

Empirical estimates of STRFs are influenced by higher-order stimulus statistics

Jörn Anemüller

+Arne Meyer, +Jörg-Hendrik Bach
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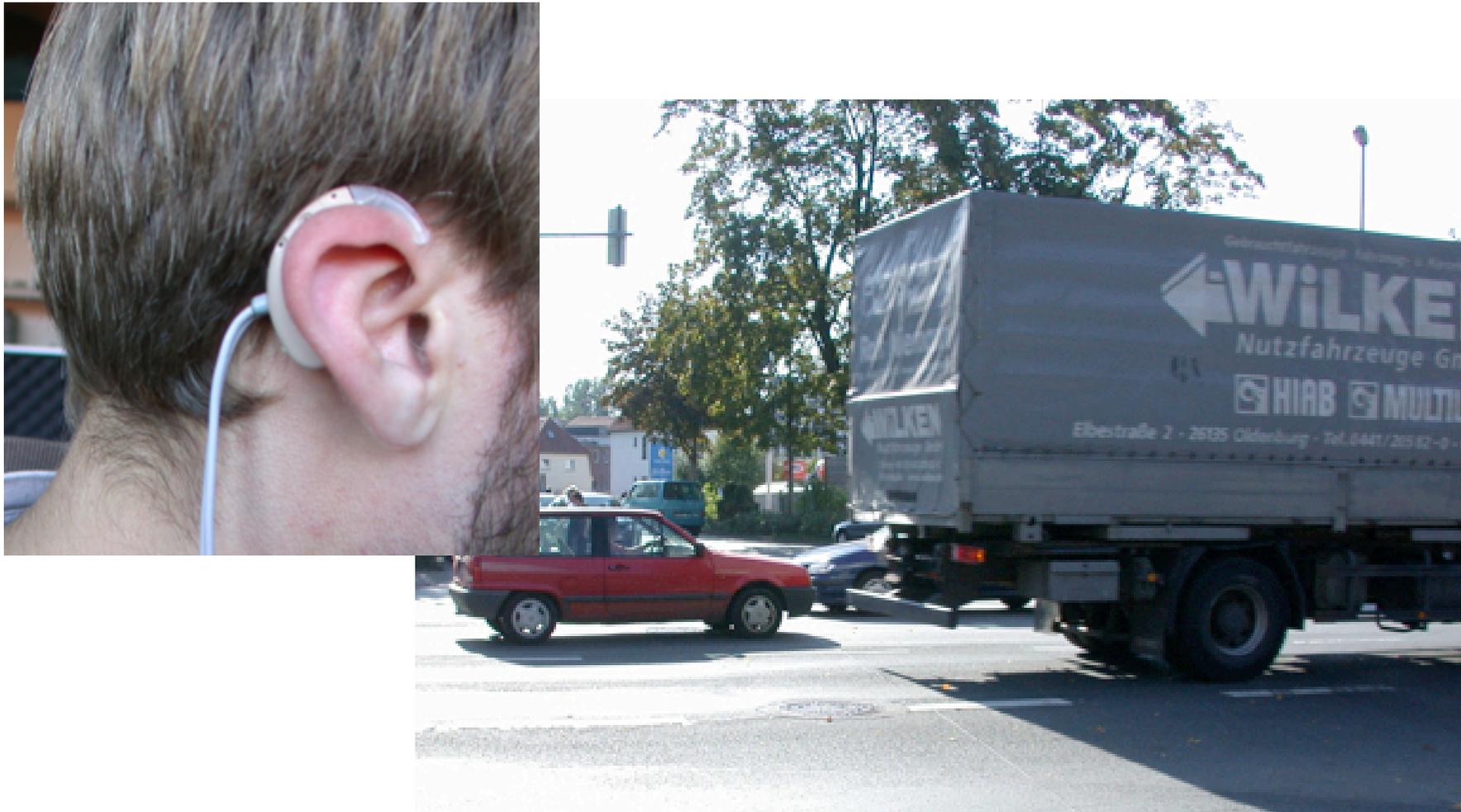
Computational Audition Group
Medical Physics Section and Cluster of Excellence Hearing4all
Carl von Ossietzky University
Oldenburg, Germany

Listening in Acoustic Scenes

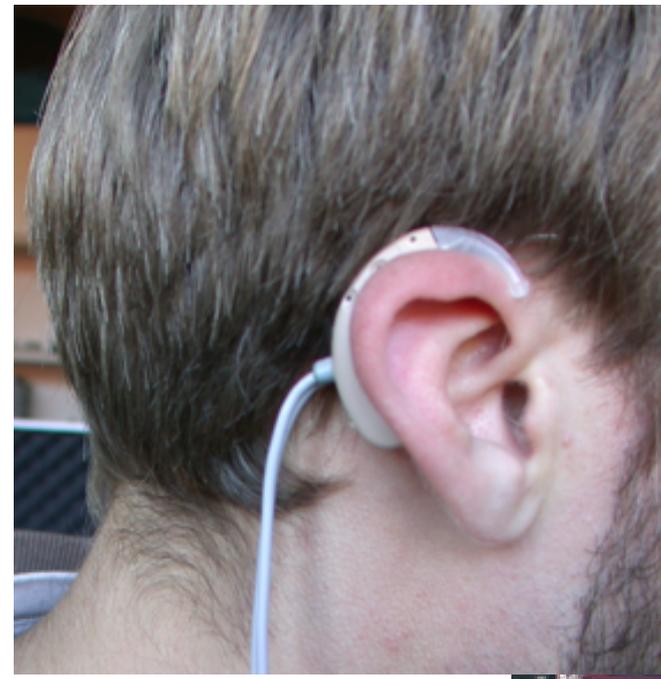
Listening in Acoustic Scenes



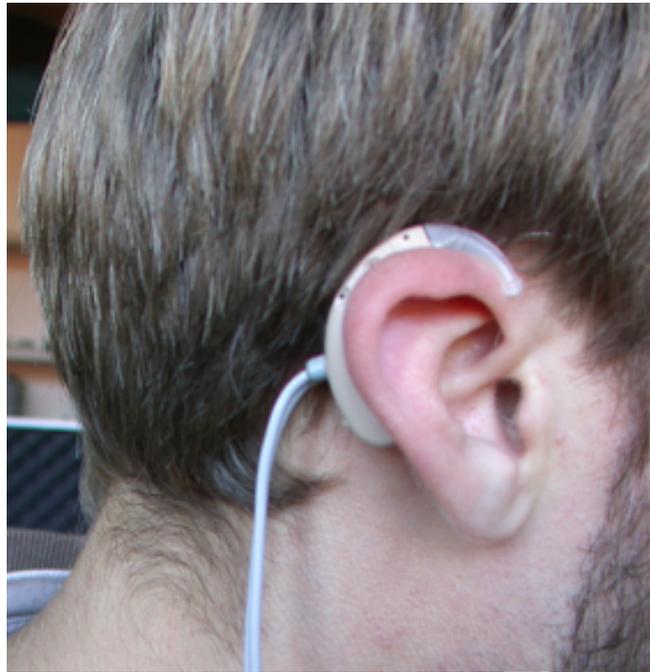
Listening in Acoustic Scenes

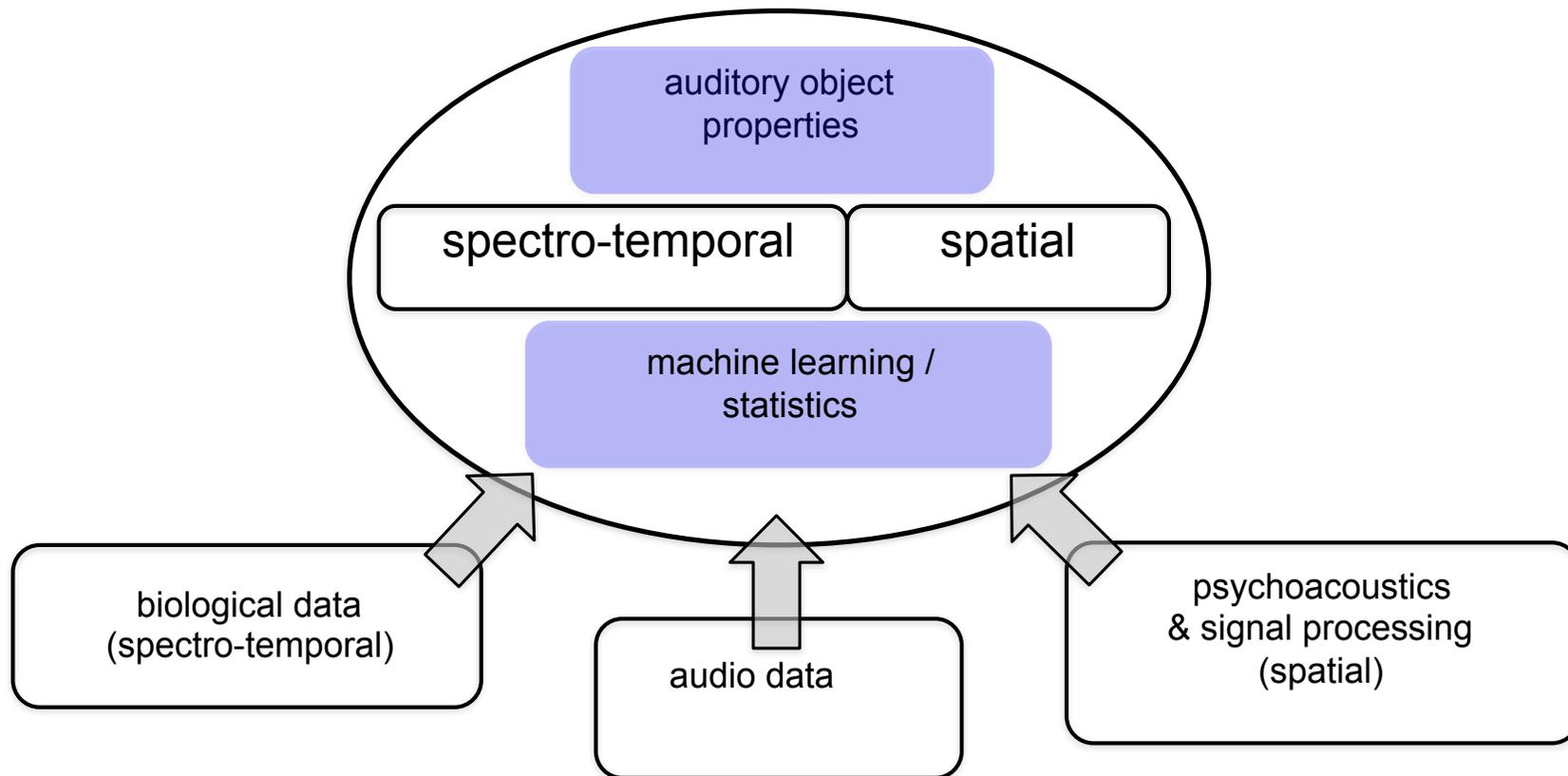


Listening in Acoustic Scene



Listening in Acoustic





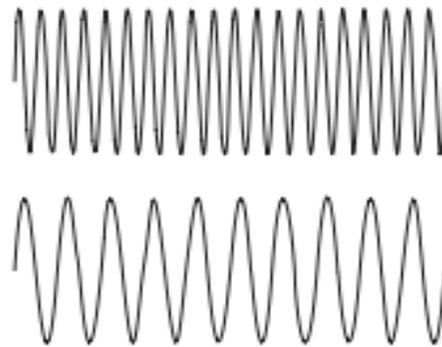
Historical approaches to neuron characterization

a Classical analytical approach

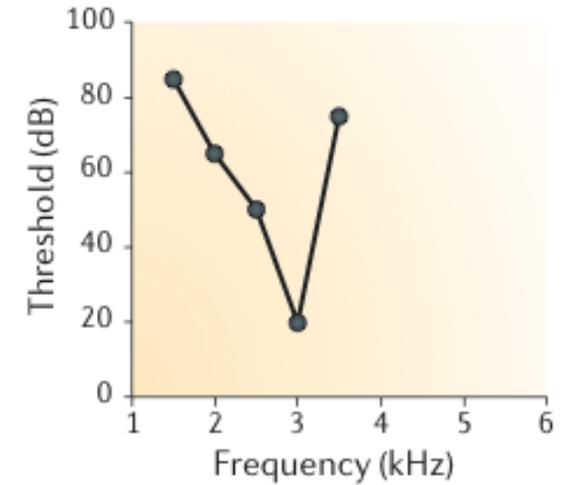
Tuning fork



Pure tones



Frequency tuning curve



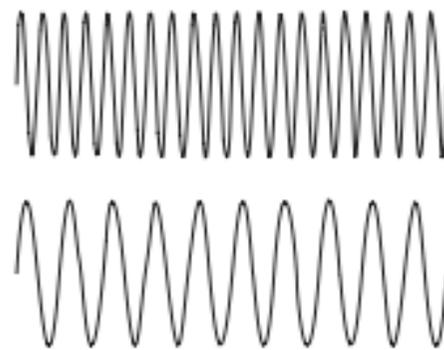
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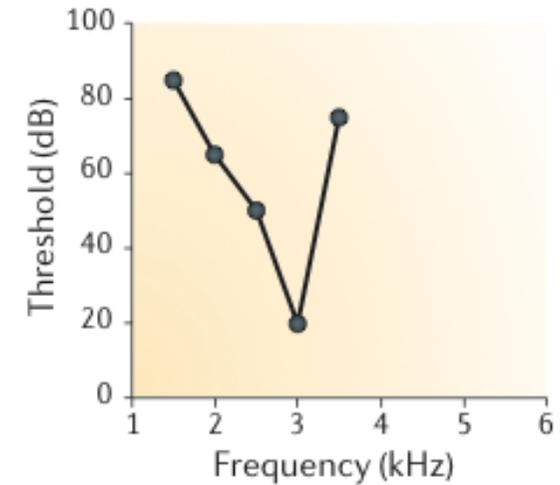
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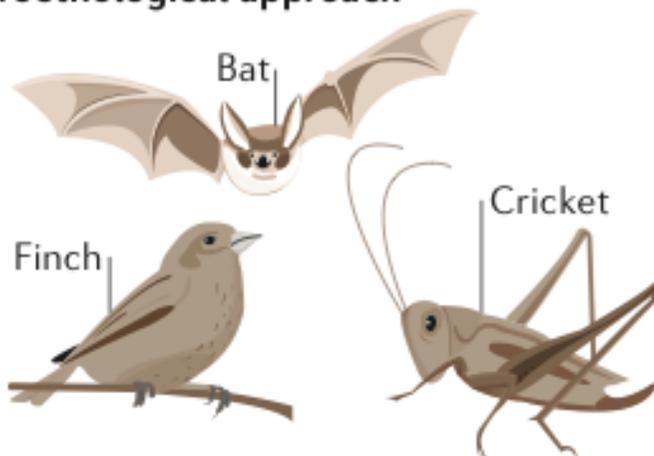
Pure tones



