Linearity and Temporal Symmetry in Primary Auditory Cortex

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Support from Office of Naval Research
MURI # N00014-97-1-05001
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
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)**

- Impulse Responses, parametrized by spectral band
- Cross-section interpretations
- Spectral Response Fields, evolving in time

**3 Stimulus Types**

- Ripple (17.2)
- TORC (5.4)
- STWN (1.0)

**Spectro-Temporally Rich Stimuli**

*Simplest Dynamic Stimulus Used*

\[ S(t,x) = \sin(2\pi w t + 2\pi x + \phi) \]

- \( x = \log(f / f_0) \)
- \( w = \text{ripple velocity}, \text{ e.g. } 4 \text{ Hz} = 4 \text{ cycles/s} \)
- \( \phi = \text{ripple density}, \text{ e.g. } 0.4 \text{ cycles/octave} = 2 \text{ cycles/5 octaves} \)

**Fourier Space representation**

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

**Extent in Fourier Space**

- Single Dynamic Ripple
- Temporally Orthogonal Ripple Combination
- Spectro-Temporal White Noise
## Reverse Correlation \( \square \) STRF

<table>
<thead>
<tr>
<th>Single Stimulus</th>
<th>Reverse Correlation from Single Stimulus</th>
<th>Reverse Correlation from Full Set</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Single Dynamic Ripple</strong></td>
<td></td>
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<tr>
<td><img src="image1" alt="Image" /></td>
<td><img src="image2" alt="Image" /></td>
<td><img src="image3" alt="Image" /></td>
</tr>
<tr>
<td><strong>Fourier Domain</strong></td>
<td><strong>Spectro-Temporal</strong></td>
<td><strong>Fourier Domain</strong></td>
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<tr>
<td><img src="image4" alt="Image" /></td>
<td><img src="image5" alt="Image" /></td>
<td><img src="image6" alt="Image" /></td>
</tr>
</tbody>
</table>
| **SNR**: 20.7  
**SNR\text{cor}**: 30.4 | **SNR**: 3.4  
**SNR\text{cor}**: 3.1 | **SNR**: 1.3  
**SNR\text{cor}**: 1.6 |

| **Temporally Orthogonal Ripple Combination** |  |  |
| ![Image](image8) | ![Image](image9) | ![Image](image10) |
| **Fourier Domain** | **Spectro-Temporal** | **Fourier Domain** | **Spectro-Temporal** |
| ![Image](image11) | ![Image](image12) | ![Image](image13) | ![Image](image14) |
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| **Spectro-Temporal White Noise** |  |  |
| ![Image](image15) | ![Image](image16) | ![Image](image17) |
| **Fourier Domain** | **Spectro-Temporal** | **Fourier Domain** | **Spectro-Temporal** |
| ![Image](image18) | ![Image](image19) | ![Image](image20) | ![Image](image21) |
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**SNR**: \( \frac{\text{Signal Power}}{\text{Signal Variance}} \)

**SNR\text{cor}**: \( \frac{\text{Power from first 50\% of STRF}}{\text{Power in last 50\% of STRF}} \)
Singular Value Decomposition (SVD)

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

\( \text{SVD} \): (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

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

\[ g = 2.9 \text{ (rank-1)} \]
\[ g = 1.9 \text{ (rank-2)} \]
\[ g = 1.7 \text{ (q-sep)} \]

\[ N = 45: \]
STRF measured with > 1 stimulus type, Anesthetized
Temporal Symmetry

Simulated STRF

Temporal cross-sections

Temporal Symmetry Index: 0.99—complete overlap

Temporal cross-sections, with Hilbert “rotations” and re-scalings

Measured STRF

Temporal cross-sections

Temporal Symmetry Index: 0.76—strong overlap

Temporal cross-sections, with Hilbert “rotations” and re-scalings

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

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)

Spectral Symmetry Definition
All spectral cross-sections equal, up to scaling and Hilbert “rotation”

Spectral Symmetry Index
Definition: (complex) correlation coefficient between 1st and 2nd (analytic) SVD spectral cross-sections
Magnitude: between 0 (no spectral symmetry) and 1 (total spectral symmetry)

Compare:

Caveats
Sustained Portion of Response only
Low Frequency (< 25 Hz) band of response only
SNR > 2
Models with Temporal Symmetry

\[ STRF^{TS}(t,x) = f_A(t)g_C(x) + f_A^0(t)g_D(x) \]

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

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

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

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

\[ STRF_2^{TS}(t,x) = STRF_1^{TS}(t,x) * h_A(t) \]

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


