Functional and Structural Implications of Non-Separability of Spectral and Temporal Responses in AI

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Introduction

- We measure the response of cells in ferret Primary Auditory Cortex (AI) to dynamic, broadband sounds.
- The dynamic, broadband sounds are simple combinations of spectro-temporal basis functions, called "moving ripples."
- By correlating the response with the stimulus, we derive Spectro-Temporal Receptive Fields (STRFs), a linear, quantitative descriptor of how a cell responds to dynamic sounds.
- The STRFs exhibit symmetries and patterns such as separability, and its generalization, quadrant separability.
- Quadrant separability does not arise from most neural networks, and can be used to rule out some models of neural connectivity.

Summary

- The STRFs measured for all units in AI are quadrant separable or fully separable.
- Quadrant separability is **incompatible** with simple summing of independent, fully separable sources.
- Summing two fully separable STRFs **is** quadrant separable if the temporal processing is in quadrature.
- There are three ways in which a fully separable STRF can become quadrant separable:
  power asymmetry, ***spectral*** asymmetry, & ***temporal*** asymmetry.
- Only power and spectral asymmetry contribute to quadrant separability in AI, **not temporal**.
- Quadrant Separability is incompatible with velocity selectivity.
- Quadrant Separability and persistence of temporal symmetry strongly constrain possible models of neural connectivity.

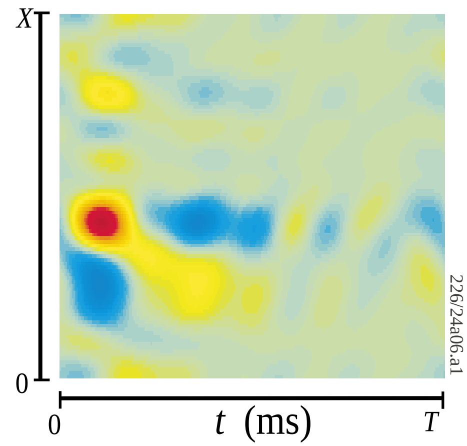
STRFs in AI

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

... or by the (Fourier domain) ripple Transfer Function (TF).

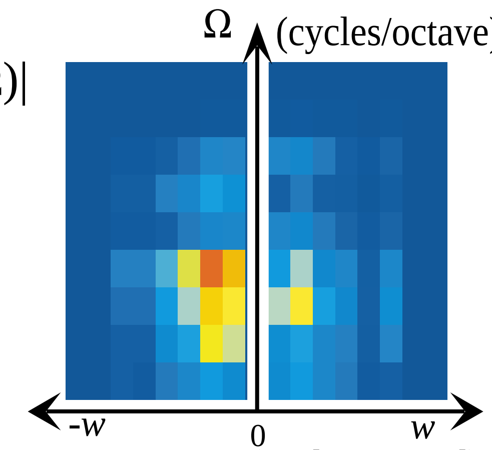
STRF(*t*,*x*)

$x = \log_2 f/fo$
(octaves)

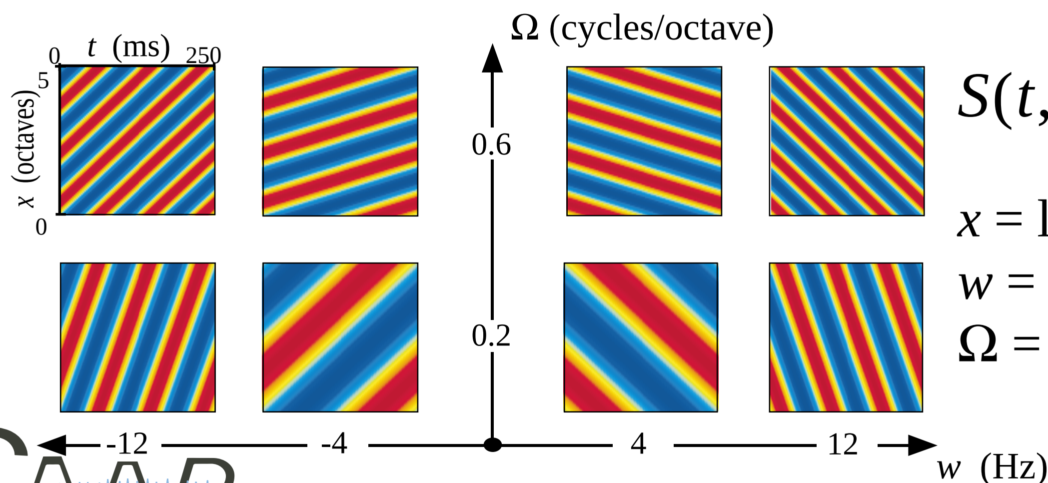


$|\mathcal{F}\{\ \}|$ ⟷

$|TF(w,\Omega)|$



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:



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

$x = \log_2[f / f_0]$
w = ripple velocity, modulation rate
Ω = ripple frequency, spectral density

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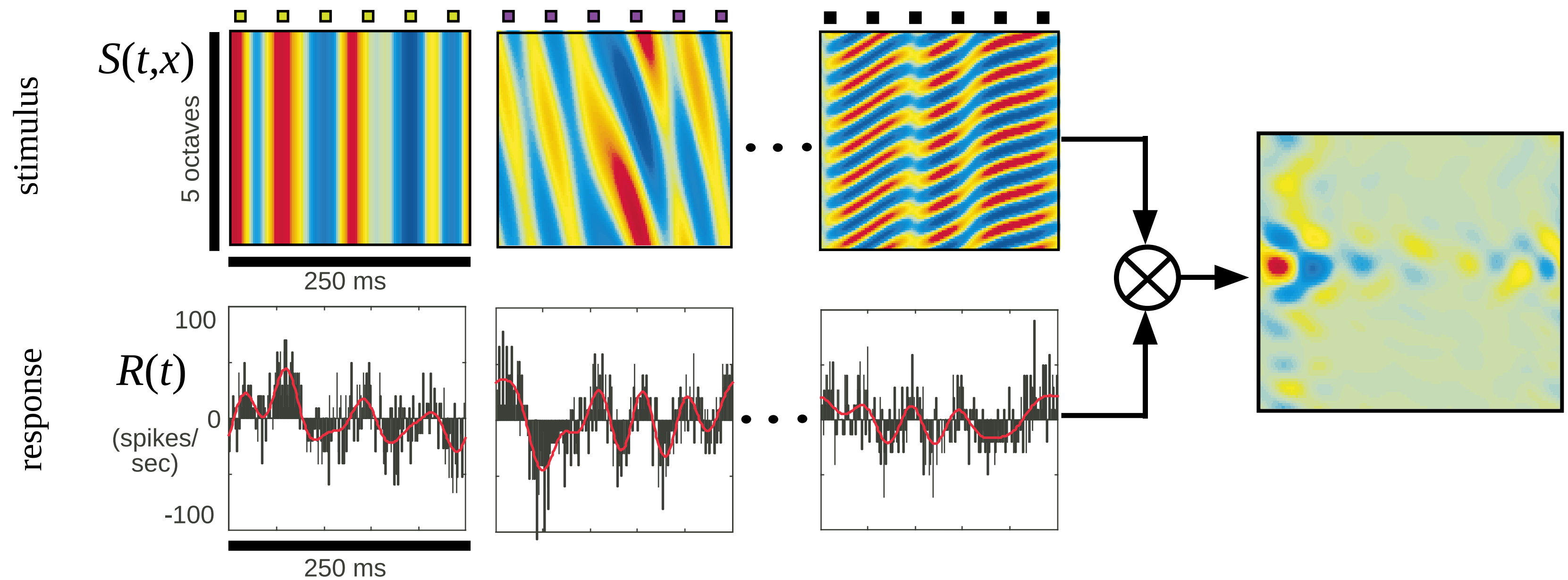
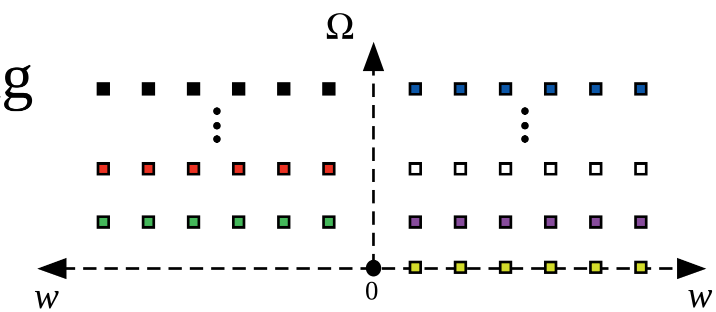
Temporally Orthogonal Ripple Combinations

- 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.