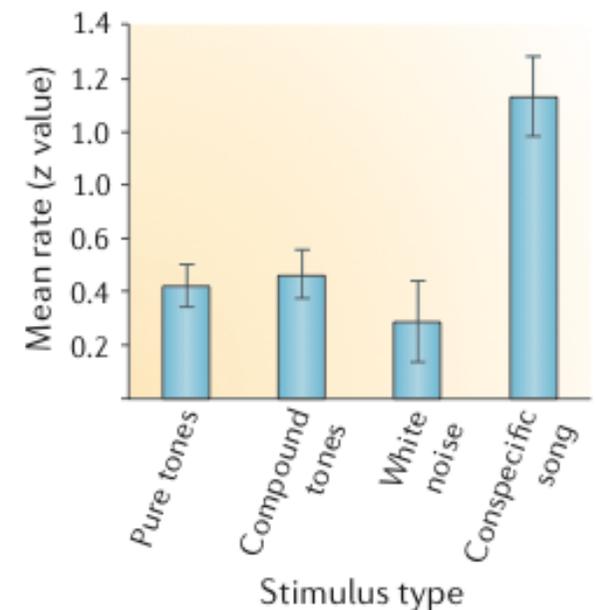
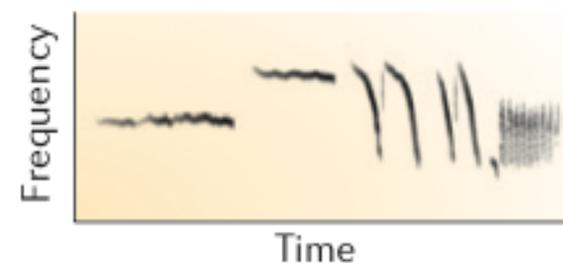
Frequency tuning curve



b Neuroethological approach



Vocalization



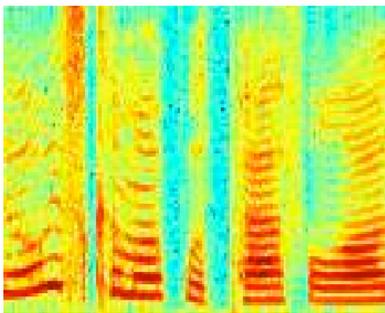
(Theunissen and Elie, 2014)

Hubel and Wiesel's visual receptive fields

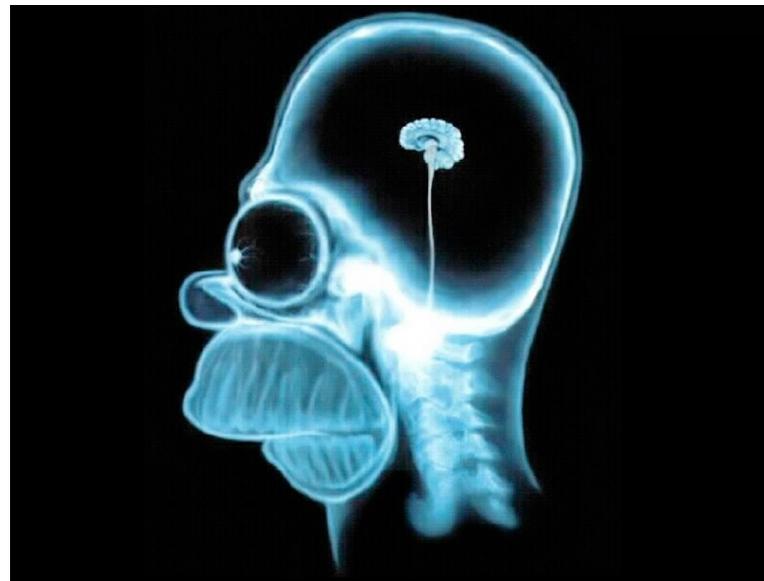
Hubel and Wiesel's visual receptive fields

Statistical approach of neural characterization

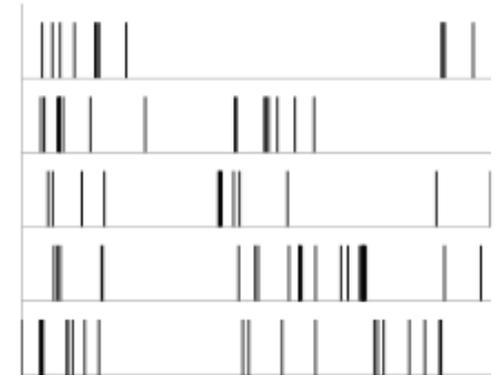
Sensory stimulus \mathbf{s}



$$p(\mathbf{r}|\mathbf{s}) = ?$$



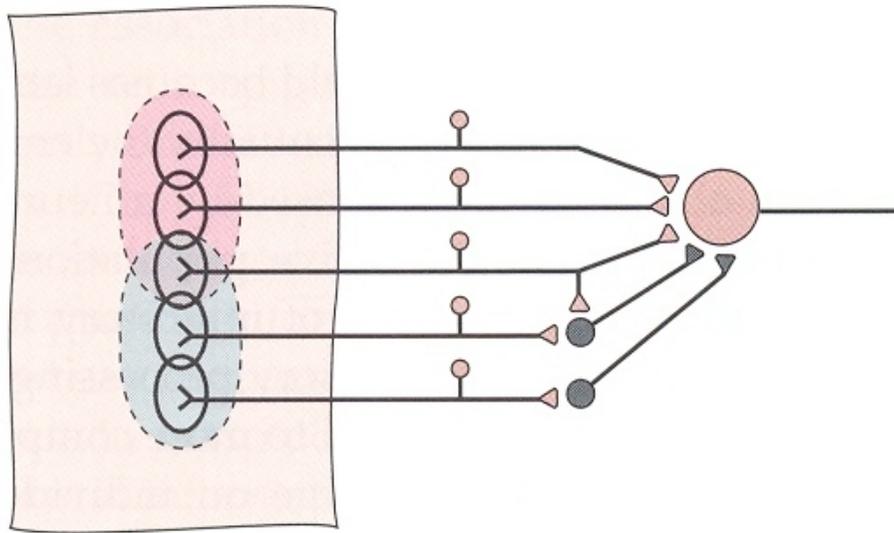
Response \mathbf{r}



- Goal: infer response properties from stimulus and evoked response

Simple cell linear receptive field model

Lateral inhibition

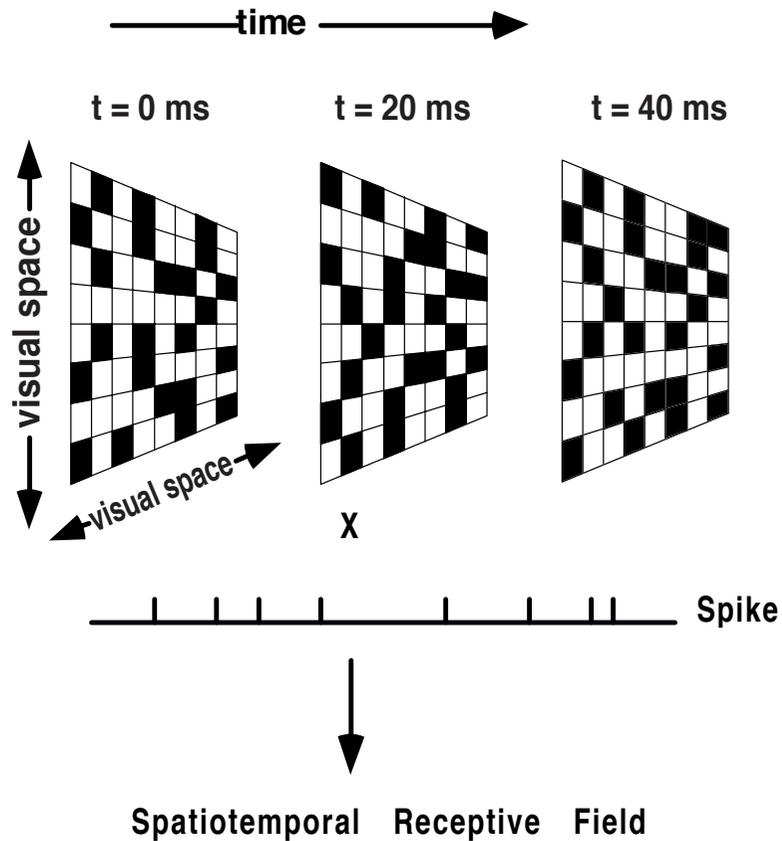


$$y = g \left(\sum_{j=1}^d w_j x_j + w_0 \right)$$

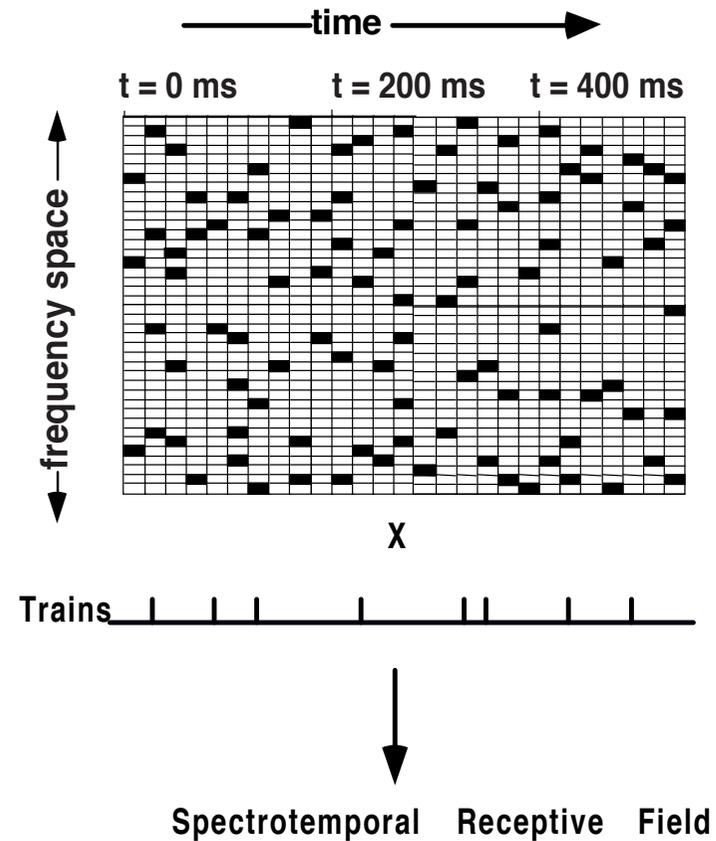
(Kandel et al., 2000)

Stimuli: White noise

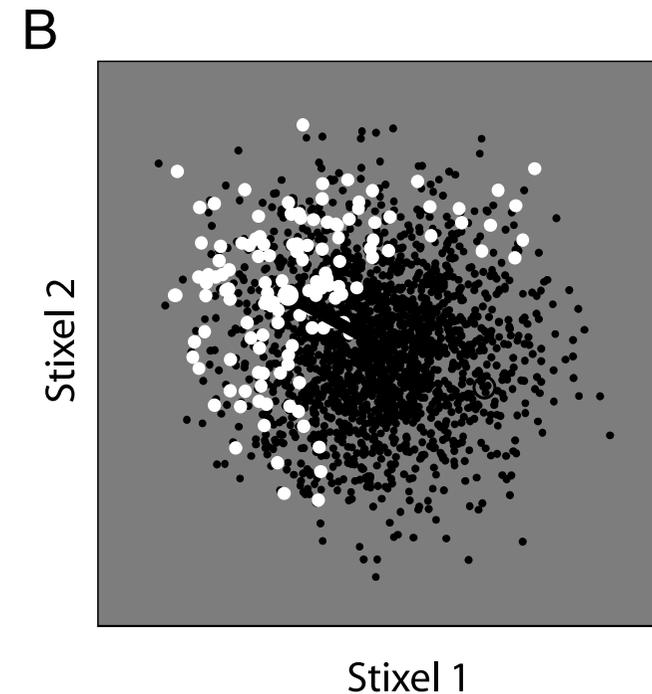
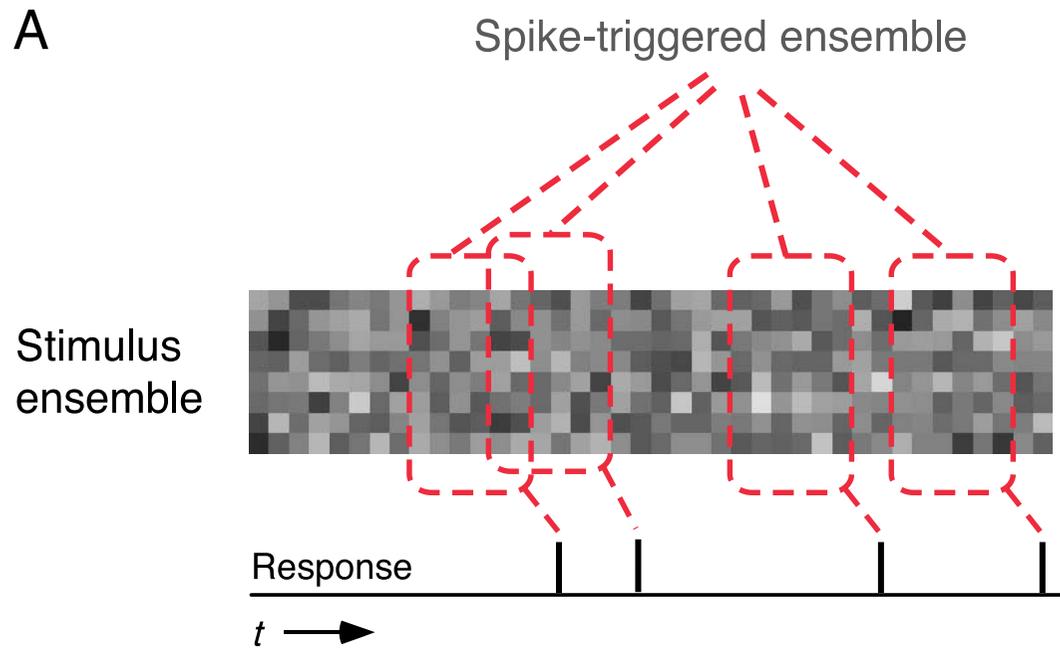
A Visual Cortex: Reverse Correlation Using 2D Visual Patterns in Time



