temporal symmetry if:

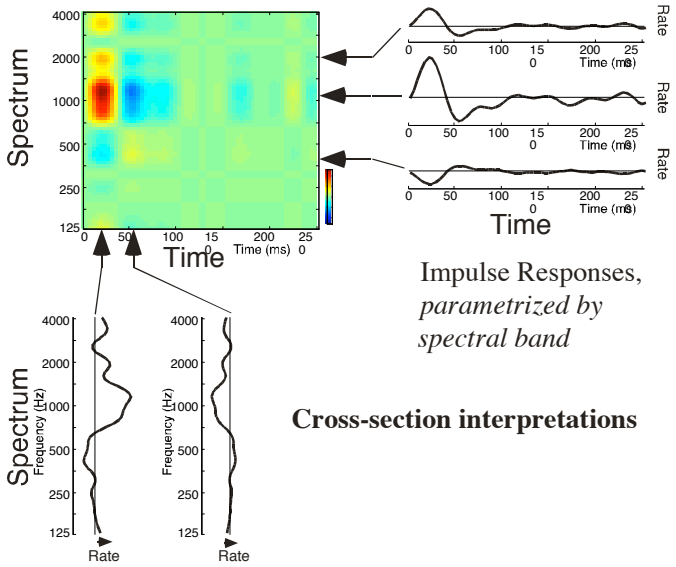
  Inputs are phase lagged

  Intracortical connections do not mix spectral response properties



# Spectro-Temporal Response Field

## Spectro-Temporal Response Field (STRF)




Spectral Response Fields, *evolving in time*

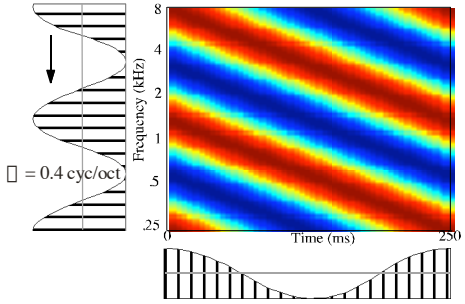
## Spectro-Temporally Rich Stimuli

*Simplest Dynamic Stimulus Used*

$S(t,x) = \sin(2\pi wt + 2\pi\Omega x + \phi)$

$x = \log_2(f / f_0)$
$w$ = ripple velocity,
e.g. 4 Hz = 4 cycles/s
$\Omega$ = ripple density,
e.g. 0.4 cycles/octave
= 2 cycles/5 octaves

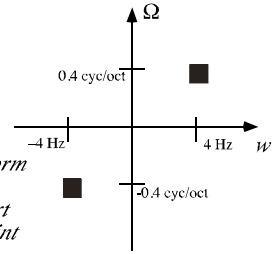
Spectro-Temporal representation (*Spectrogram*)




c.f. visual contrast gratings

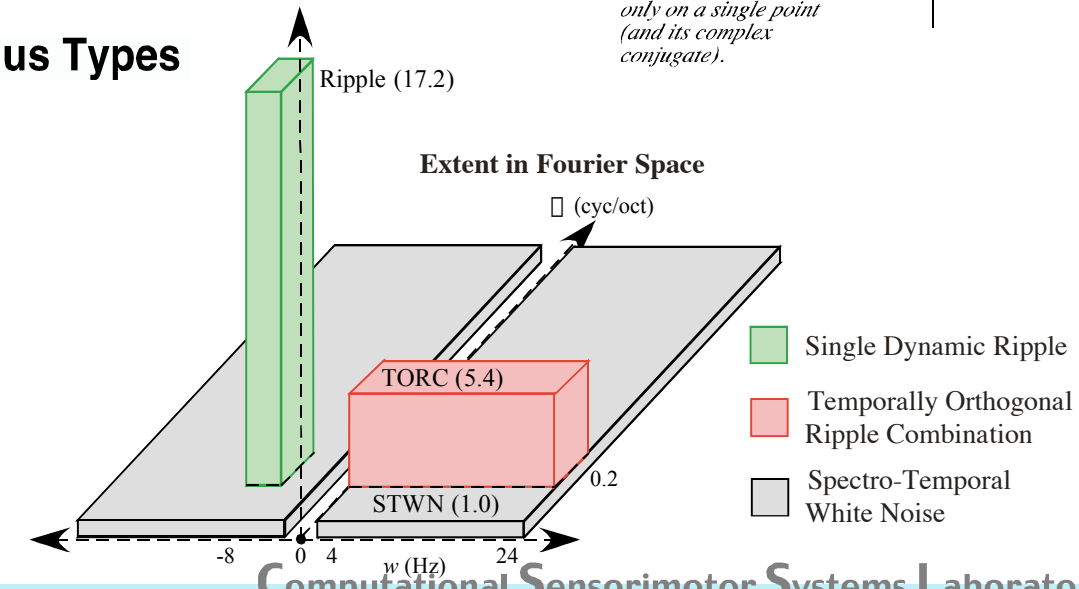
$\int [.] \exp(\pm 2\pi j\Omega x \pm 2\pi j wt)$