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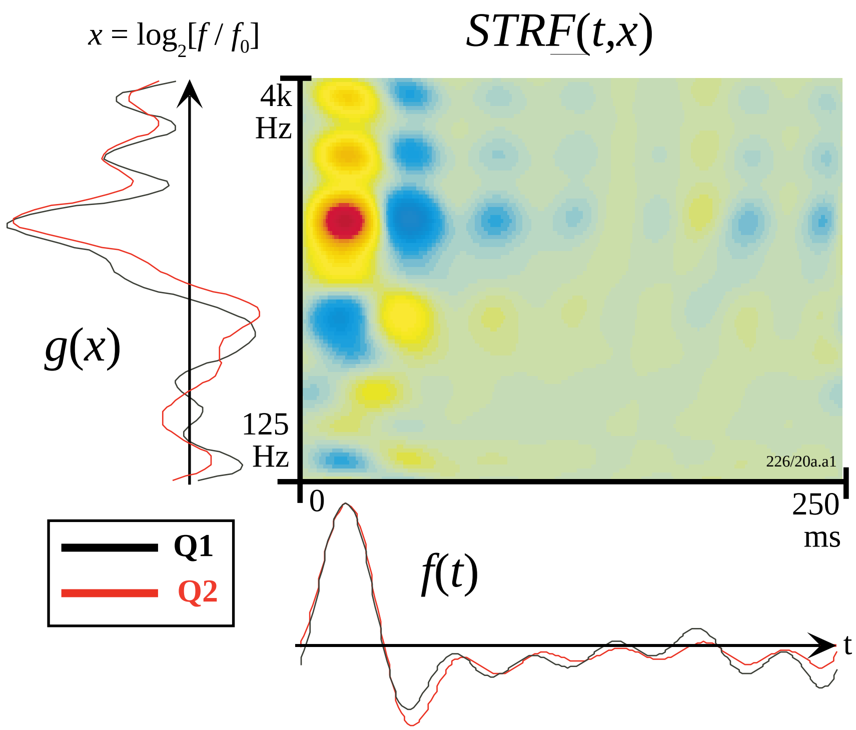
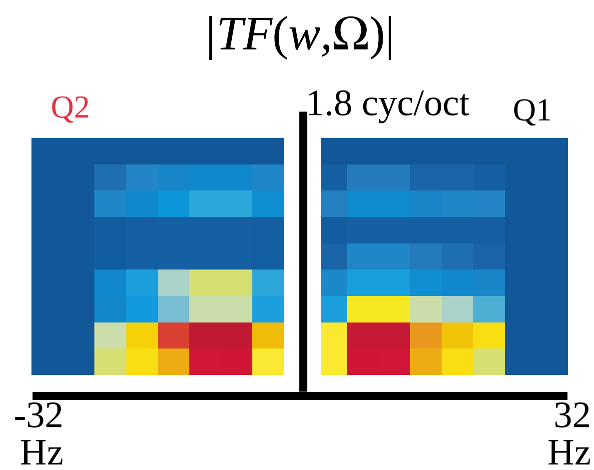
Fully Separable STRF



$|\mathcal{F}\{\ \}|$
$\longleftrightarrow$



The STRF and TF are a product of a single spectral response function with a single temporal response function.

Shown above are the impulse responses $f(t)$ and receptive fields $g(x)$ derived from quadrant 1 (black) and quadrant 2 (red) of the transfer function by inverse Fourier transformation.

$$STRF(t,x) = f(t)\, g(x)$$

$$f(t) \overset{|\mathcal{F}\{\ \}|}{\longleftrightarrow} F(w)$$

$$g(x) \overset{|\mathcal{F}\{\ \}|}{\longleftrightarrow} G(\Omega)$$

$$TF(w,\Omega) = F(w)\, G(\Omega)$$

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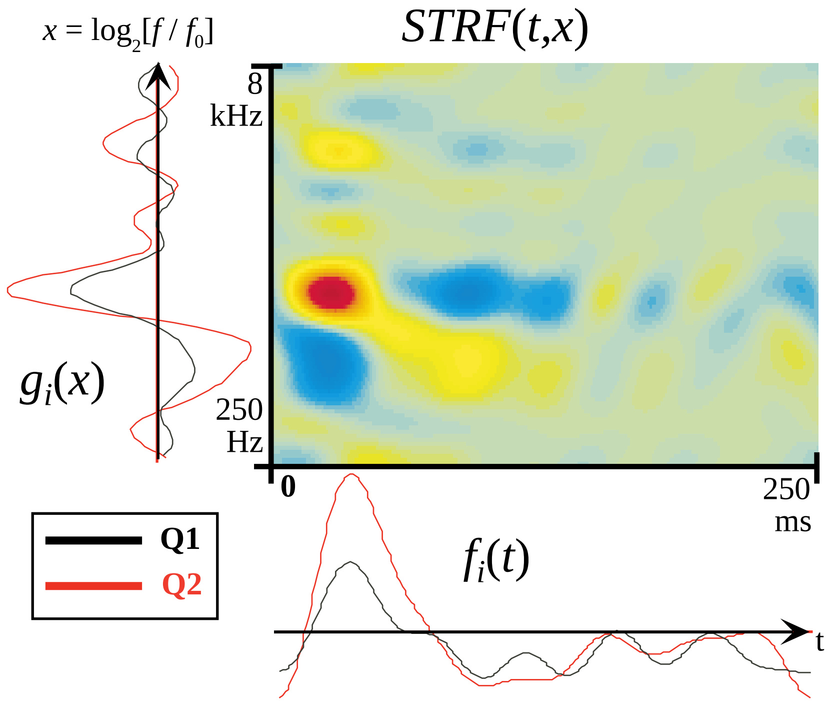
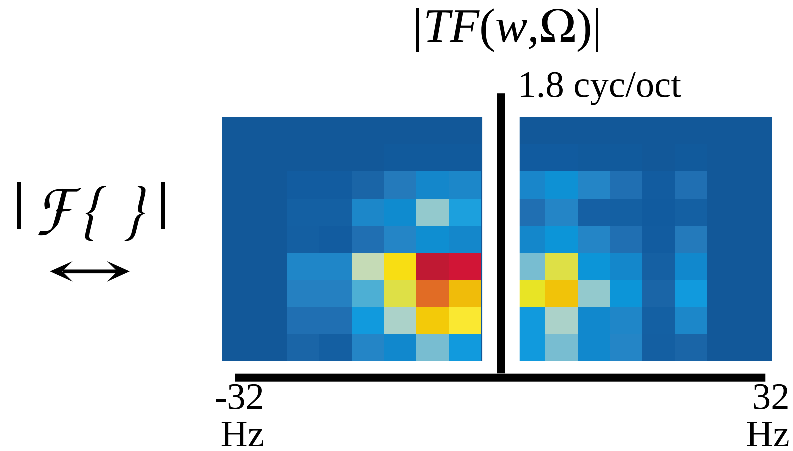
Quadrant Separable STRF





This neuron responded twice as strong to rising frequencies than it did to falling frequencies.