B Auditory Cortex: Reverse Correlation Using 1D Auditory Patterns (Chords) in Time

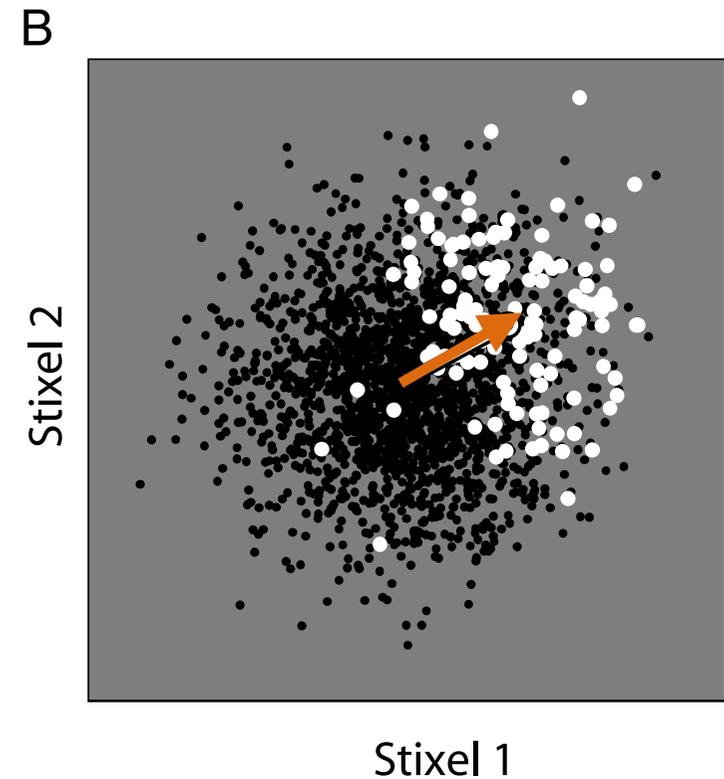
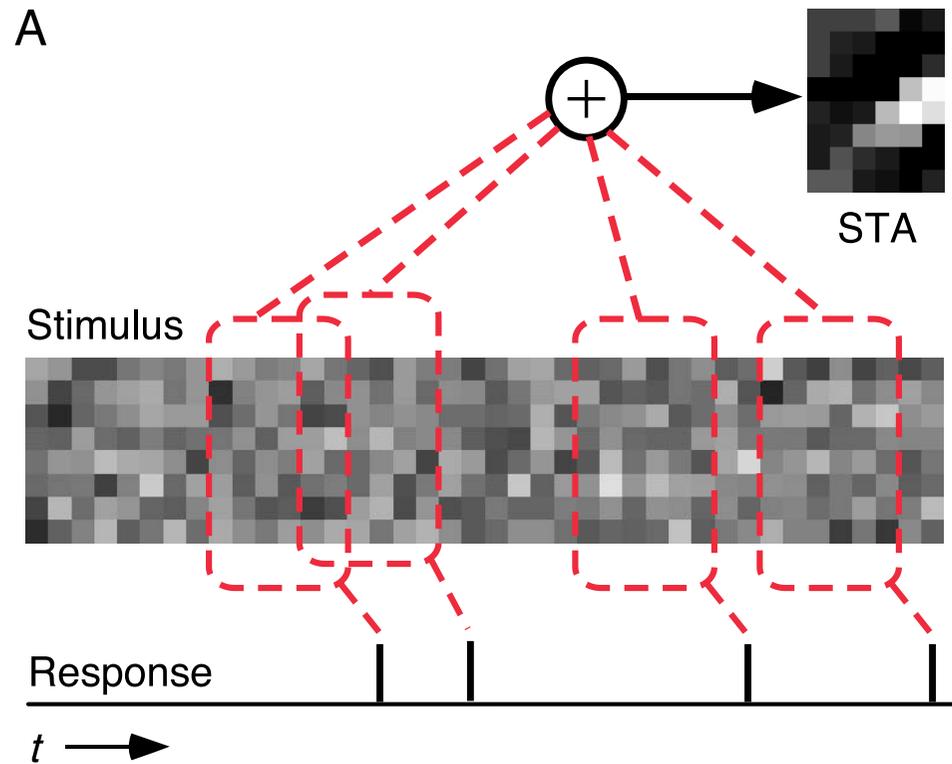


Stimulus = Point in feature space



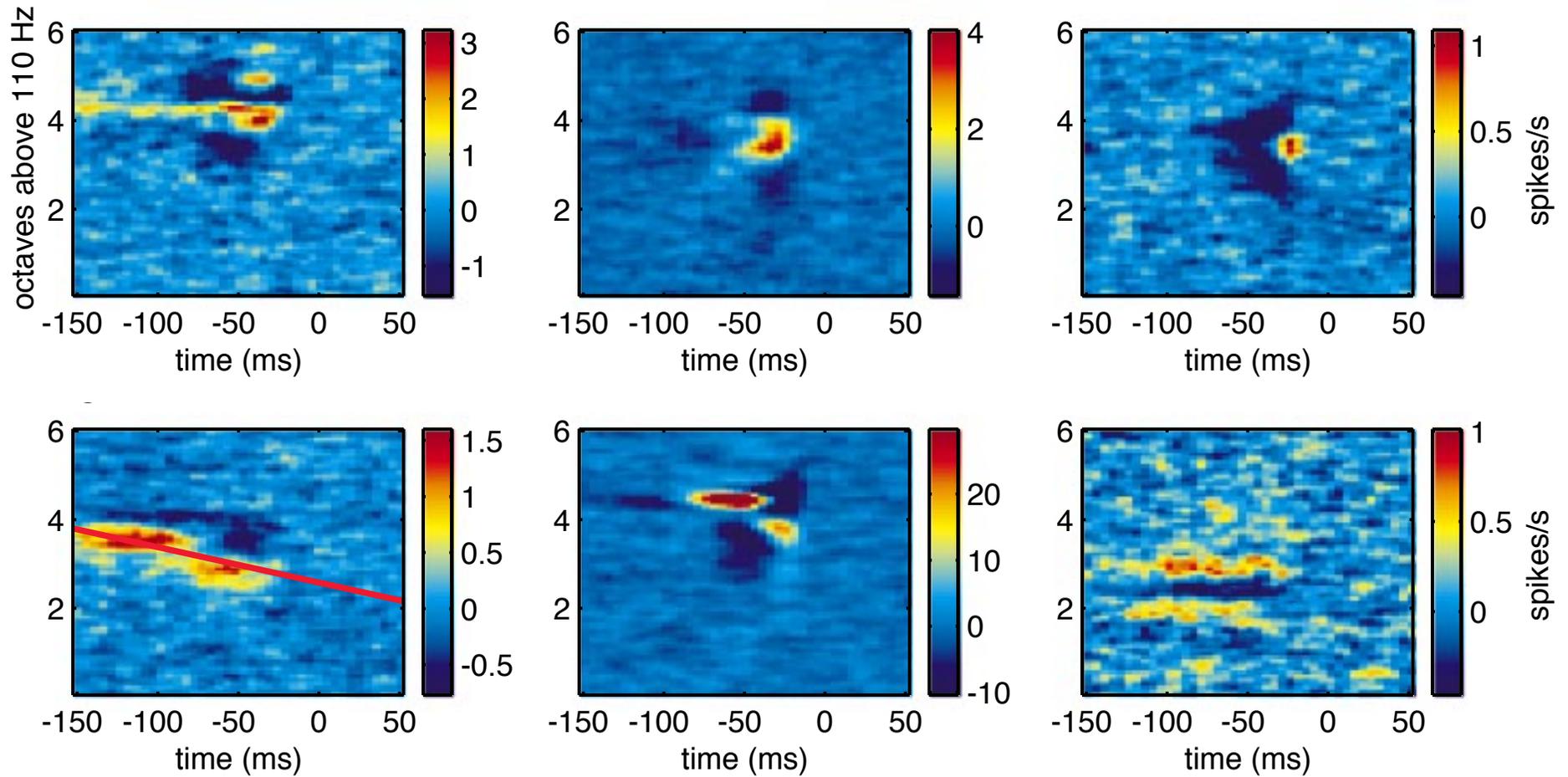
Eggermont, Johannesma, Aertsen (1983)
Schwartz, Pillow, Rust, Simoncelli (2006)

Spike triggered average (STA)

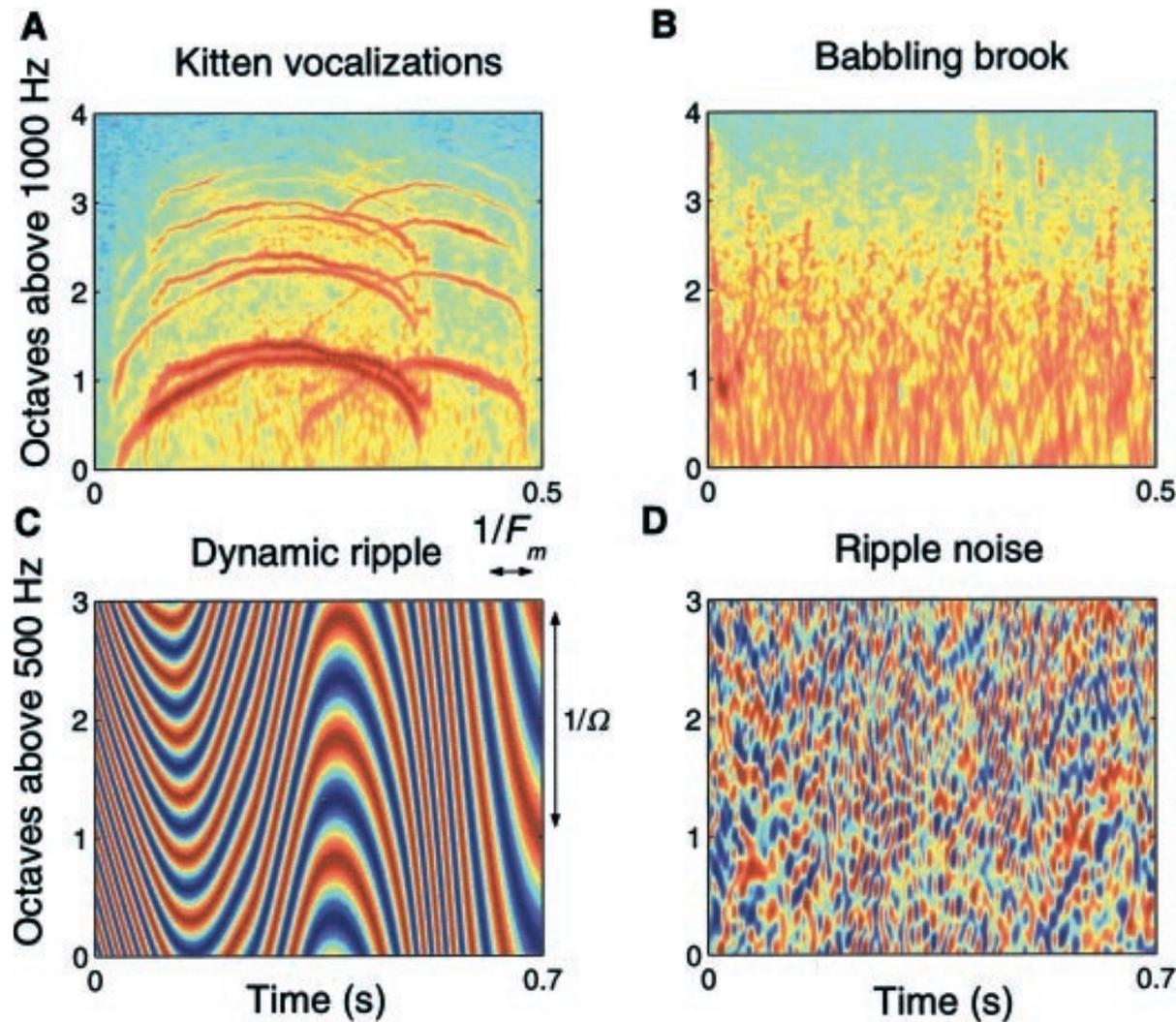


Eggermont, Johannesma, Aertsen (1983)
Schwartz, Pillow, Rust, Simoncelli (2006)