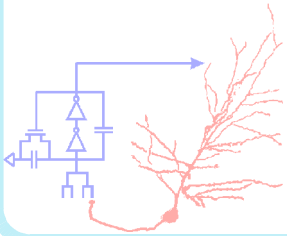
Fourier Space representation



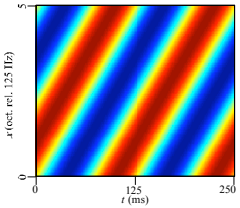
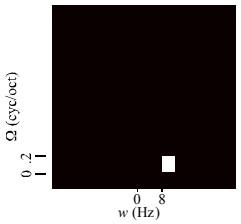
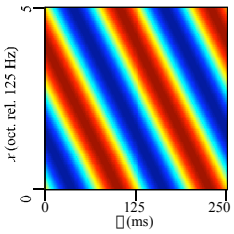
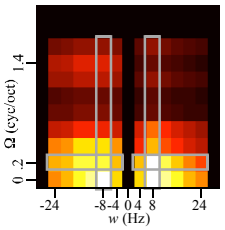
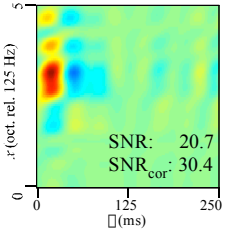
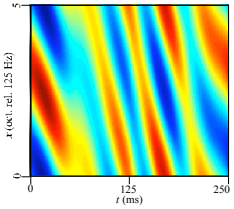
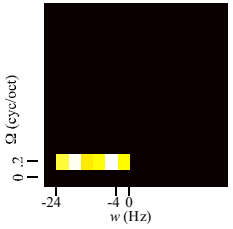
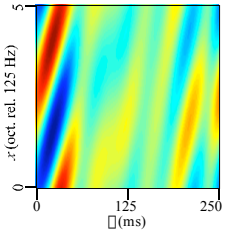
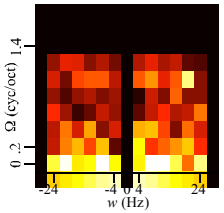
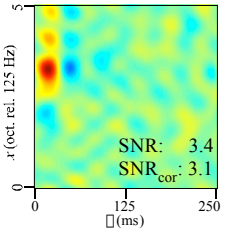
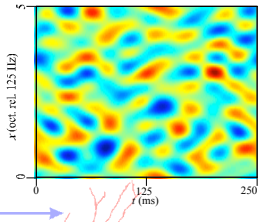
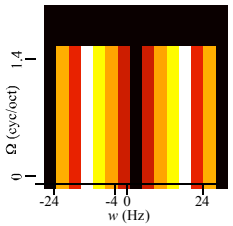
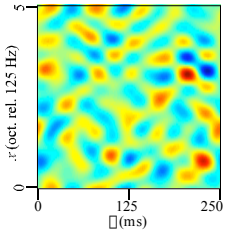
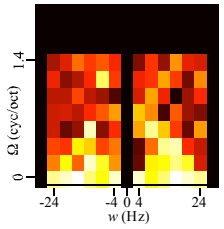
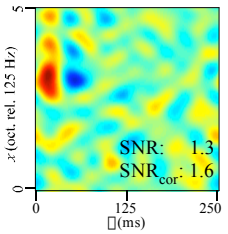

*The Fourier transform of a single moving sinusoid has support only on a single point (and its complex conjugate).*