The STRF is not separable, but each quadrant of the transfer function is, i.e., there are different spectral and temporal responses for upwards and downwards frequency modulation.

$$f_i(t) \overset{|\mathcal{F}\{\ \}|}{\longleftrightarrow} F_i(w)$$

$$g_i(x) \overset{|\mathcal{F}\{\ \}|}{\longleftrightarrow} G_i(\Omega)$$

$$T(w,\Omega) = \begin{cases} F_1(w)\, G_1(\Omega) & w > 0, \Omega > 0 \\ F_2(w)\, G_2(\Omega) & w < 0, \Omega > 0 \end{cases}$$

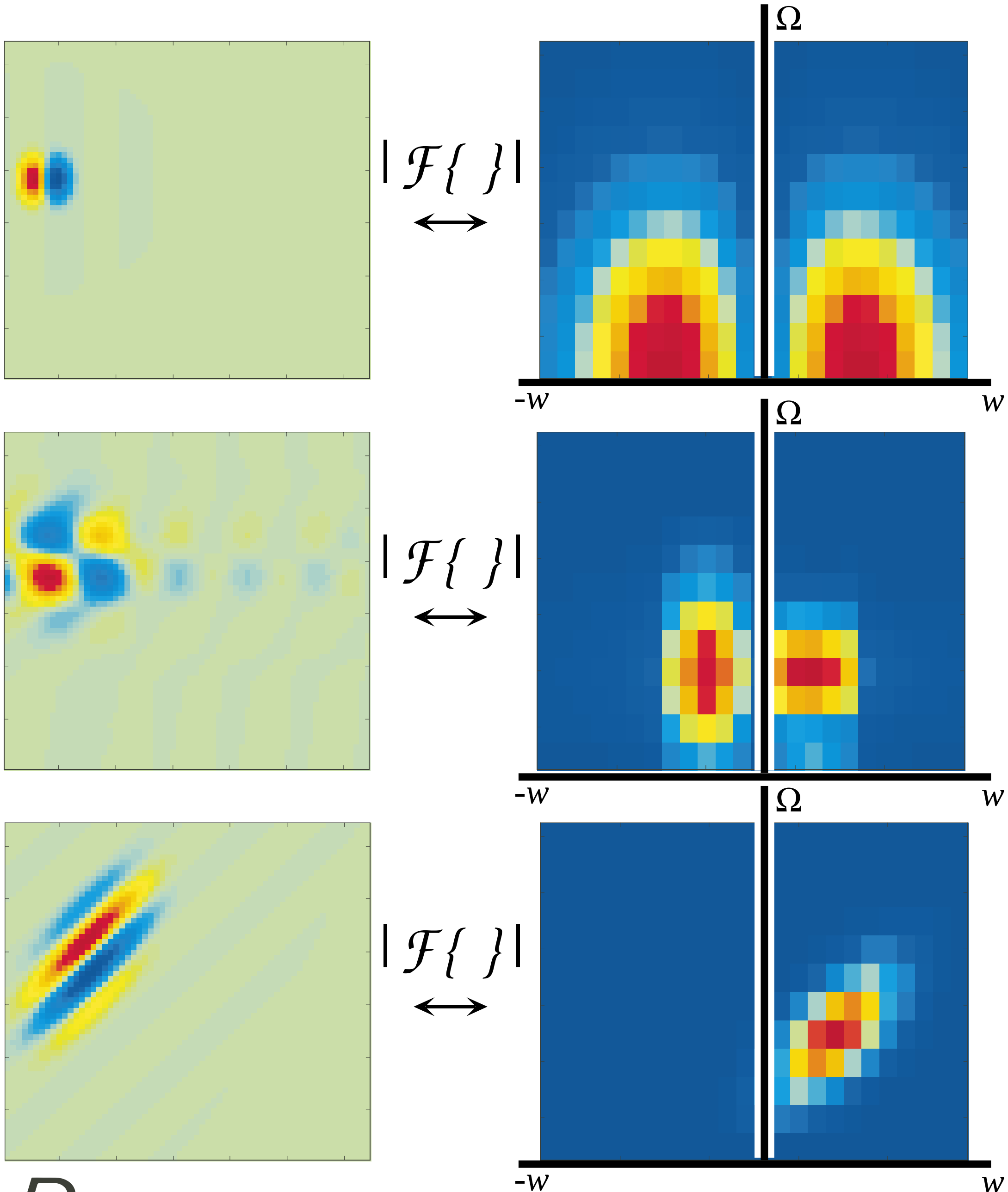
and for $\Omega > 0$: $T(w,\Omega) = T^*(-w,-\Omega)$

Examples & Counterexamples

Fully Separable

Quadrant Separable

Velocity Selective is *Inseparable*



Quadrant separability is incompatible with velocity selectivity.

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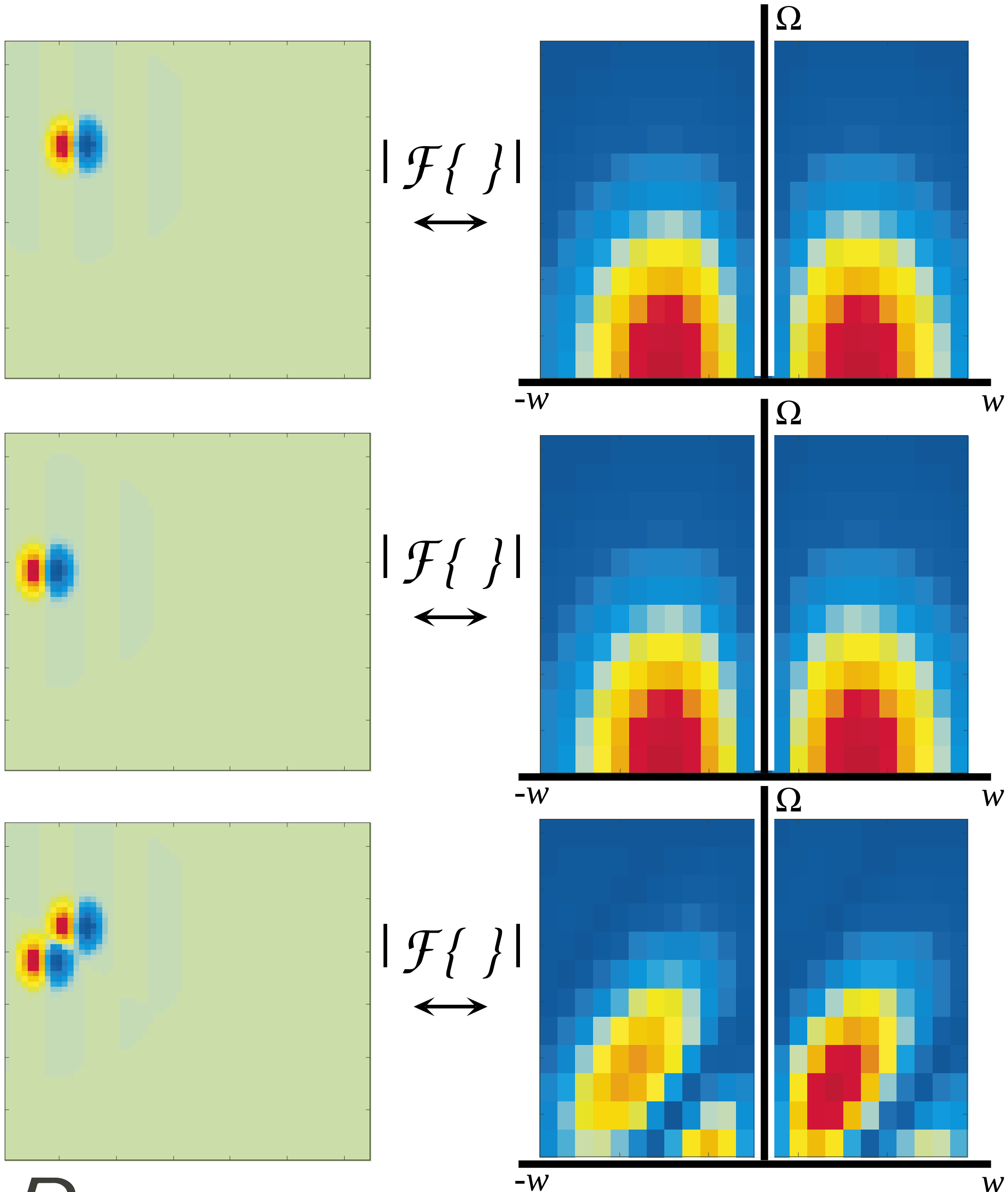
A Counterexample