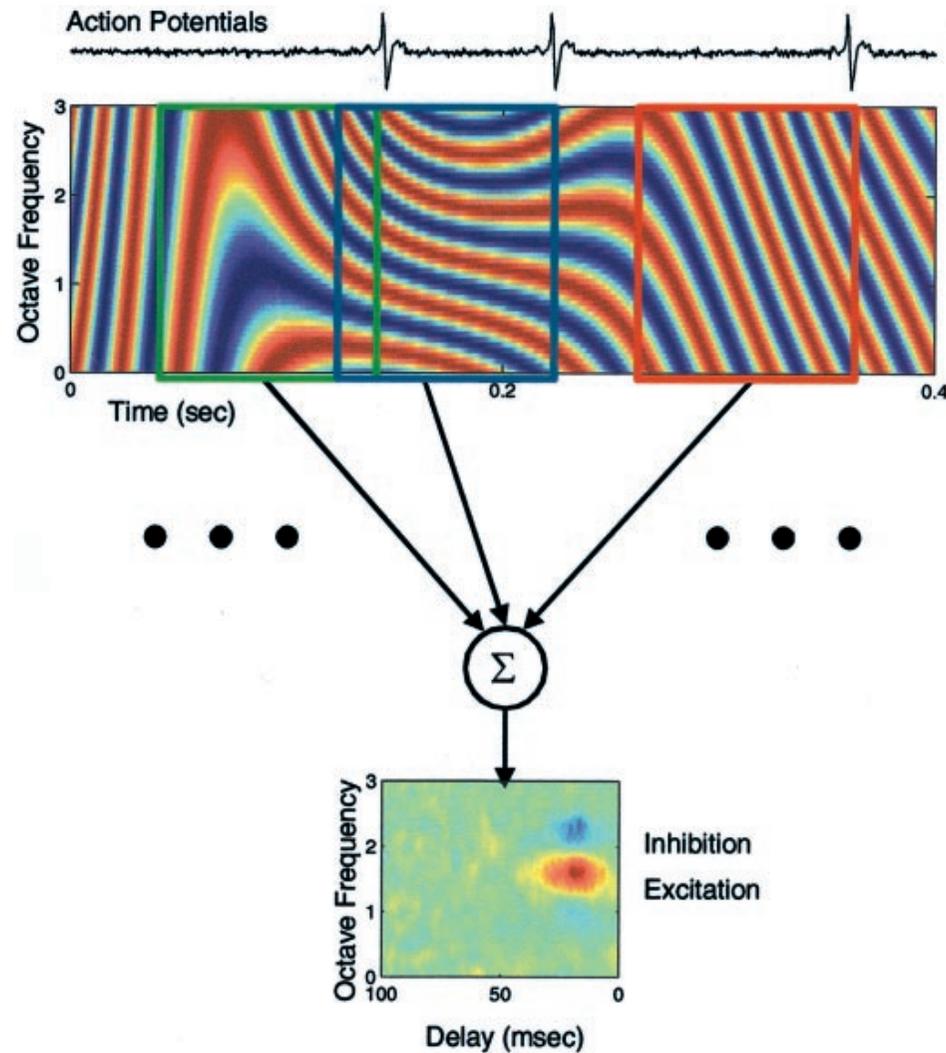
Response characteristics in A1



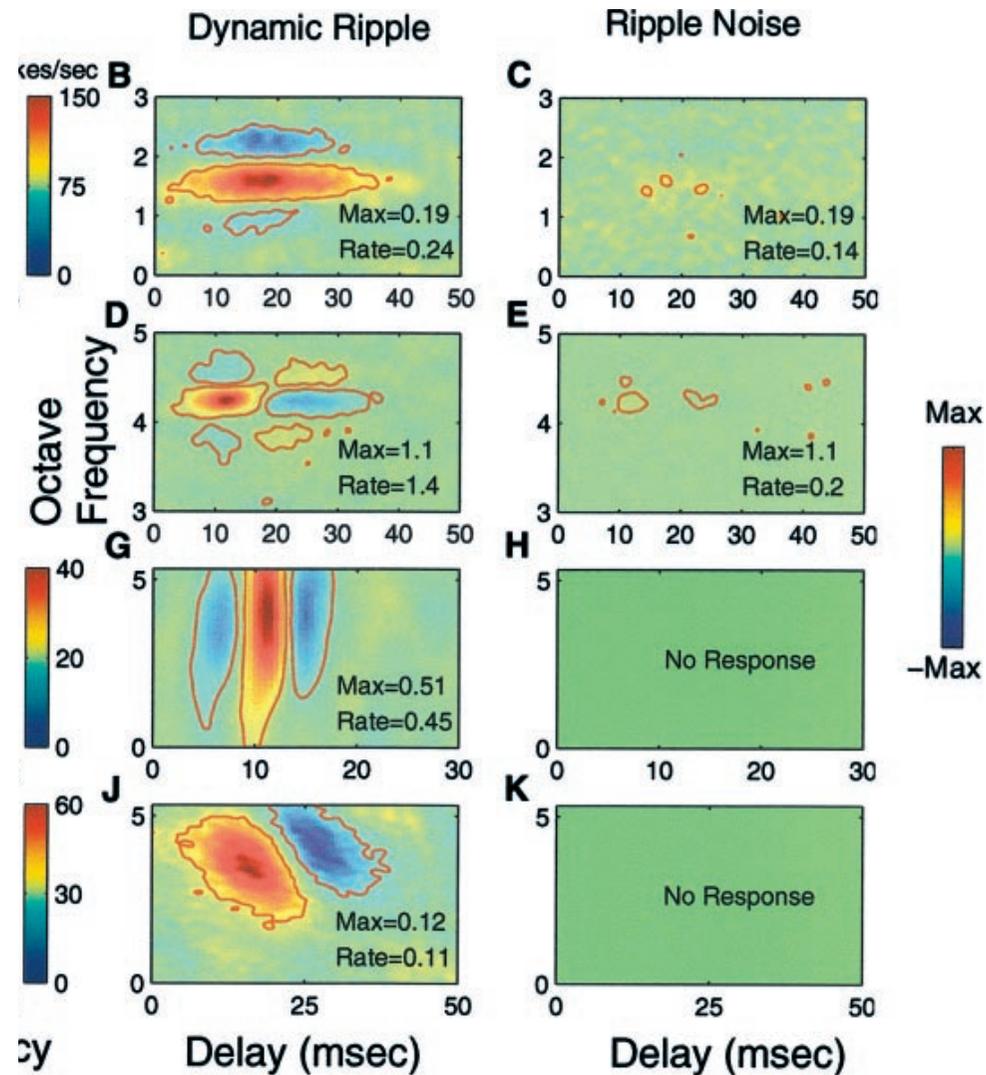
Stimuli: Dynamic moving ripples (DMR) and ripple noise



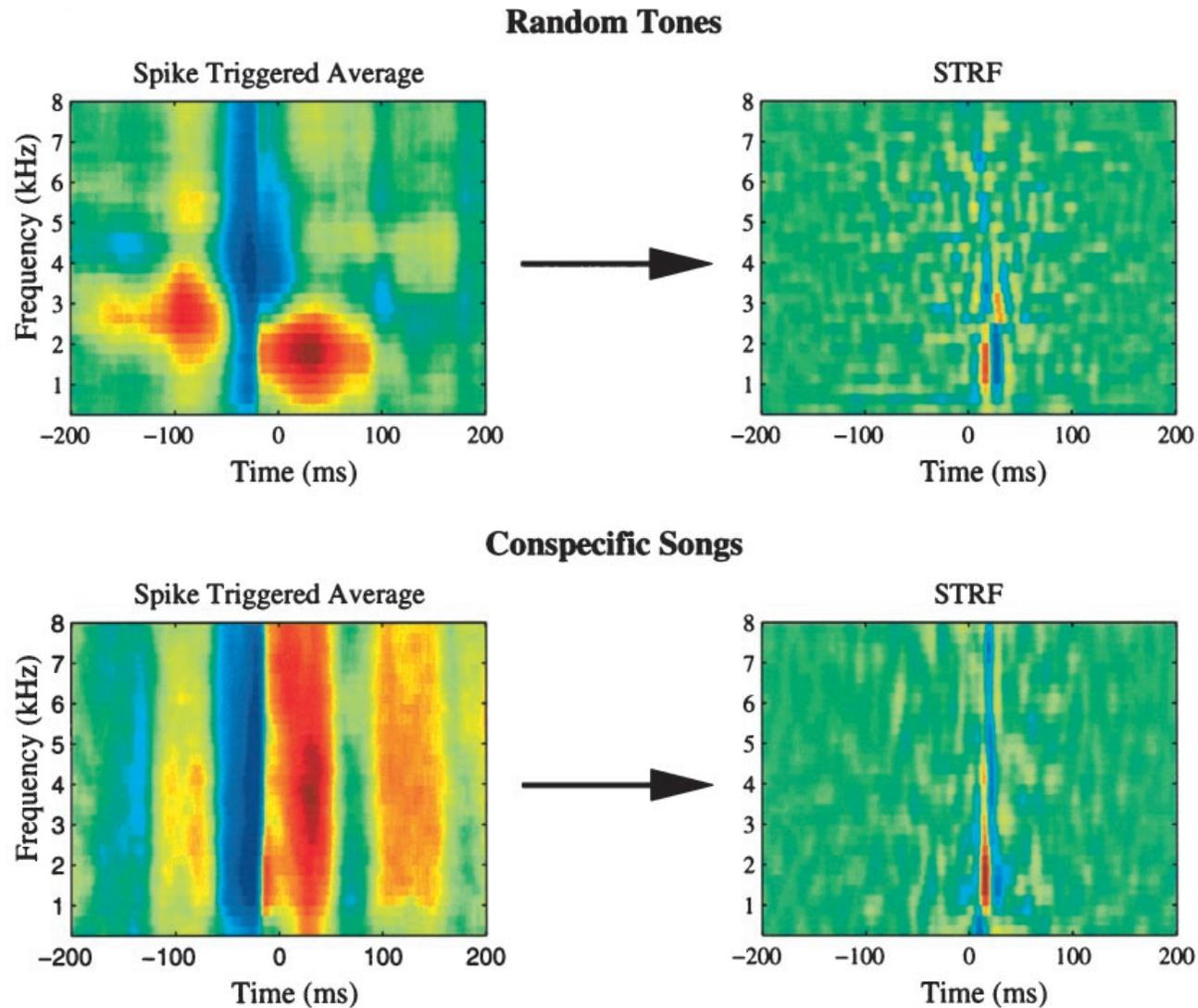
STRF estimation with STA



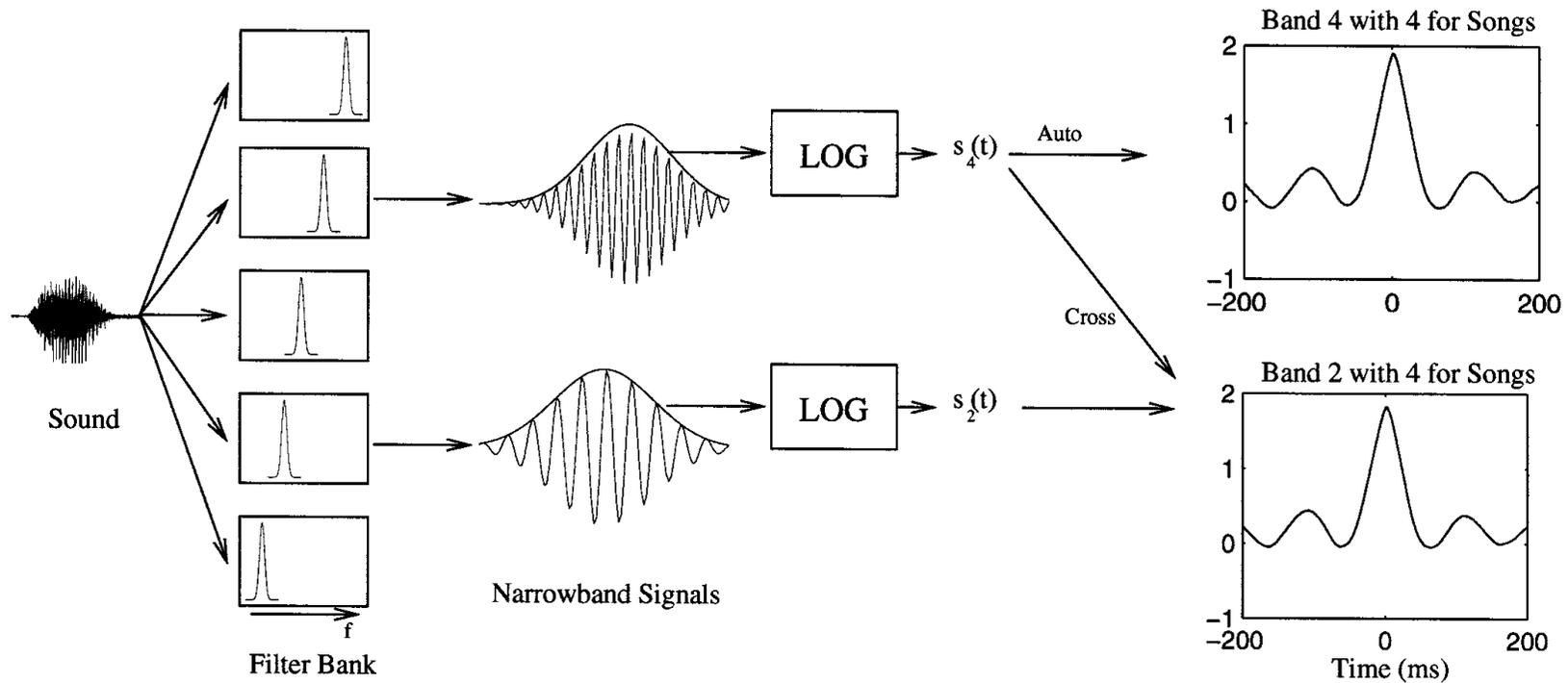
Response characteristics in IC



STRF for natural stimuli



STA not optimal for correlated stimuli



Correcting for stimulus correlations

- Normalized reverse correlation (NRC)