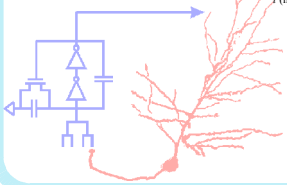
## 3 Stimulus Types



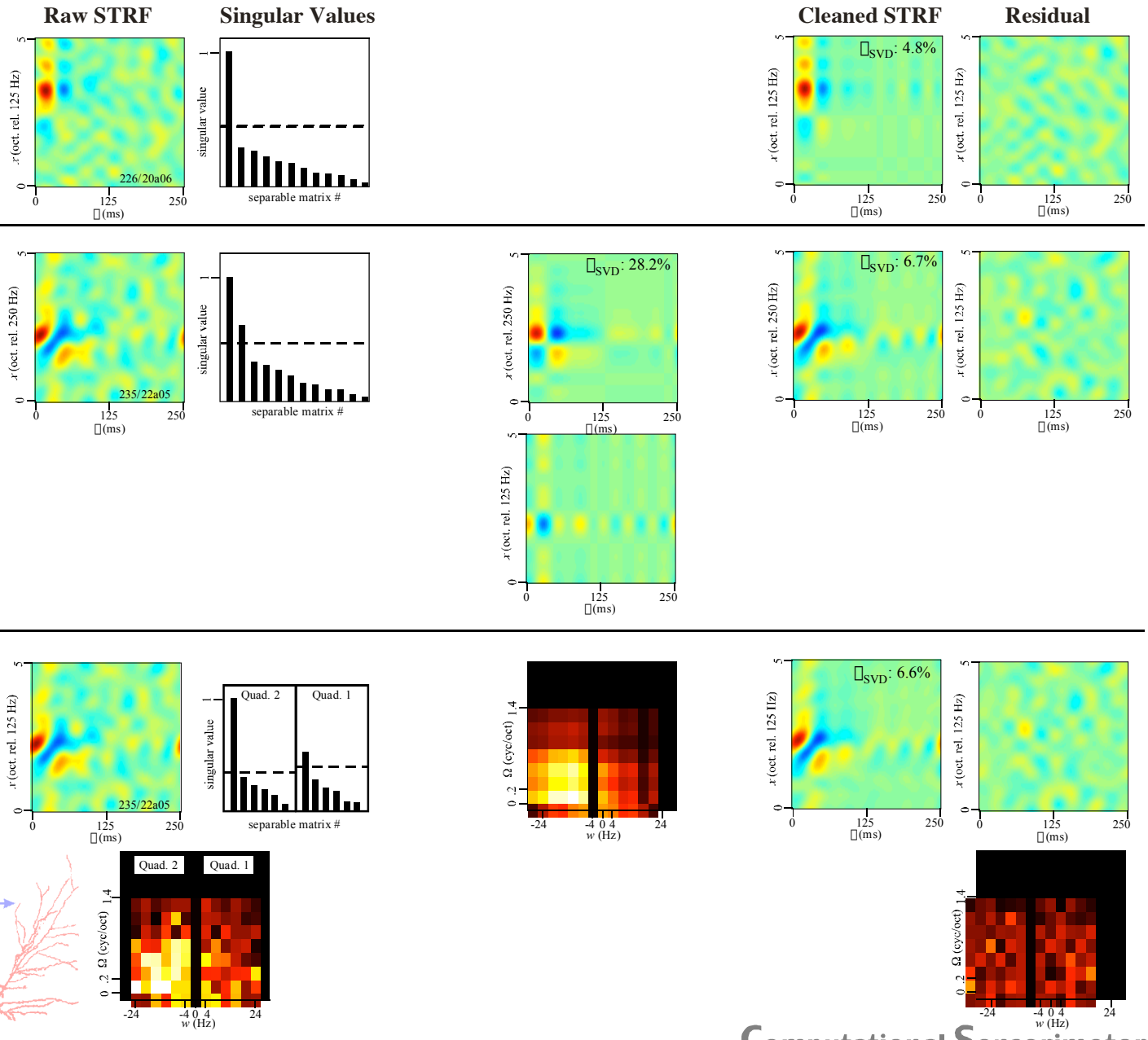
# Reverse Correlation  STRF

| | *Single Stimulus* | *Reverse Correlation from Single Stimulus* | | *Reverse Correlation from Full Set* | |
|---|---|---|---|---|---|
| | | **Fourier Domain** | **Spectro-Temporal** | **Fourier Domain** | **Spectro-Temporal** |
| **Single Dynamic Ripple** |  |  |  |  |   |
| **Temporally Orthogonal Ripple Combination** |  |  |  |  |   |
| **Spectro-Temporal White Noise** |  |  |  |  |   |



SNR: (Signal Power) / (Signal Variance)
SNR$_{cor}$: (Power from first 50% of STRF) / (Power in last 50% of STRF)