Fully Separable

Fully Separable (displaced)

Sum of two Fully Separable is *Inseparable*



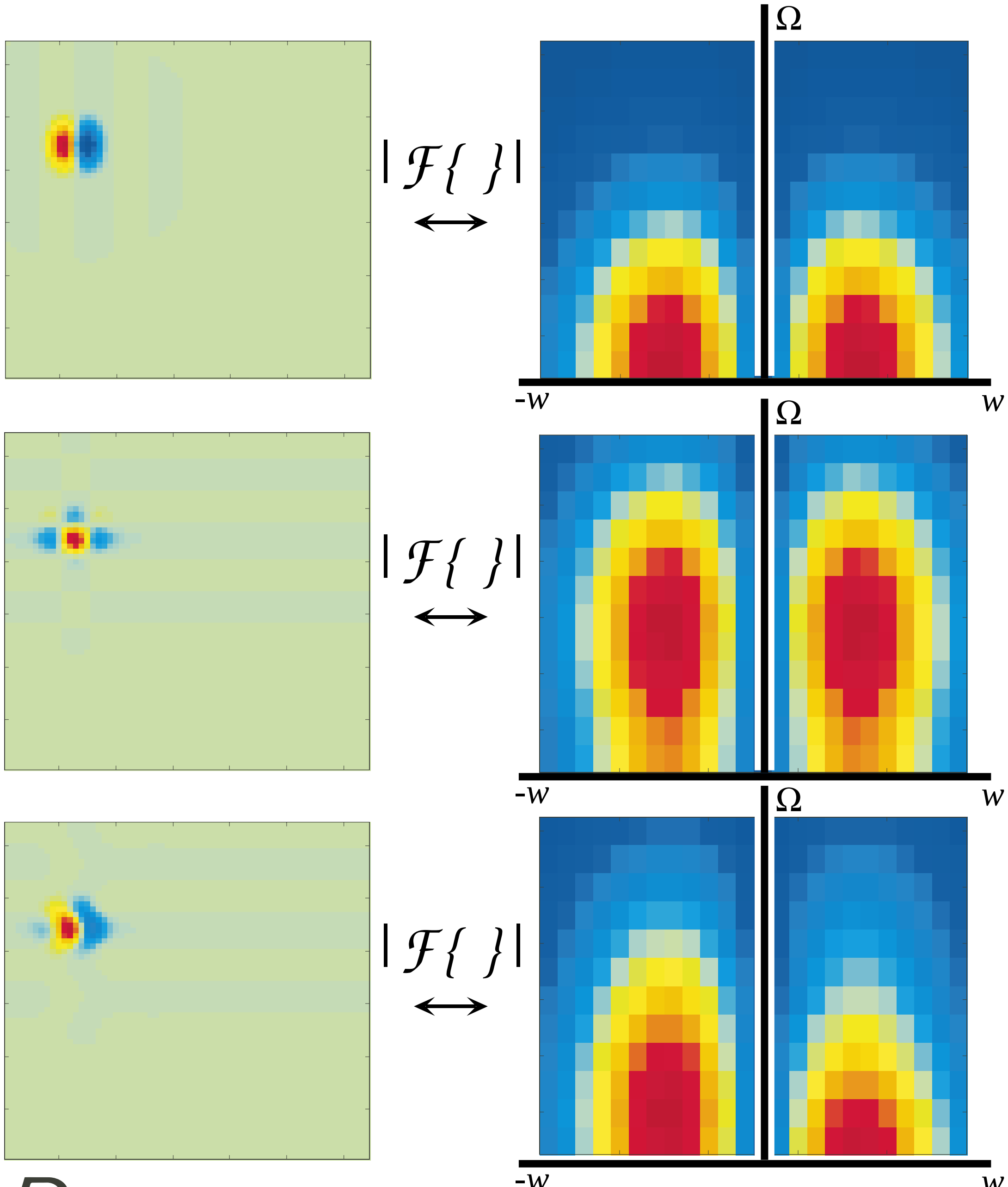
Naive sum of two fully separable STRFs is inseparable.

An Example

Fully Separable

Same Fully Separable but Lagged (& shifted spectrally)

Sum of Non-Lagged and Lagged is *Separable*



Sum of two fully separable STRFs is separable if the temporal processing is in quadrature.

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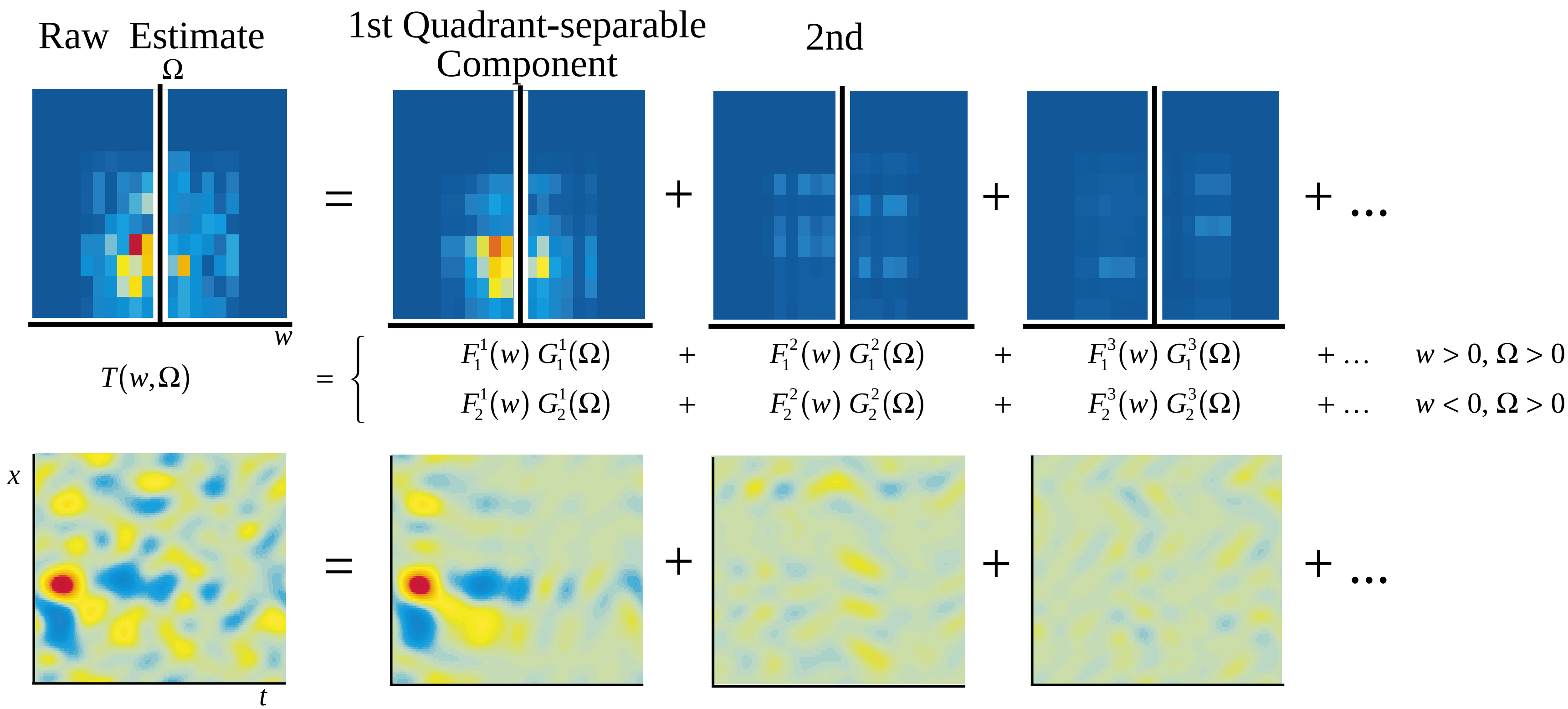
Measuring Separability with SVD