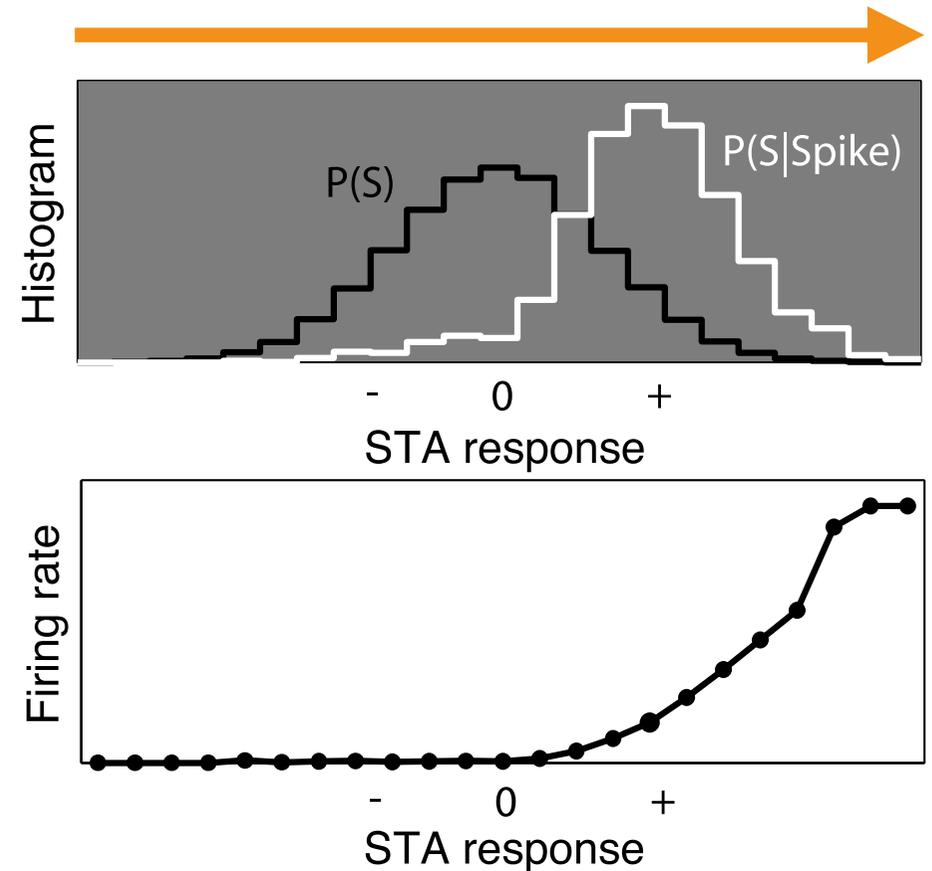
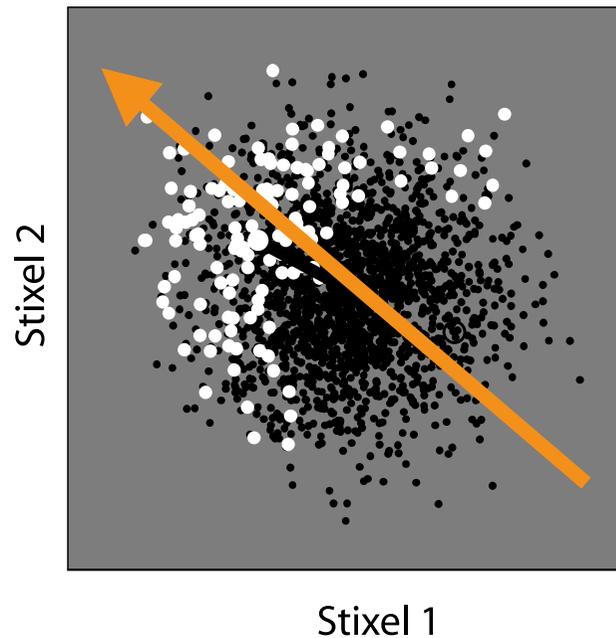
$$r = Sh + e$$

$$h_{\text{ideal}} = \frac{1}{T} C_{ss}^{-1} S^T r \quad C_{ss} = S^T S / T$$

- Ridge Regression
Regularize C_{ss} with additive diagonal term
(Often done on spike rate)

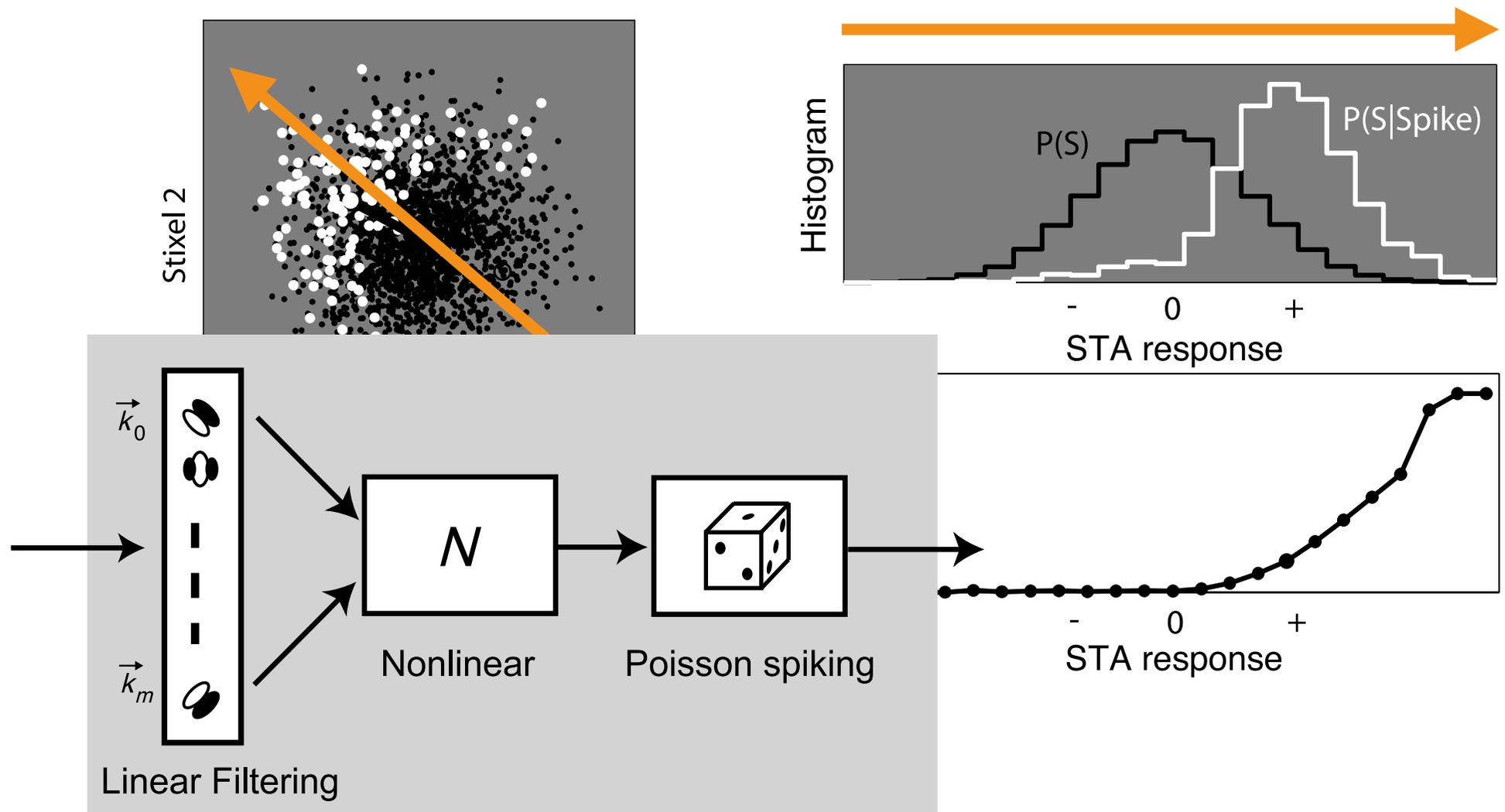
Machens, Wehr, Zador (2004); David, Mesgarani,
Shamma (2007); Park, Pillow (2011)

Linear-nonlinear Poission (LNP) model



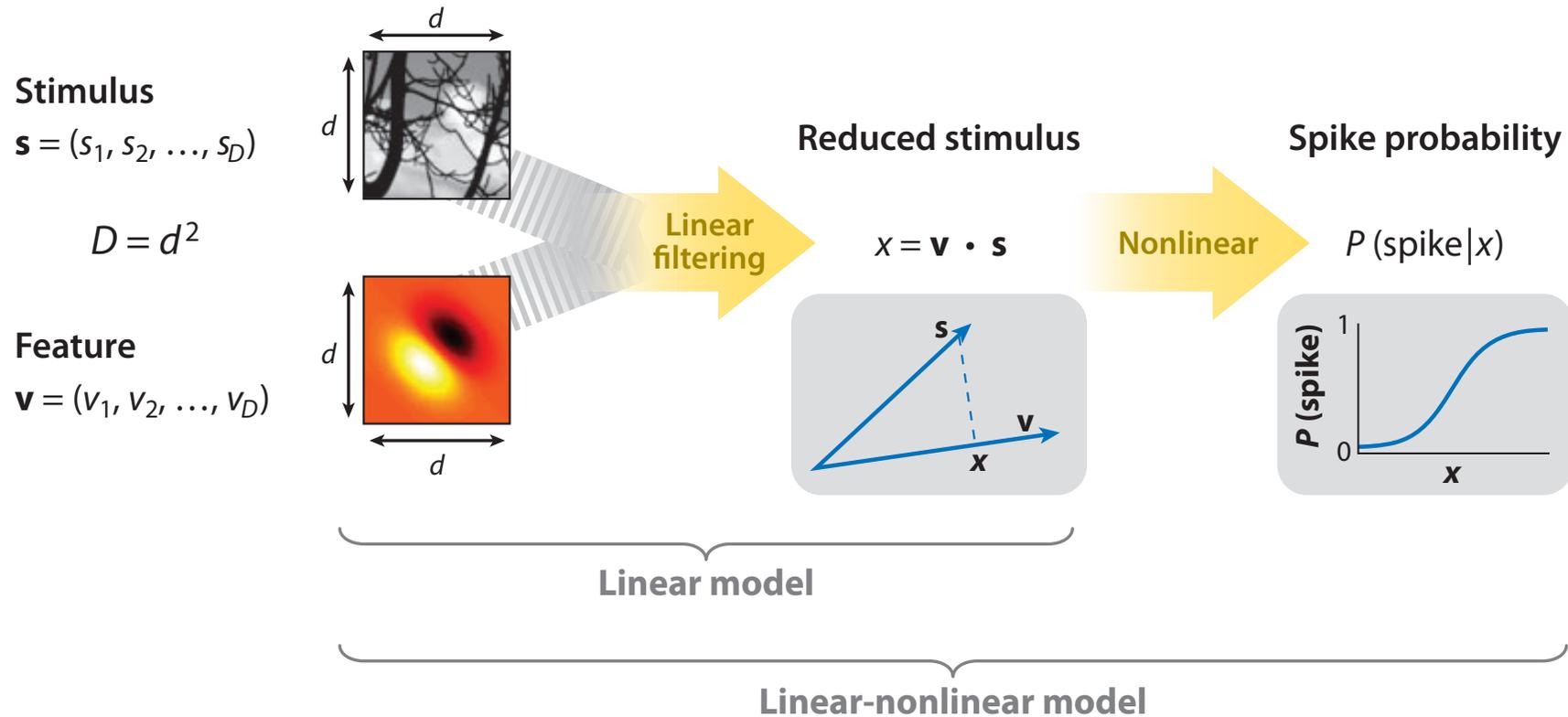
Chichilniski, 2001; Schwartz, Pillow, Rust, Simoncelli (2006)

Linear-nonlinear Poission (LNP) model



Chichilniski, 2001; Schwartz, Pillow, Rust, Simoncelli (2006)

LNP estimation: generalized linear models (GLM) and maximally informative dimensions (MID)

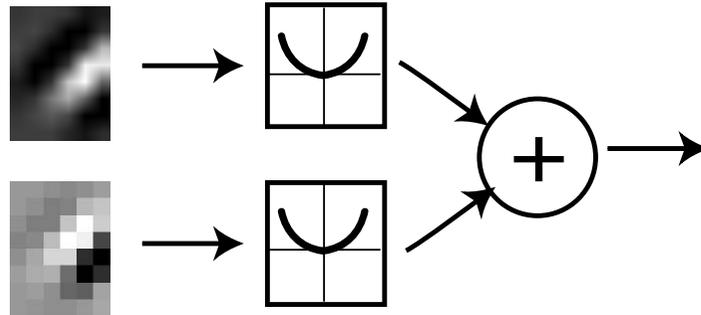


GLM: maximize likelihood based on prior distribution

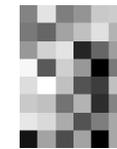
MID: search for directions that preserve stimulus information

Subspace approach: Spike-triggered covariance (STC)

Model neuron:



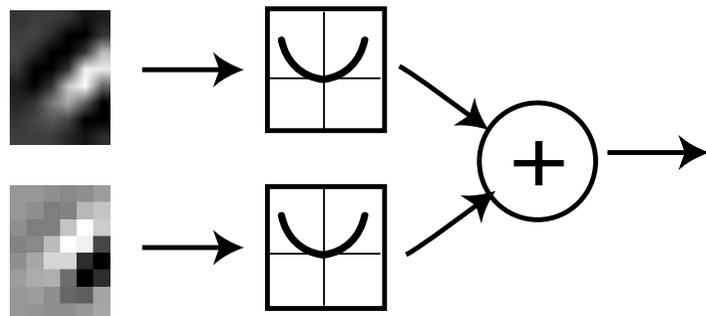
STA analysis:



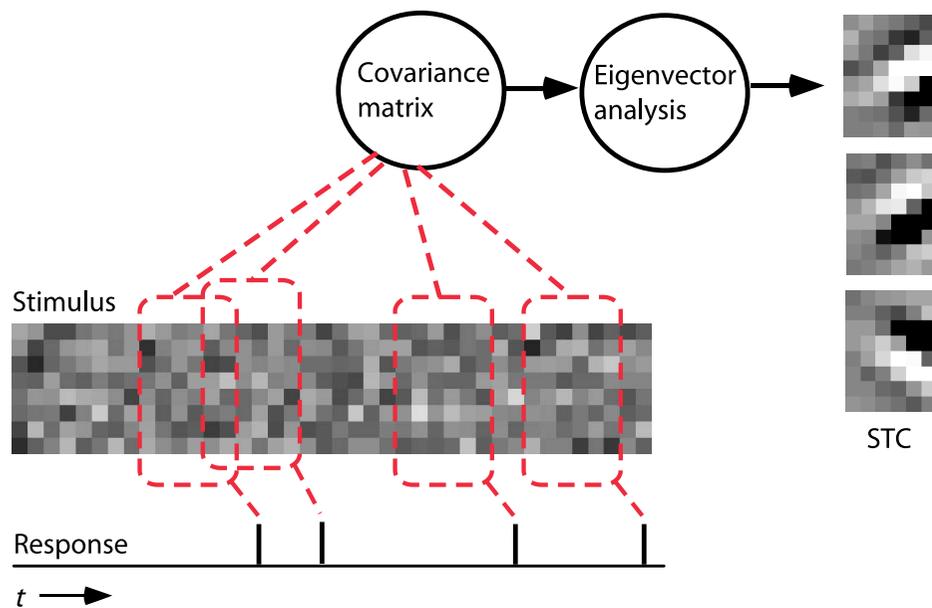
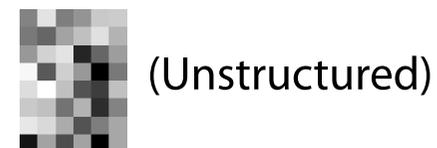
(Unstructured)