# Singular Value Decomposition (SVD)




Estimated Noise Threshold:
Max. Singular Value of STRF over last 50% of STRF

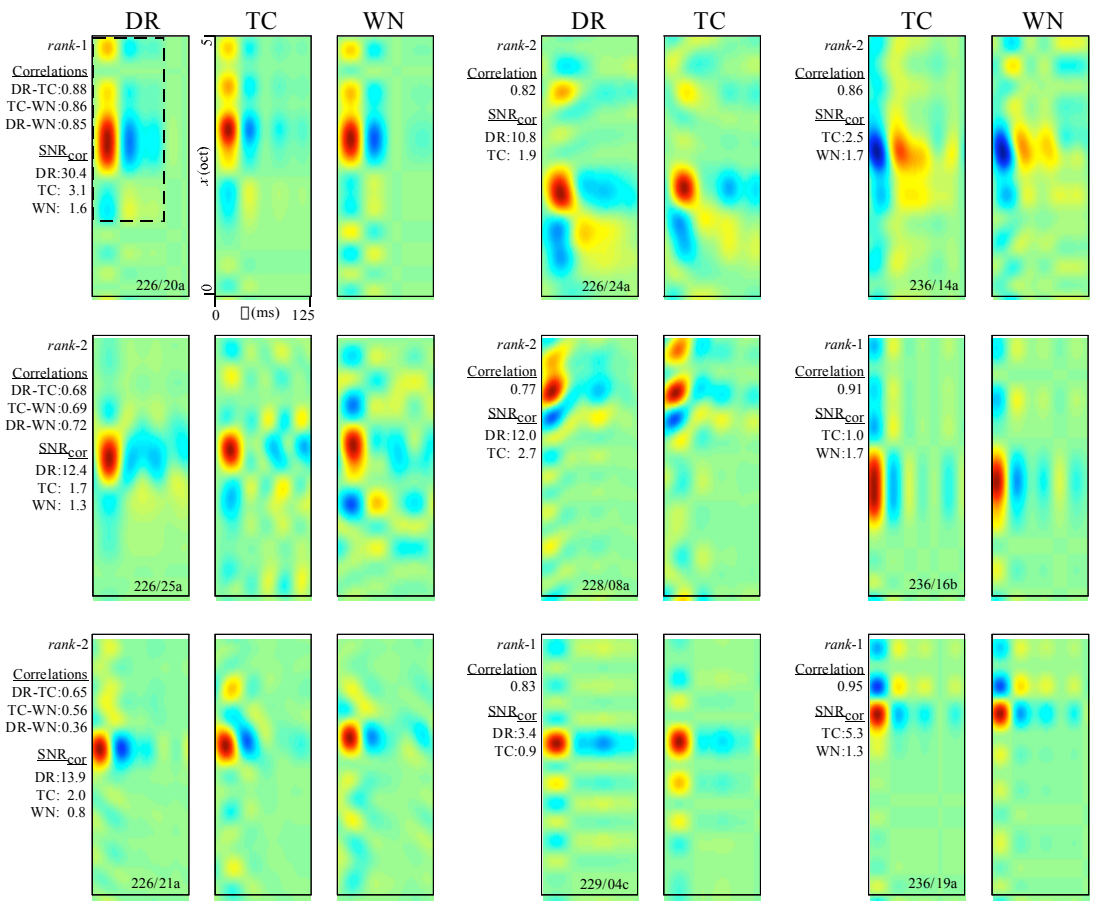
$\Delta_{SVD}$:
(unbiased) estimator of STRF power remaining in residual

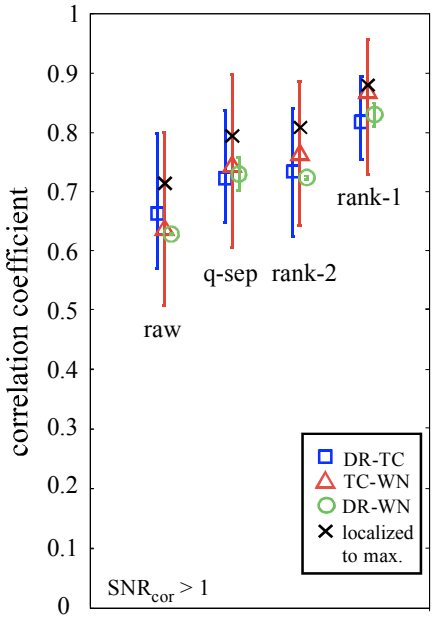
lower values = better approximations

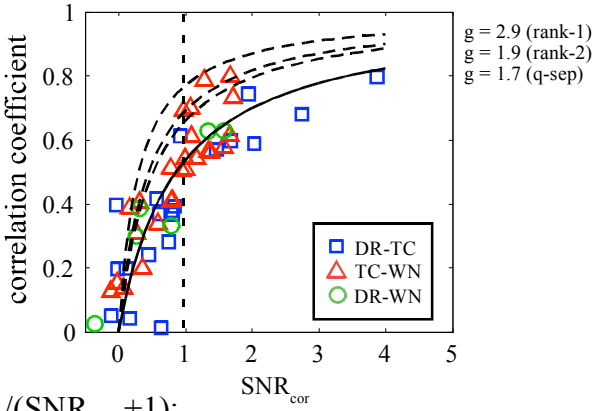
**SVD used to estimate optimal approximation**