- Singular Value Decomposition (SVD) can be used to estimate the separability of a Transfer Function (possibly corrupted by noise). It decomposes the Transfer Function into a sum of Quadrant Separable Transfer Functions, ordered by their power.

- We apply SVD to each quadrant of the transfer function. Below, an STRF and the three most significant quadrant-separable components, derived from SVD:



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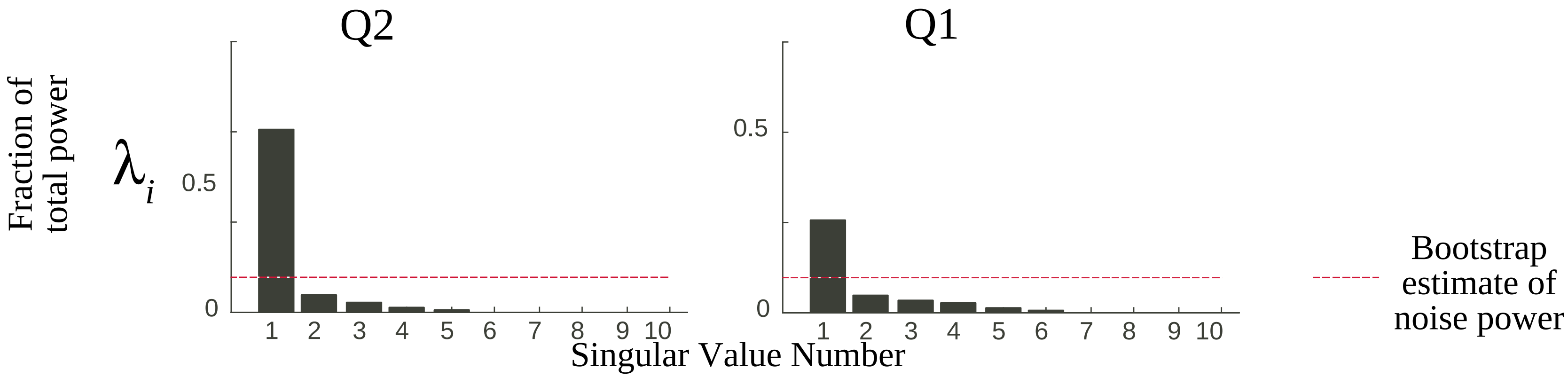
SVD Example



- SVD naturally picks out high SNR components of a matrix.
- Large jumps in the singular values separate signal from noise.
- Jumps straddle bootstrap estimate of noise.
- Noise can be removed by discarding lower-magnitude components.
- All cells (31) measured in AI have a single dominant SVD component in each quadrant.

All units measured in AI are quadrant separable (or fully separable).

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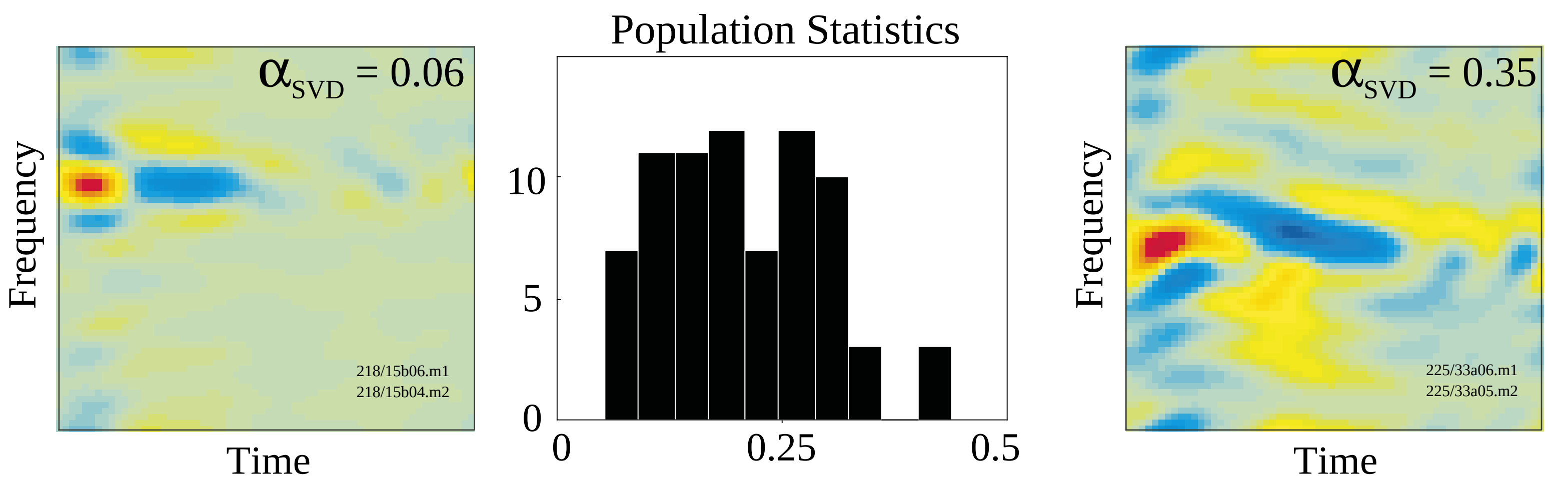
Measure of Inseparability

- SVD supplies a natural measure of inseparability, α_{SVD}

$$\alpha_{SVD} = \left(1 - \frac{\lambda_1^2}{\sum_i \lambda_i^2}\right)$$

- $\alpha_{SVD} \approx 0$ is fully separable
- $\alpha_{SVD} > 0.3$ is strongly inseparable