Subspace approach: Spike-triggered covariance (STC)

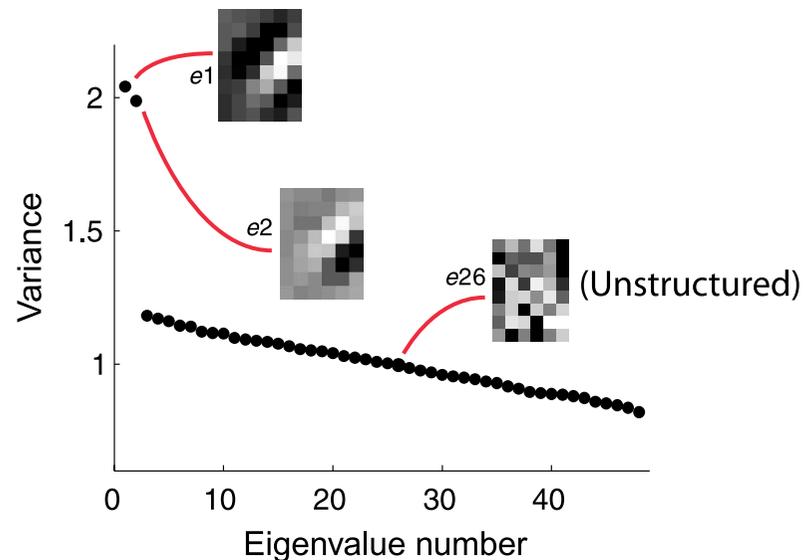
Model neuron:



STA analysis:



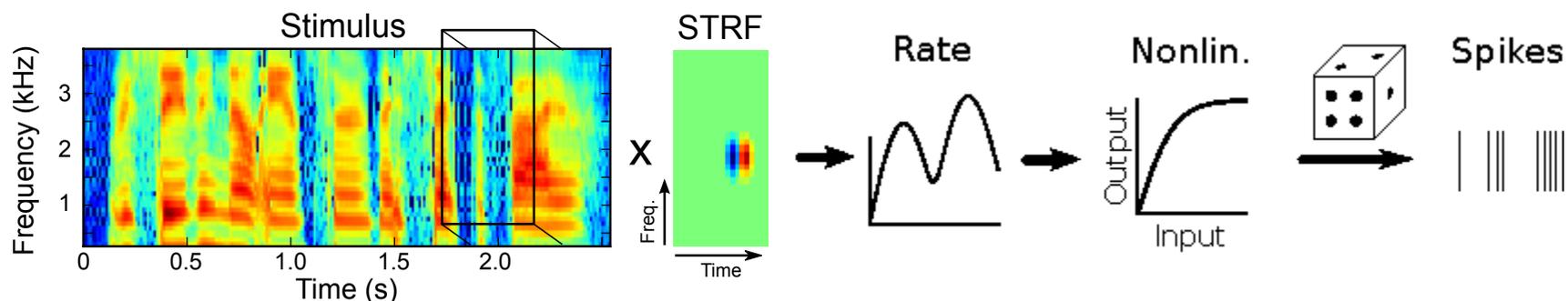
STC analysis:



From sounds to spikes

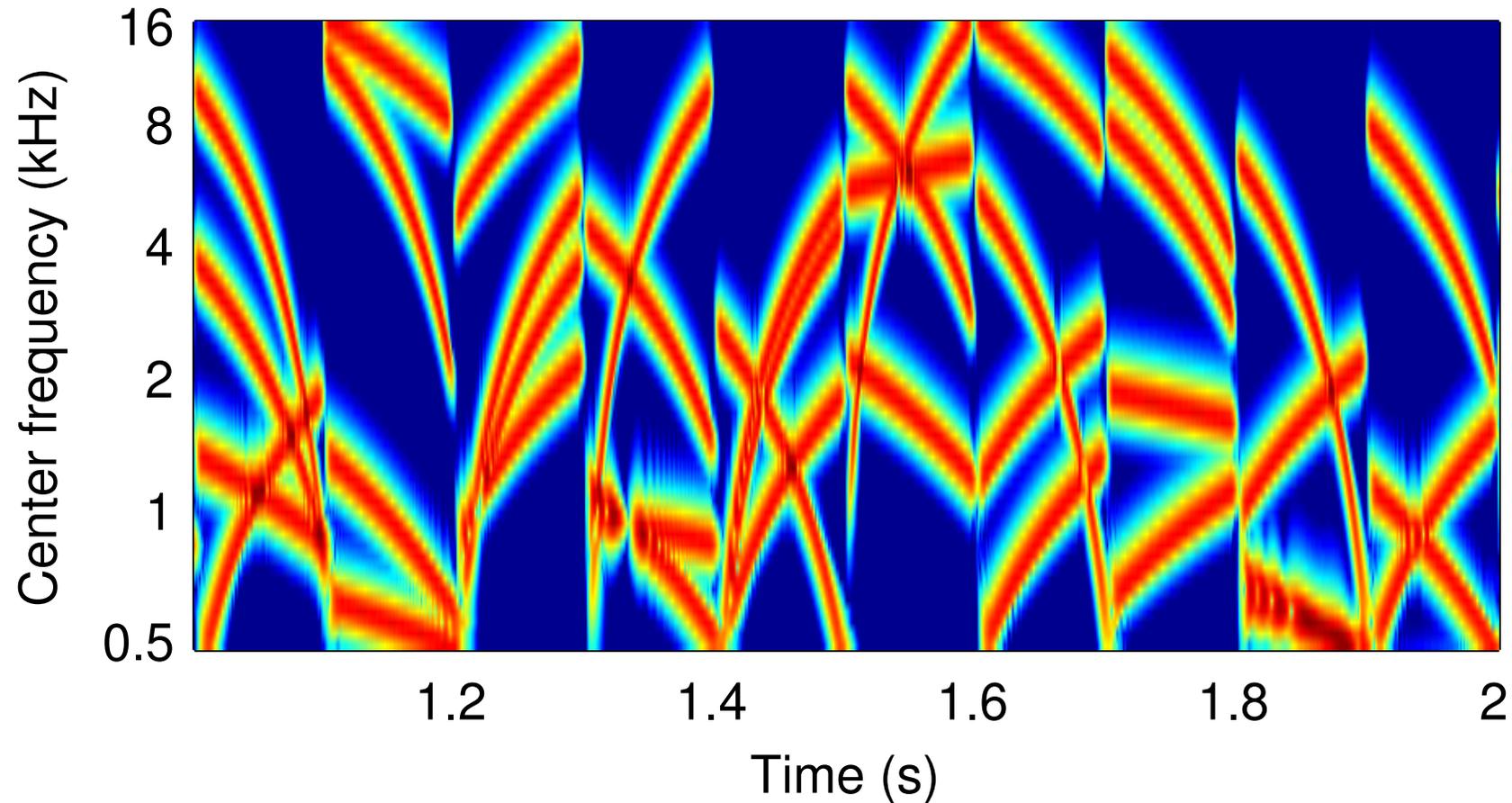


Classic STRF model:



- Separation into **linear part** (= receptive field or kernel **k**) and **static memoryless nonlinearity** (Chichilnisky 2001)
- Once we know **k** estimation of the nonlinearity is quite simple!
- White noise approach: Estimation of linear part using (normalized) reverse correlation method (Bussgang Theorem 1952)
- BUT: need Gaussian (symmetric) stimuli!

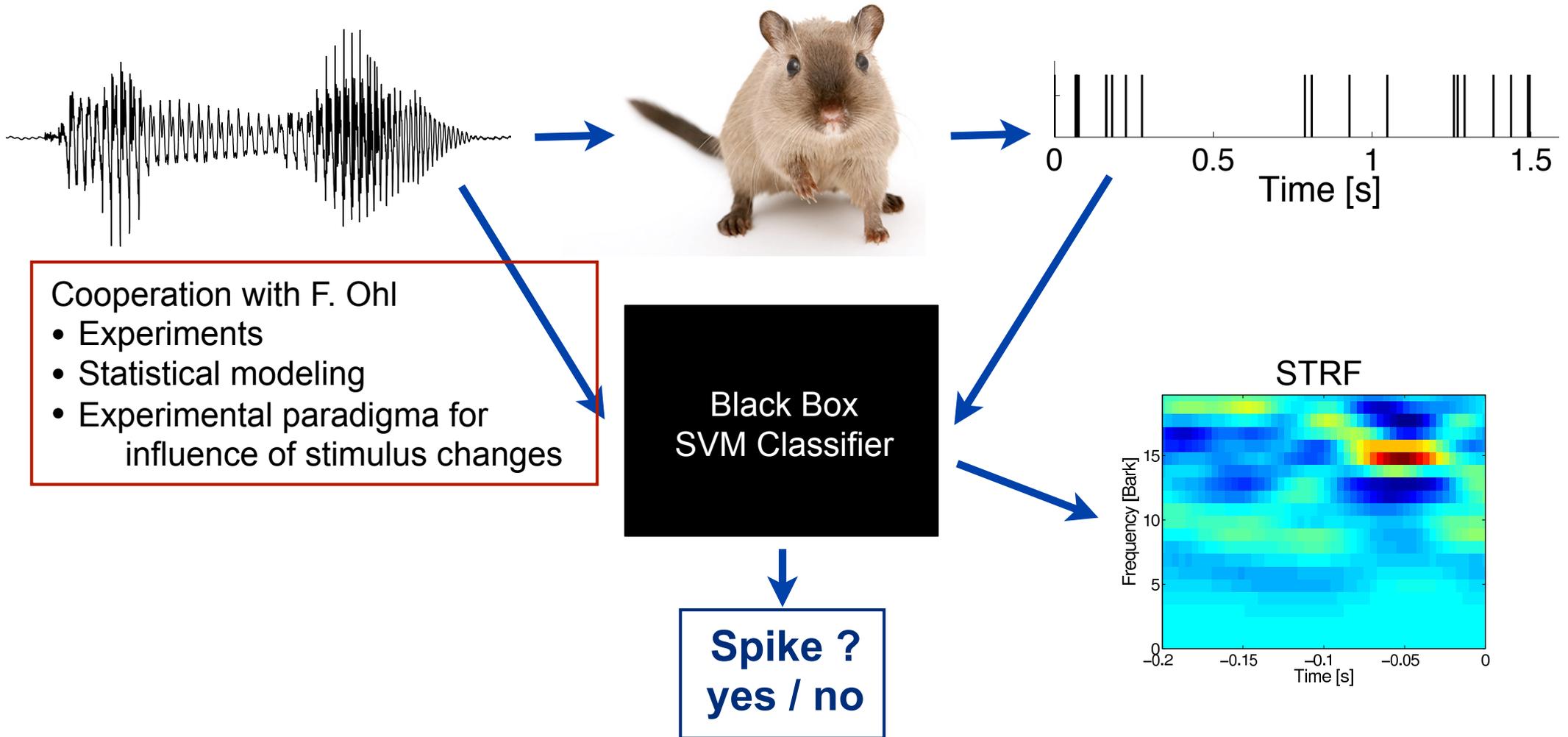
Stimuli: Bank of frequency-modulated tones (FM-Bank)



Meyer, Diepenbrock, Happel, Ohl, Anemüller (2014)

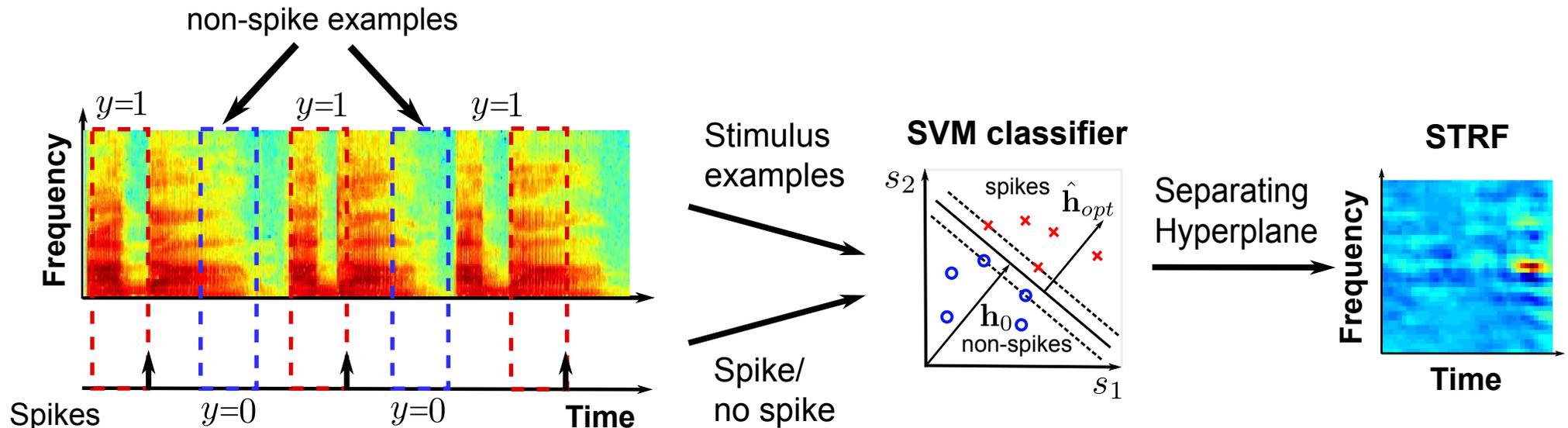
Classification-based receptive field (CbRF) estimation