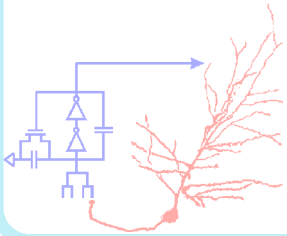
**SVD not used to estimate rank**

# STRF Linearity/Robustness



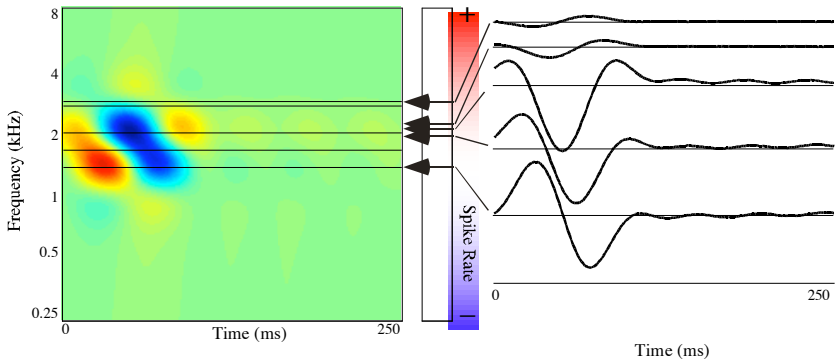
$N = 45$:
STRF measured with > 1 stimulus type,
Anesthetized

$SNR_{cor}/(SNR_{cor}+1)$:
Prediction of Purely Linear System + Noise

$g\ SNR_{cor}/(g\ SNR_{cor}+1)$:
Prediction of Purely Linear System + Noise + Noise Reduction (via SVD)

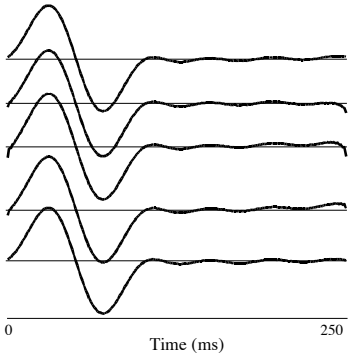
# Temporal Symmetry

## Simulated STRF

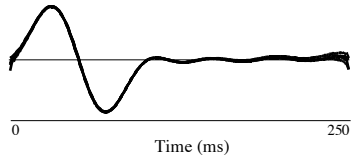



Temporal cross-sections



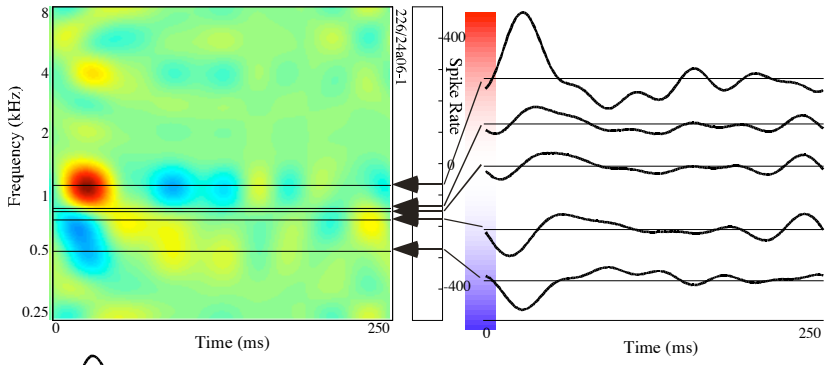

Temporal cross-sections, with Hilbert "rotations" and re-scalings




same, overlaid

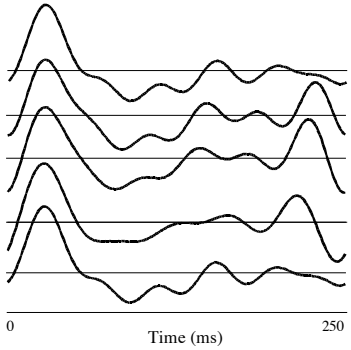
Temporal Symmetry Index: 0.99—complete overlap

## Measured STRF




Temporal cross-sections

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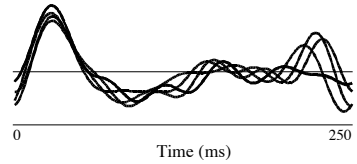



same, overlaid

Temporal Symmetry Index: 0.76—strong overlap

**Temporal Symmetry Definition**

All temporal cross-sections equal, up to scaling and Hilbert "rotation" $f^{\theta}(t) = \sin\theta\ \hat{f}(t) + \cos\theta\ f(t)$

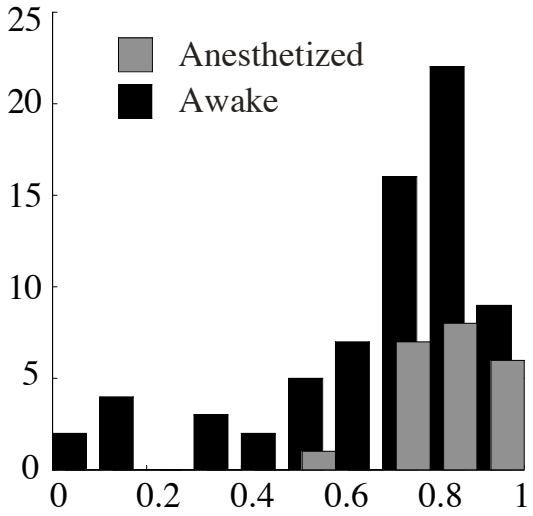
**Temporal Symmetry Index**

Definition: (complex) correlation coefficient between 1st and 2nd (analytic) SVD temporal cross-sections