Symmetry by Power

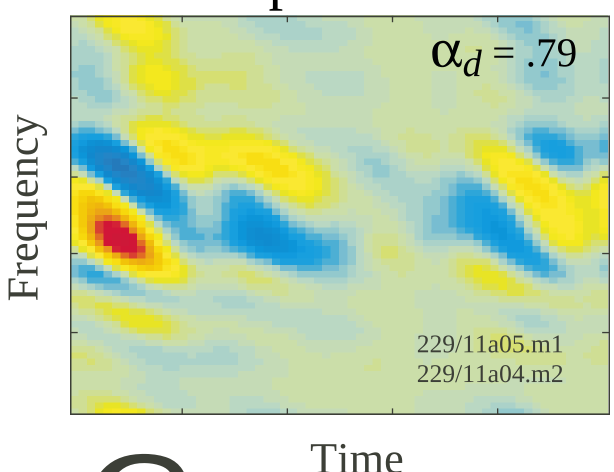
- α_d: Power asymmetry breaks full separability, producing quadrant separability

$$\alpha_d = (P_1 - P_2)/(P_1 + P_2)$$

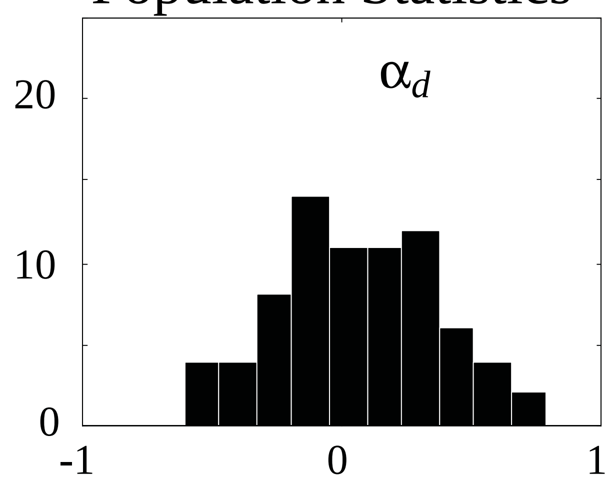
$$P_1 = (\text{Power in quadrant 1}) = (\lambda_1)^2$$
$$P_2 = (\text{Power in quadrant 2}) = (\lambda_2)^2$$

- $\alpha_d \approx 0$ is symmetric in power
- $|\alpha_d| > 0.3$ is quite asymmetric in power—strongly inseparable

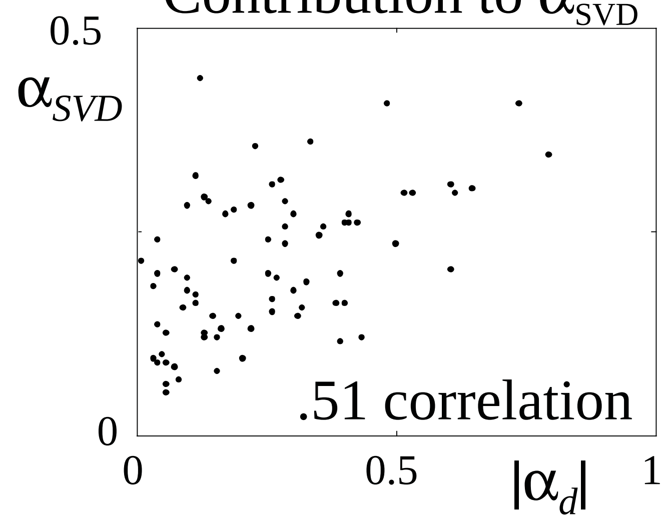
Example STRF



Population Statistics



Contribution to α_{SVD}



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Spectral Symmetry

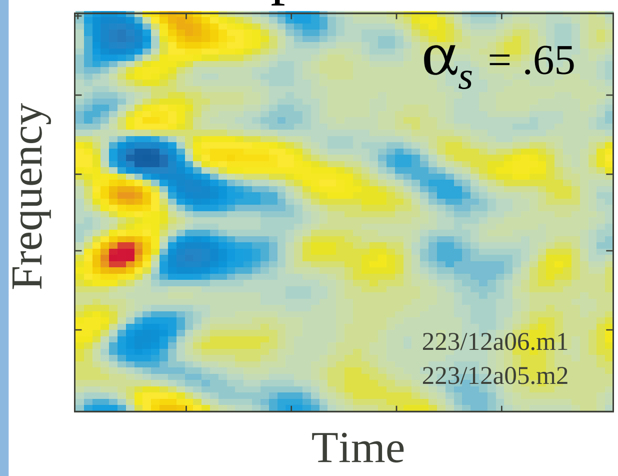
- α_s: Asymmetry between spectral cross-sections $G_i(\Omega)$:

$$\alpha_s = 1 - \left| \frac{\sum_{\Omega>0} G_1(\Omega)\, G_2^*(\Omega)}{\sqrt{\sum_{\Omega>0} |G_1(\Omega)|^2\, |G_2(\Omega)|^2}} \right|$$

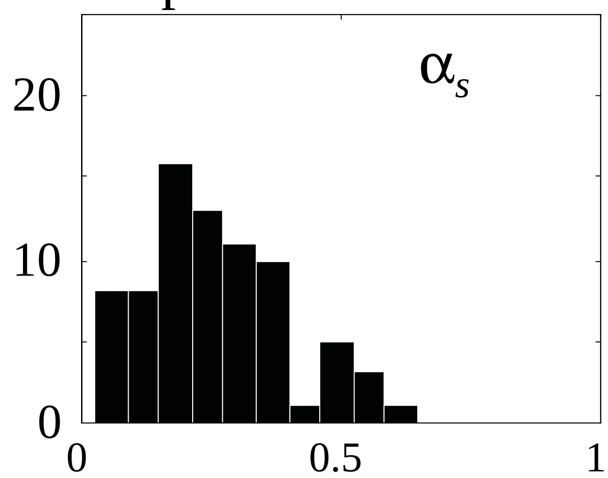
where the quantity inside the big absolute value bars is the (complex) correlation between $G_1(\Omega)$ and $G_2(\Omega)$

- $\alpha_s \approx 0$ is spectrally symmetric
- $\alpha_s > 0.3$ is spectrally asymmetric—strongly inseparable

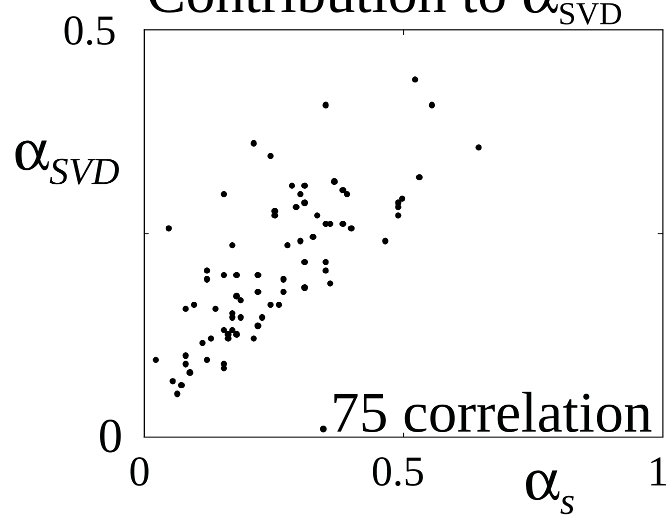
Example STRF



Population Statistics



Contribution to α_{SVD}



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Temporal Symmetry

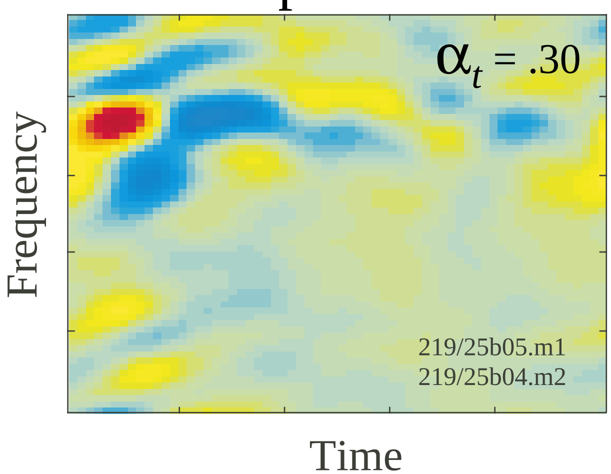
- α_t: Asymmetry between temporal cross-sections $F_i(w)$:

$$\alpha_t = 1 - \left| \frac{\sum_{w>0} F_1(w)\, F_2(-w)}{\sqrt{\sum_{w>0} \left|F_1(w)\right|^2 \left|F_2(-w)\right|^2}} \right|$$