Training a classifier to predict spike trains

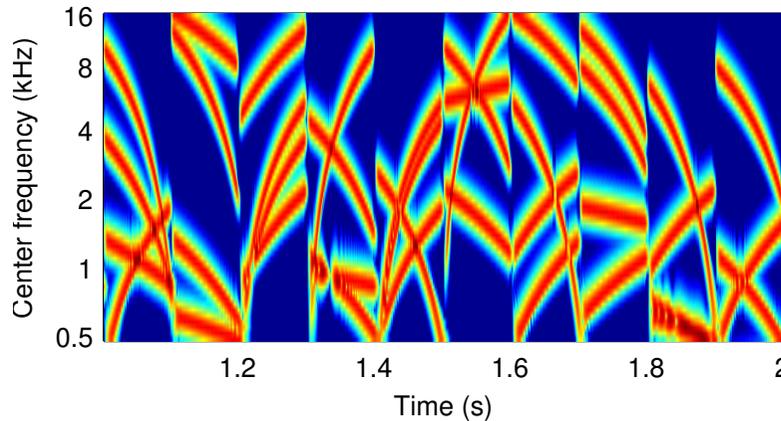


Classification-based receptive field estimation (CbRF)

Spectro-temporal receptive field (STRF) estimation



STRF estimation from gerbil neurons



stimulation with
frequency-modulated
tone complexes

Unit A



Unit B



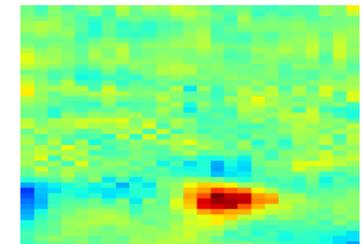
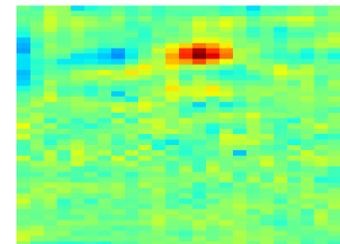
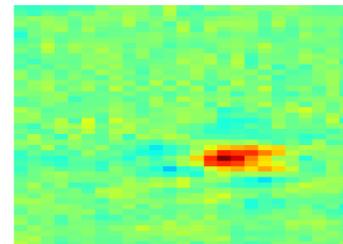
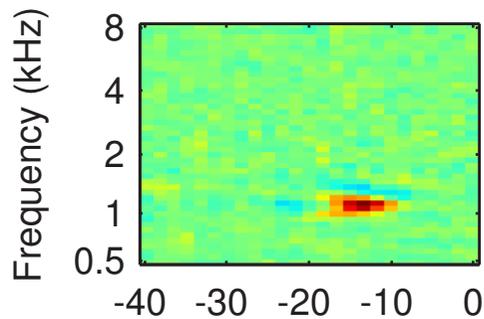
Unit C



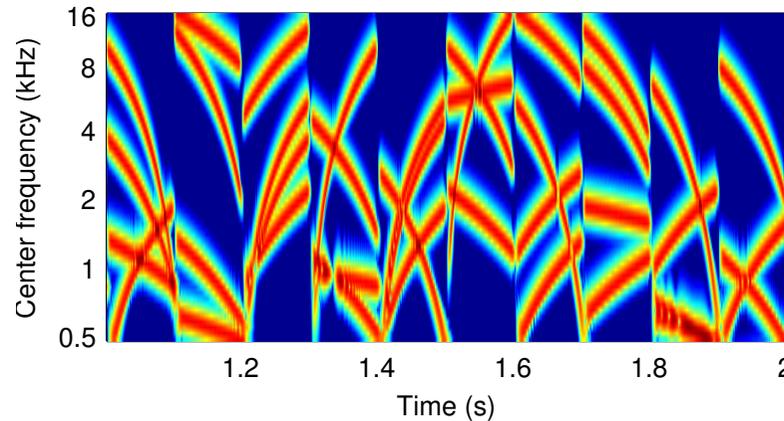
Unit D



CbRF



STRF estimation from gerbil neurons



stimulation with
frequency-modulated
tone complexes

Unit A



Unit B



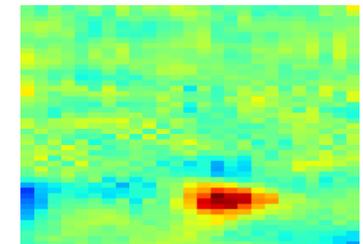
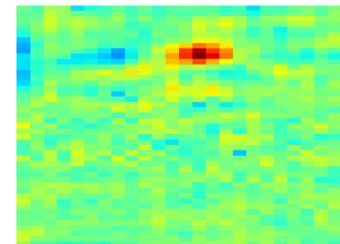
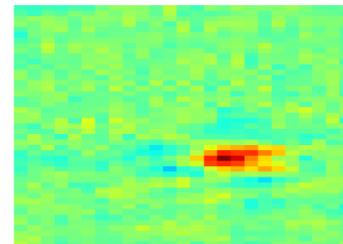
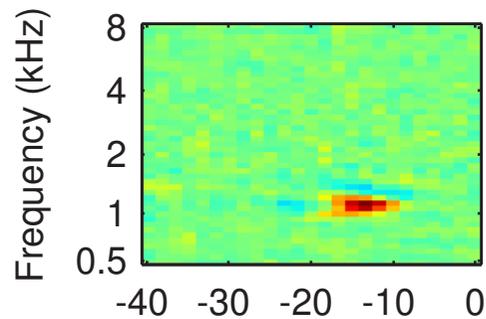
Unit C



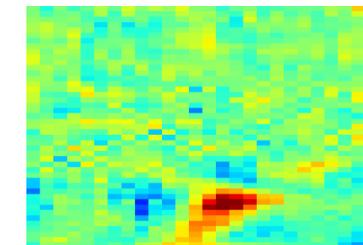
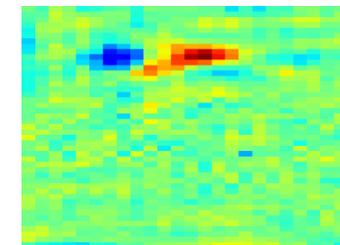
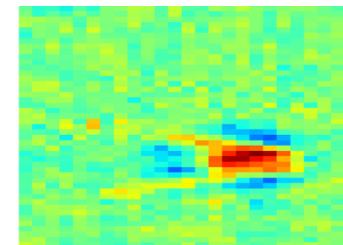
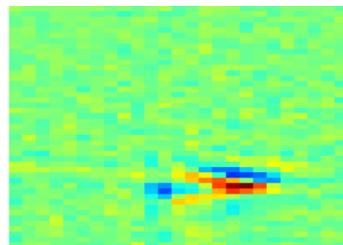
Unit D



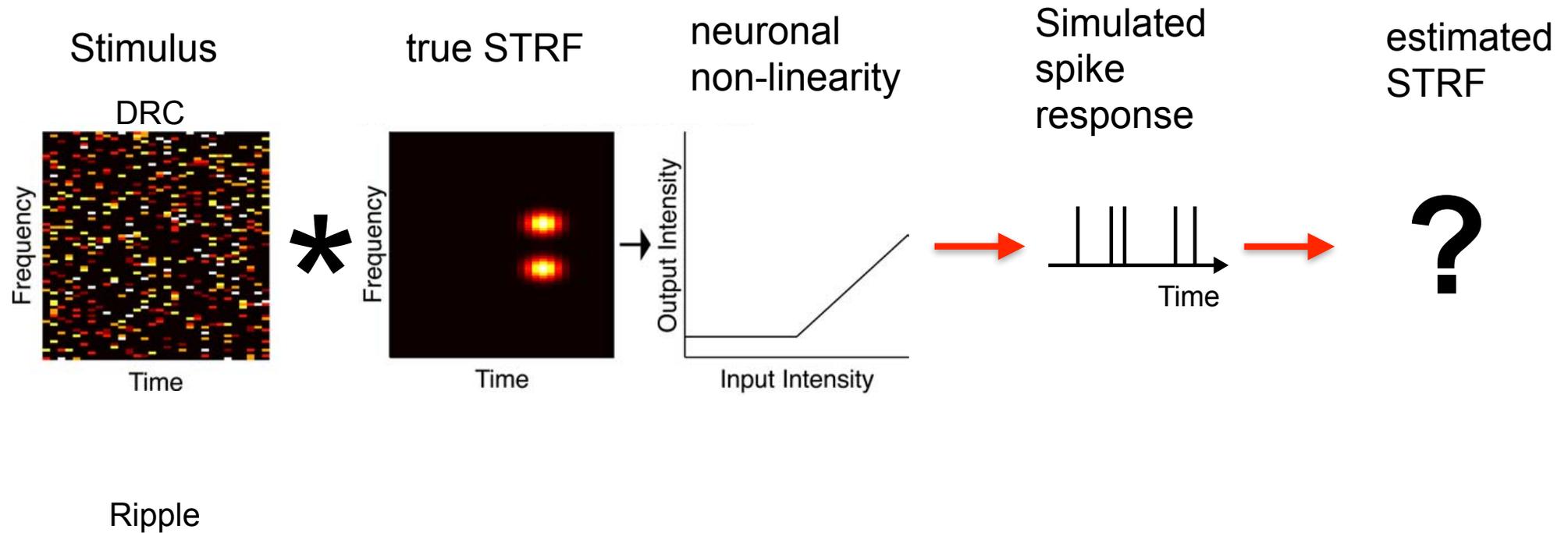
CbRF



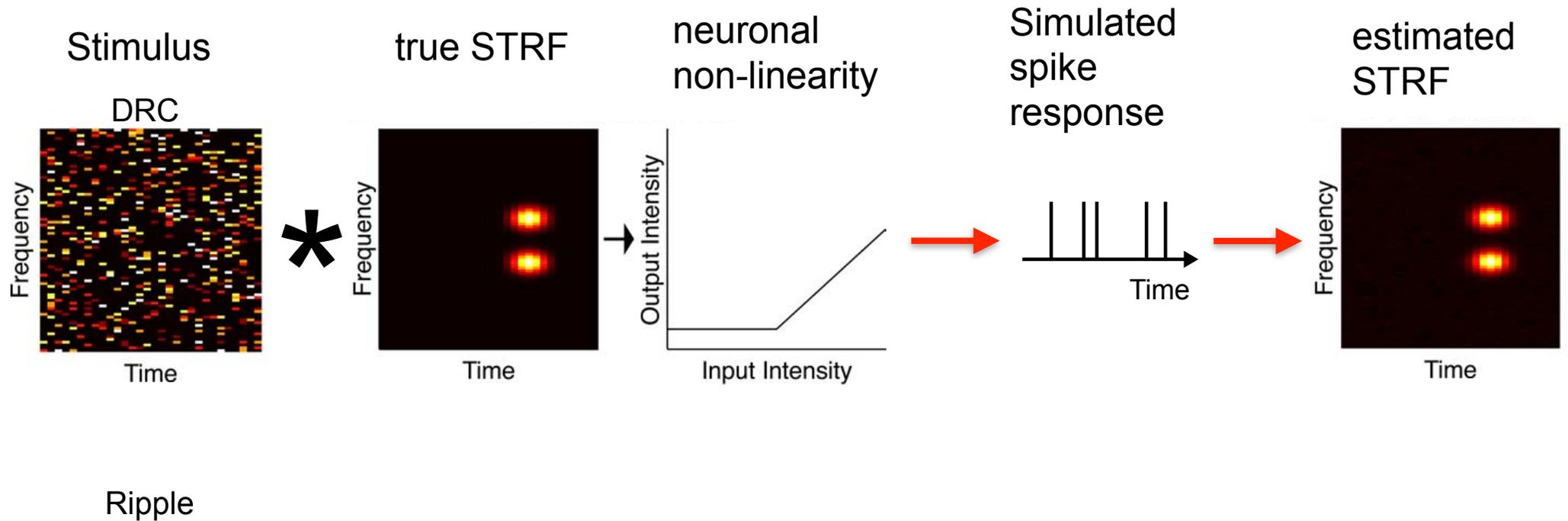
Ridge



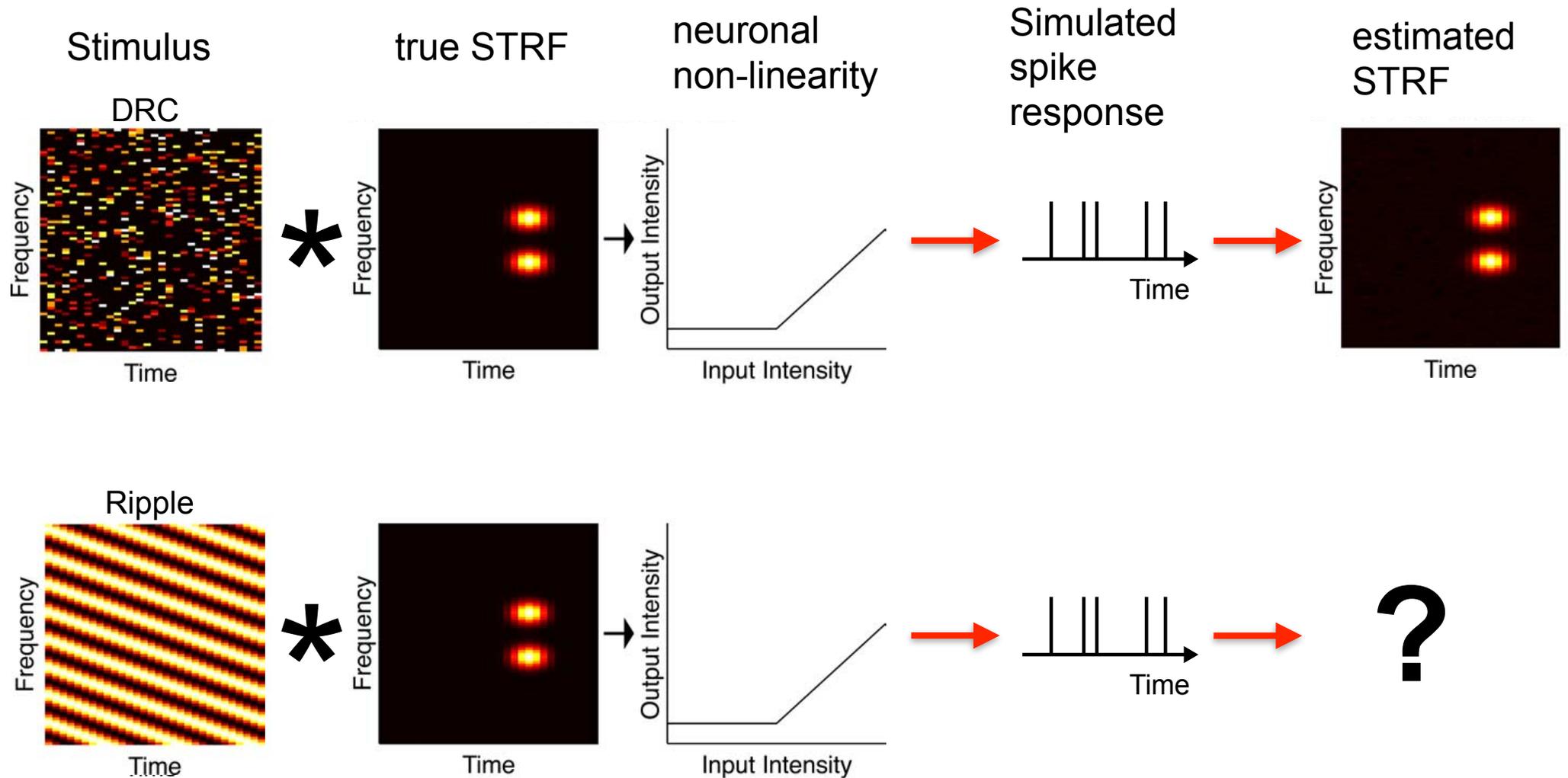
Higher-order stimulus statistics influences STRF estimation results