Magnitude: between 0 (no temporal symmetry) and 1 (total temporal symmetry)

# Temporal Symmetry Statistics

**Temporal Symmetry Index**



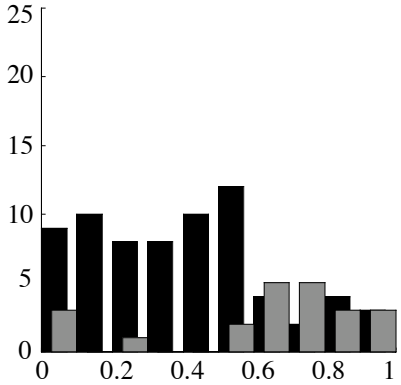

**SVD approximations by rank, across population**

Anesthetized:
49/73 Rank 1 (temporally symmetric, not shown)
22/73 Rank 2 (shown at left)
2/73 Rank 3 (not temporally symmetric)

Awake:
72/145 Rank 1 (temporally symmetric, not shown)
70/145 Rank 2 (shown at left)
3/145 Rank 3 (not temporally symmetric)

**Compare:**

**Spectral Symmetry Index**

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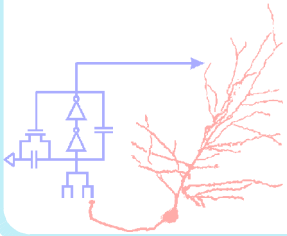
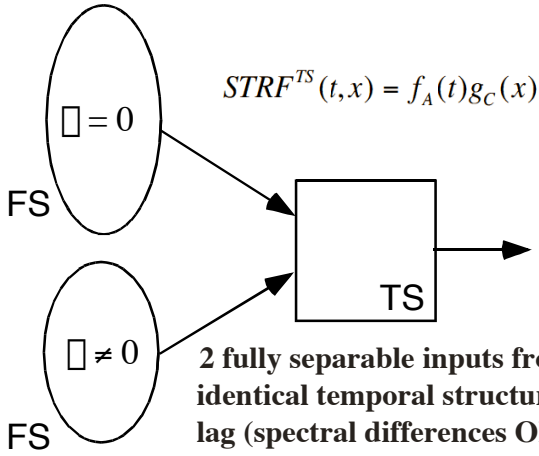


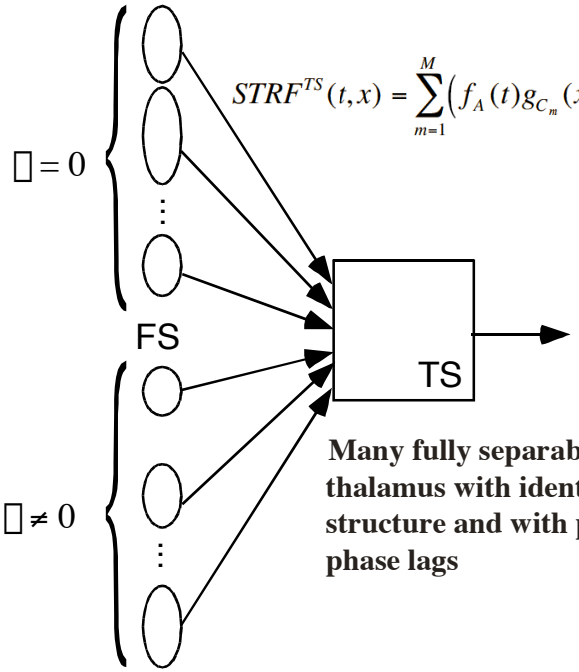
**Caveats**
Sustained Portion of Response only
Low Frequency (< 25 Hz) band of response only
SNR > 2