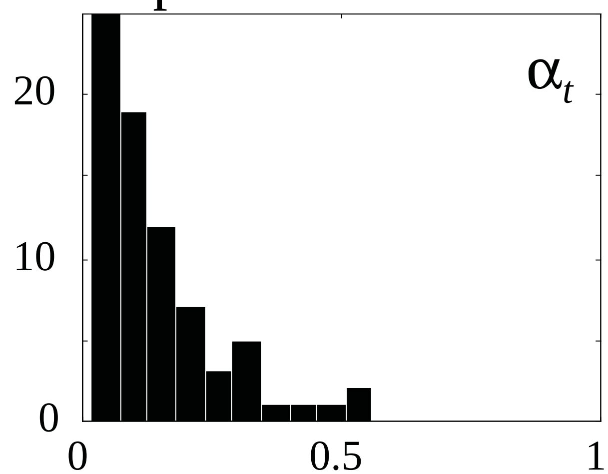
where the quantity inside the big absolute value bars is the (complex) correlation between $F_1(w)$ and $F_2^*(-w)$

- $\alpha_t \approx 0$ is temporally symmetric
- $\alpha_t > 0.3$ is temporally asymmetric—strongly inseparable

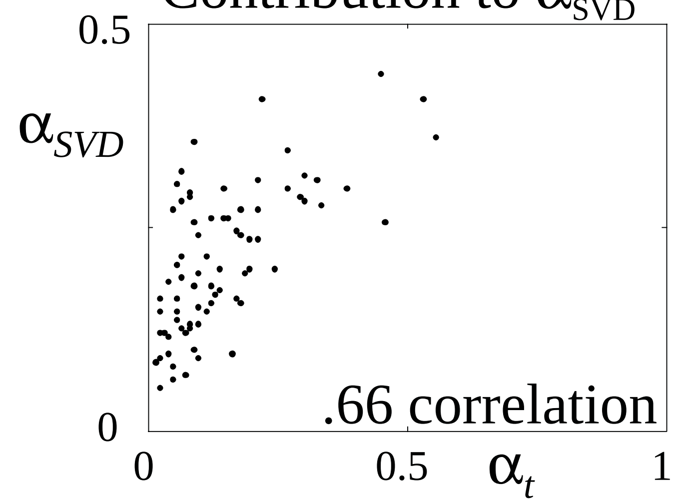
Example STRF



Population Statistics



Contribution to α_{SVD}



Distribution is strongly skewed toward temporal symmetry.

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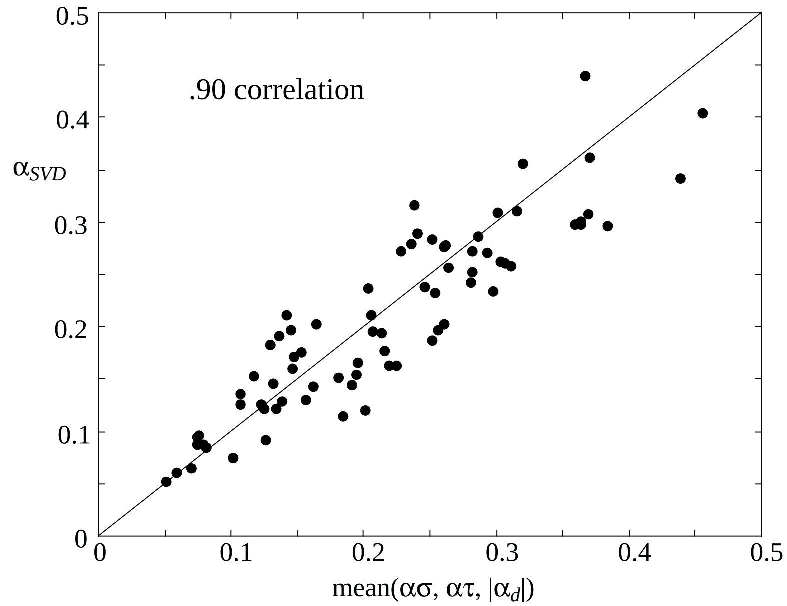
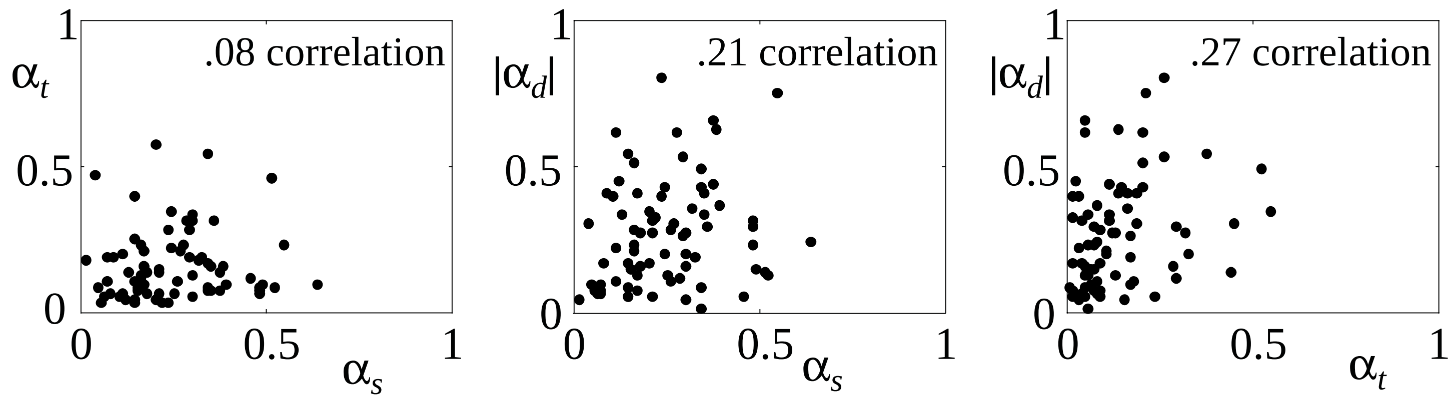
Symmetry Correlations