# Models with Temporal Symmetry



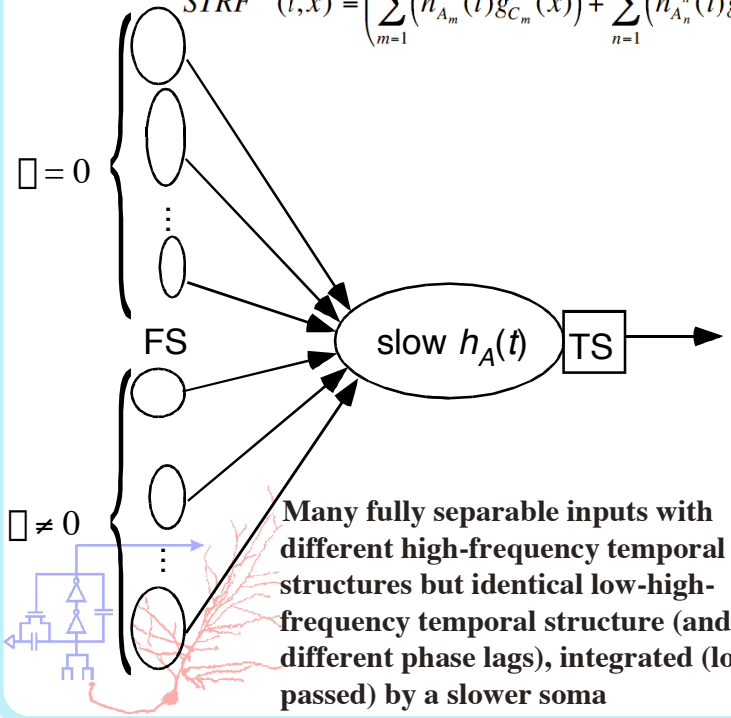

$$STRF^{TS}(t,x) = f_A(t)g_C(x) + f_A^{\theta}(t)g_D(x)$$

**2 fully separable inputs from thalamus with identical temporal structure but with phase lag (spectral differences OK)**



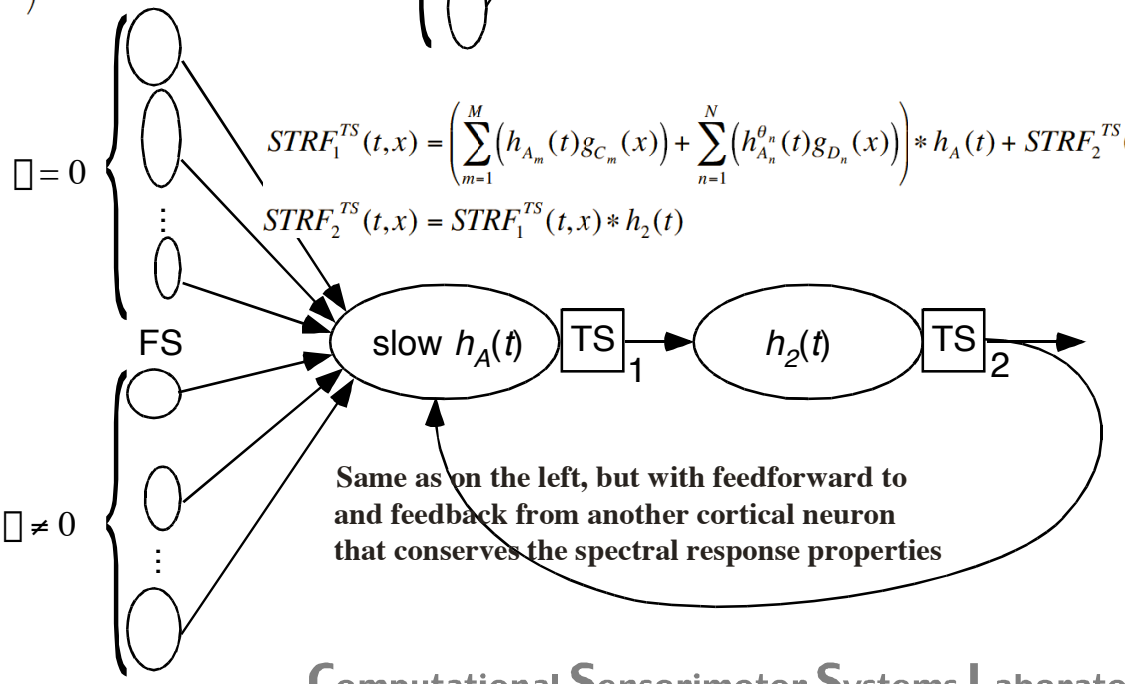

$$STRF^{TS}(t,x) = \sum_{m=1}^{M}\left(f_A(t)g_{C_m}(x)\right) + \sum_{n=1}^{N}\left(f_A^{\theta_n}(t)g_{D_n}(x)\right)$$

**Many fully separable inputs from thalamus with identical temporal structure and with possibly different phase lags**




$$STRF^{TS}(t,x) = \left(\sum_{m=1}^{M}\left(h_{A_m}(t)g_{C_m}(x)\right) + \sum_{n=1}^{N}\left(h_{A_n}^{\theta_n}(t)g_{D_n}(x)\right)\right) * h_A(t)$$

**Many fully separable inputs with different high-frequency temporal structures but identical low-high-frequency temporal structure (and different phase lags), integrated (low-passed) by a slower soma**