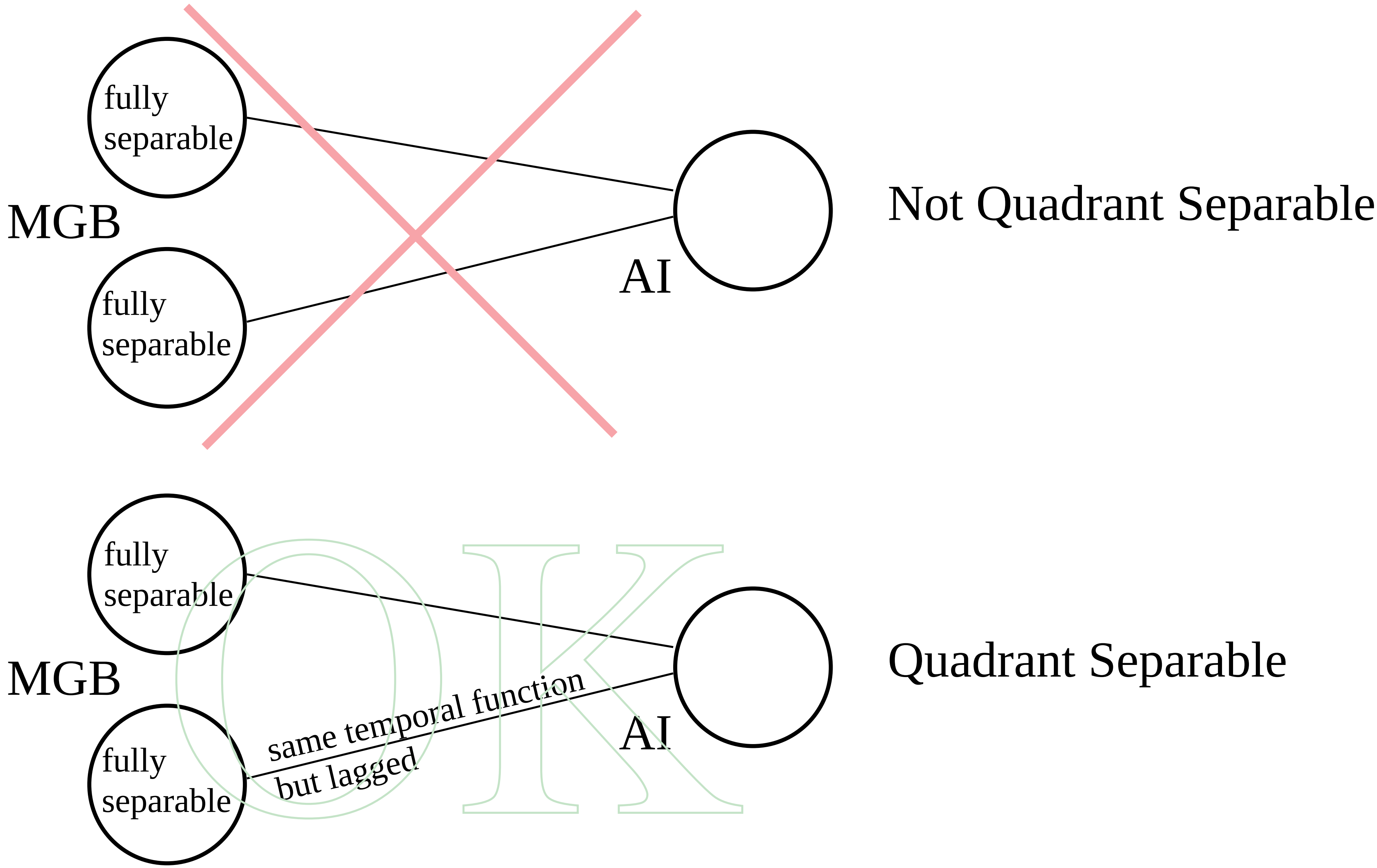
- Mean of 3 separate symmetry measures correlates well with full separability index.



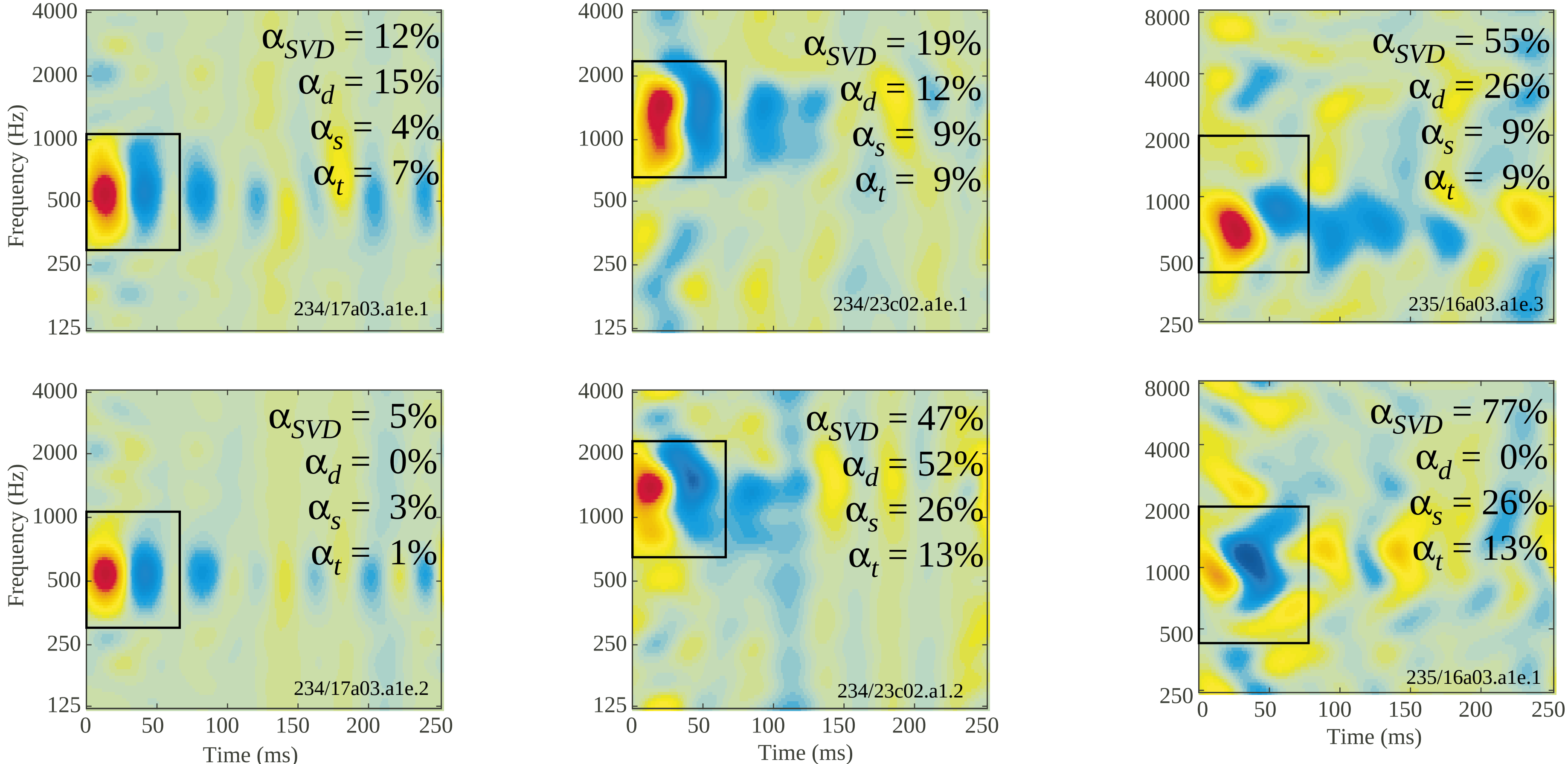
- Individual indices only partially correlated with each other.



Models


fully separable
fully separable
MGB
AI
Not Quadrant Separable
fully separable
fully separable
MGB
same temporal function but lagged
AI
OK
Quadrant Separable

Example STRF Recording Pairs



Very similar,
Both fully separable

ε = (20%, 15%) $\quad \alpha_s^{corr} = \begin{bmatrix} 4\% & 6\% \\ 3\% & 4\% \end{bmatrix}$

$\alpha_t^{corr} = \begin{bmatrix} 2\% & 7\% \\ 4\% & 5\% \end{bmatrix}$

Different,
Upper fully separable,
Lower quadrant separable

ε = (40%, 25%) $\quad \alpha_s^{corr} = \begin{bmatrix} 6\% & 10\% \\ 23\% & 12\% \end{bmatrix}$

$\alpha_t^{corr} = \begin{bmatrix} 6\% & 5\% \\ 20\% & 7\% \end{bmatrix}$

Very different,
Both quadrant separable
(somewhat noisy though)

ε = (60%, 60%) $\quad \alpha_s^{corr} = \begin{bmatrix} 32\% & 55\% \\ 40\% & 25\% \end{bmatrix}$

$\alpha_t^{corr} = \begin{bmatrix} 21\% & 32\% \\ 27\% & 59\% \end{bmatrix}$

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Selected References

Spectro-Temporal Correlation Methods

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