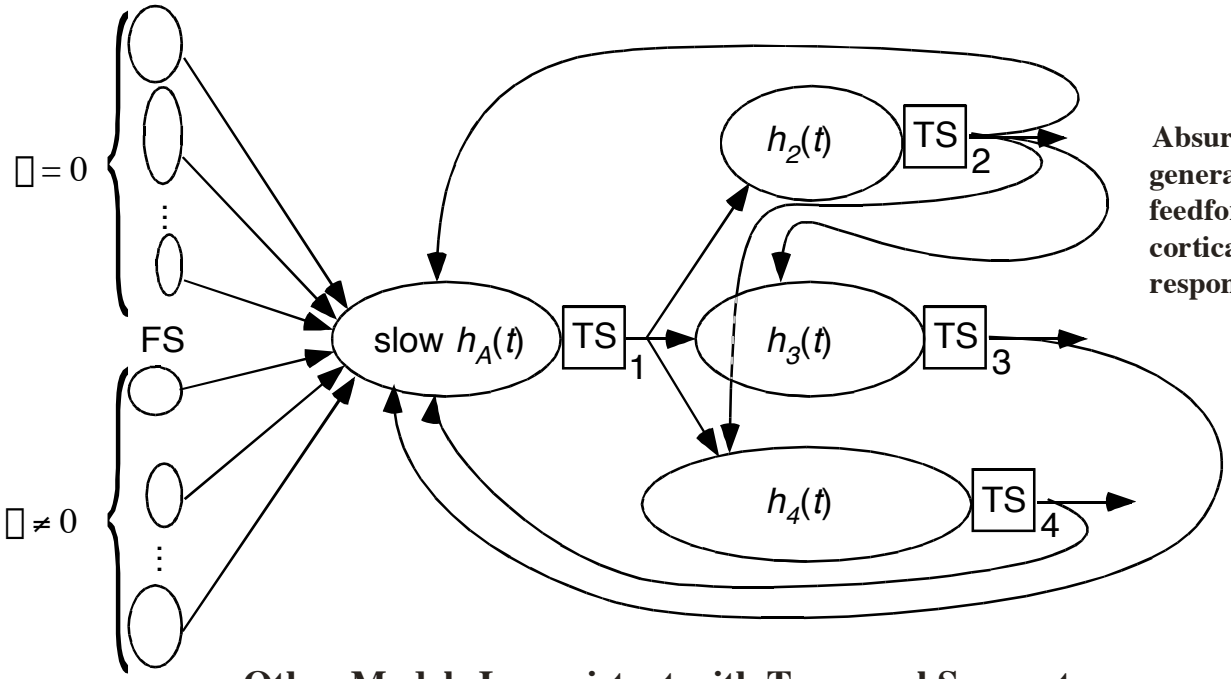



$$STRF_1^{TS}(t,x) = \left(\sum_{m=1}^{M}\left(h_{A_m}(t)g_{C_m}(x)\right) + \sum_{n=1}^{N}\left(h_{A_n}^{\theta_n}(t)g_{D_n}(x)\right)\right) * h_A(t) + STRF_2^{TS}(t,x)$$

$$STRF_2^{TS}(t,x) = STRF_1^{TS}(t,x) * h_2(t)$$

**Same as on the left, but with feedforward to and feedback from another cortical neuron that conserves the spectral response properties**

# Models continued



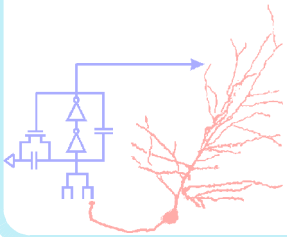

**Absurdly but plausibly complicated generalization—with additional feedforward and feedback among cortical cells that conserve the spectral response properties**

**Other Models Inconsistent with Temporal Symmetry:**

- Inputs from thalamus with identical temporal structure but with time lag instead of phase lag
- Feedforward to and feedback from another cortical neuron that changes the spectral response properties

**Caveats**

- Physiological, not Anatomical
- Sustained Portion of Response only
- Only for broadband dynamic stimuli
- Describes linear response components only
- Lag might arise from any of several mechanisms (e.g. inhibition, synaptic depression)



# Suggested Reading

Depireux DA, Simon JZ, Klein DJ, Shamma SA. 2001. Spectro-temporal response field characterization with dynamic ripples in ferret primary auditory cortex. *J Neurophysiol* 85: 1220-34

Eggermont JJ, Johannesma PM, Aertsen AM. 1983. Reverse-correlation methods in auditory research. *Q Rev Biophys* 16: 341-414

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Stewart GW. 1993. Determining Rank in the Presence of Error. In *Linear algebra for large scale and real-time applications*, ed. MS Moonen, GH Golub, BLRd Moor. Dordrecht: Kluwer Academic Publishers