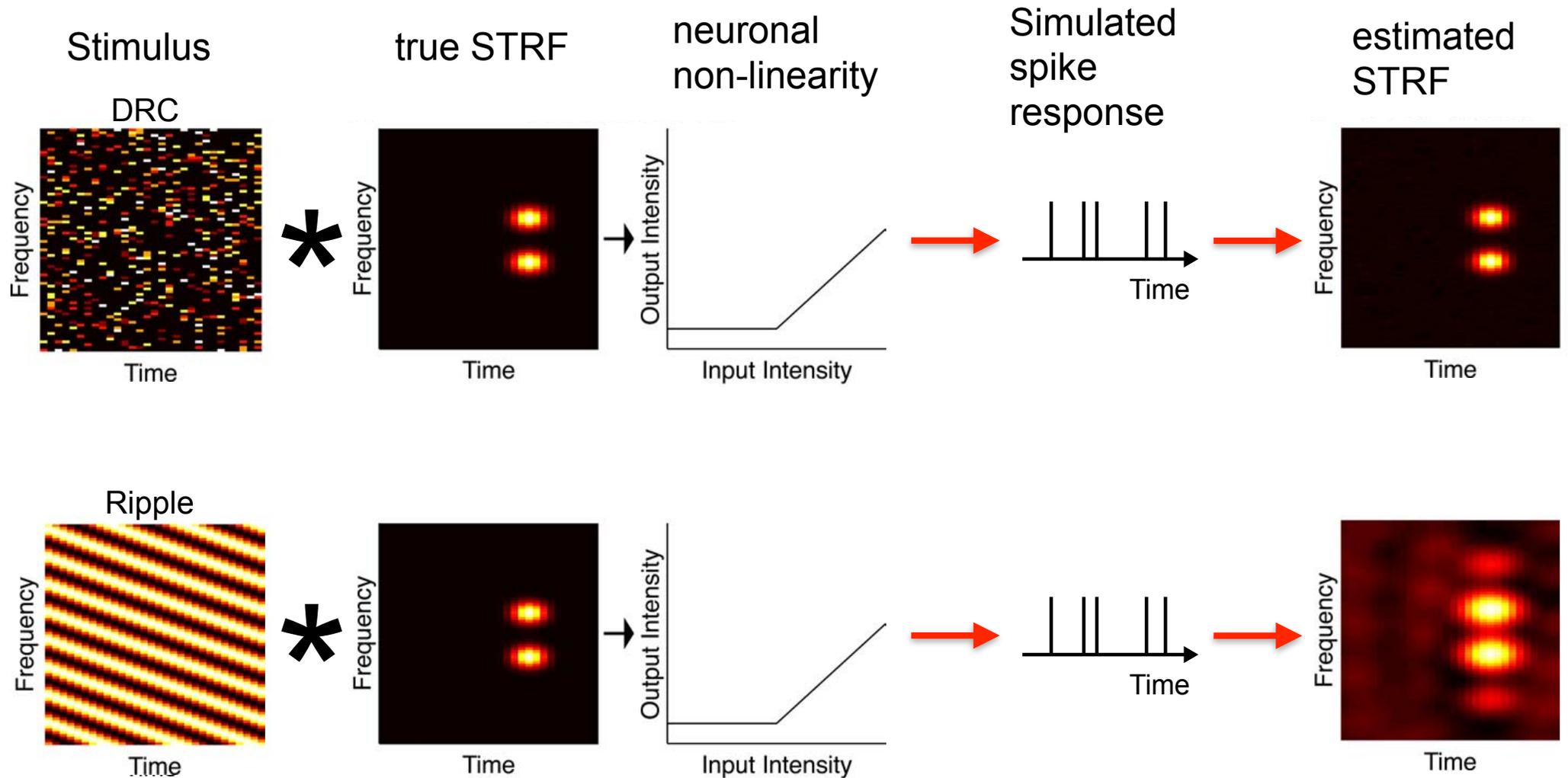
Higher-order stimulus statistics influences STRF estimation results



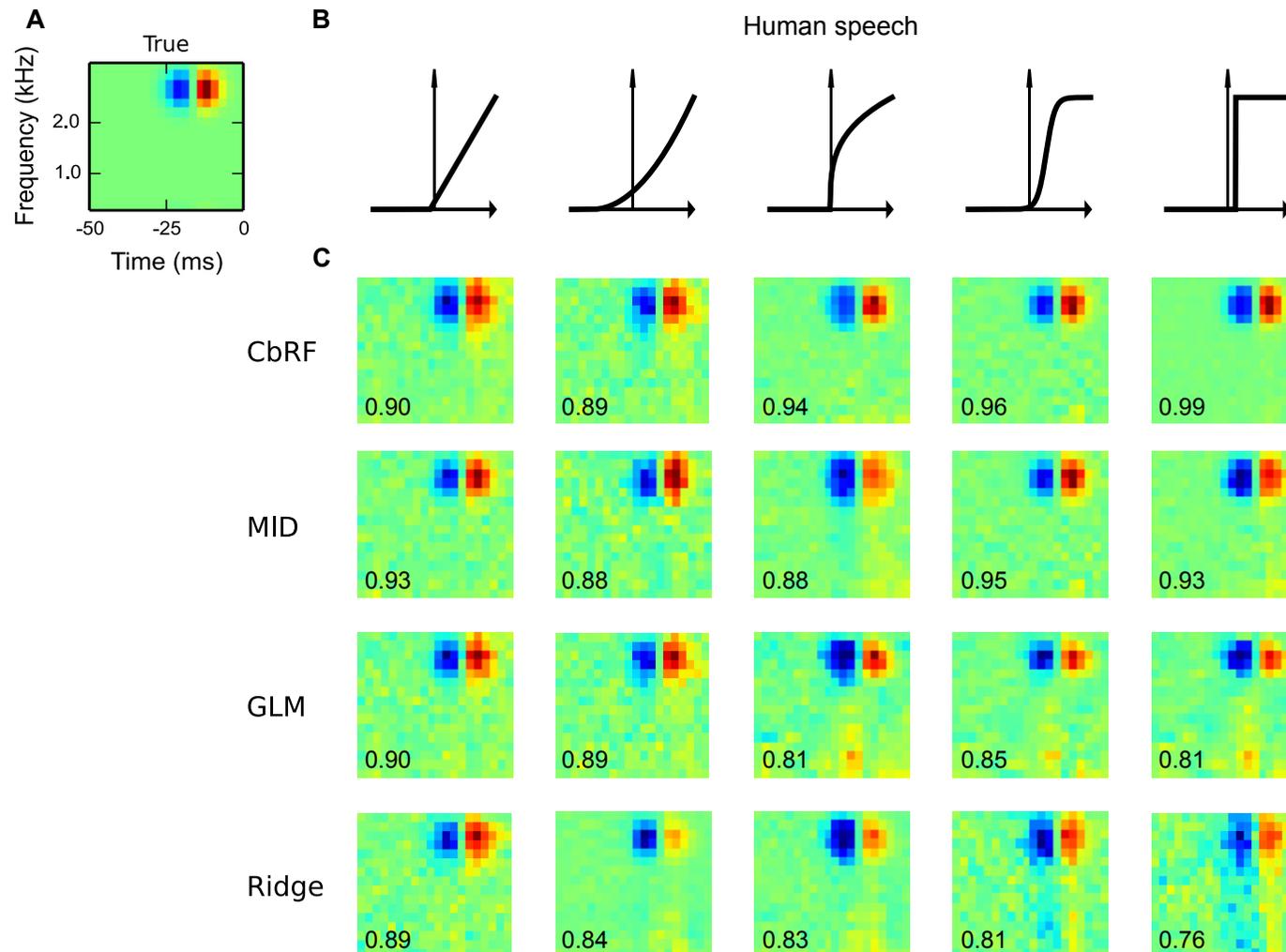
Higher-order stimulus statistics influences STRF estimation results



Higher-order stimulus statistics influences STRF estimation results

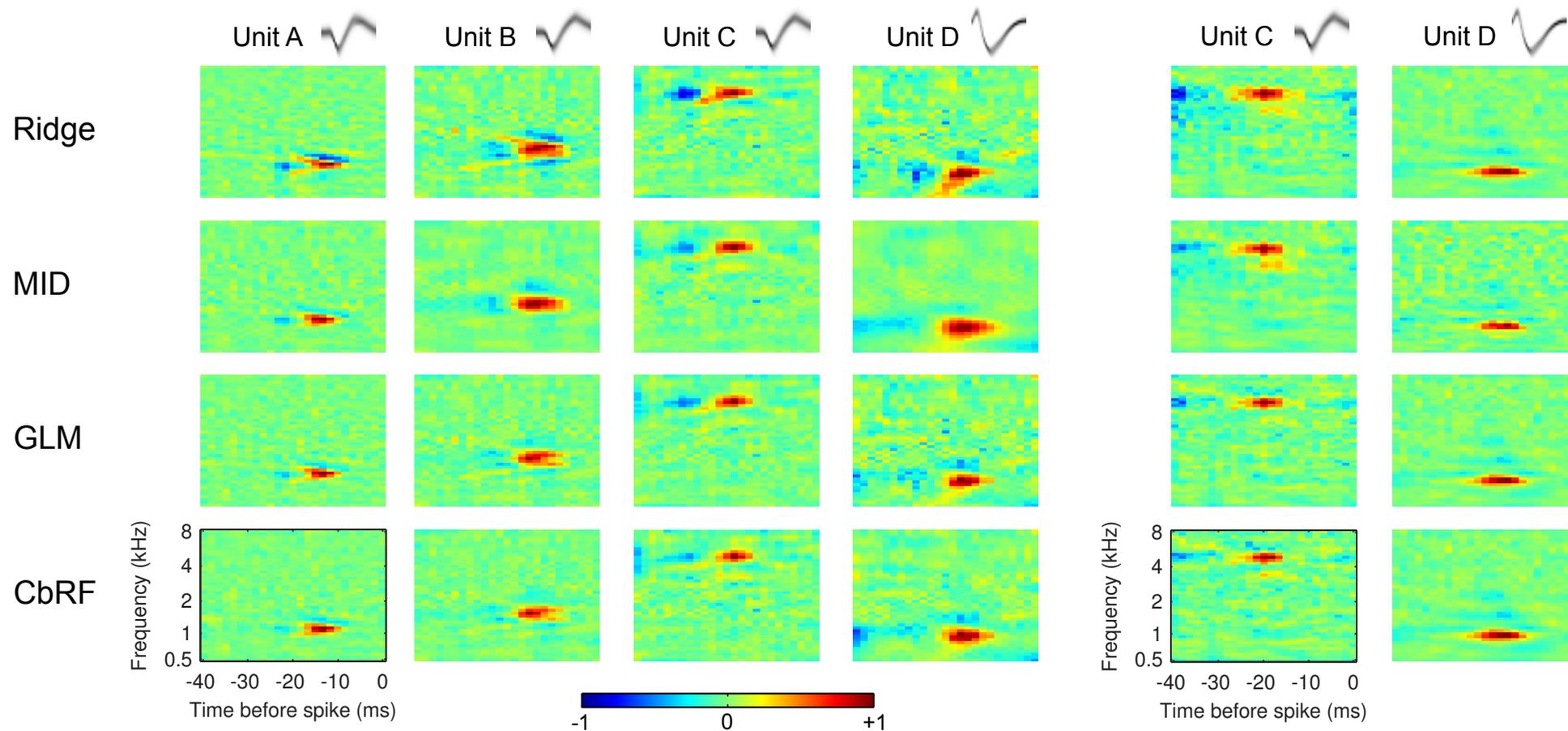
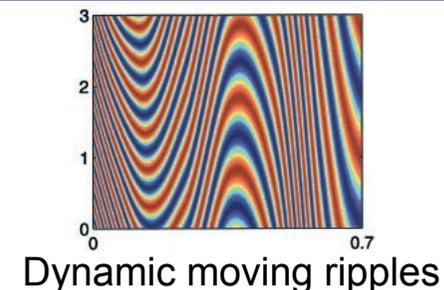
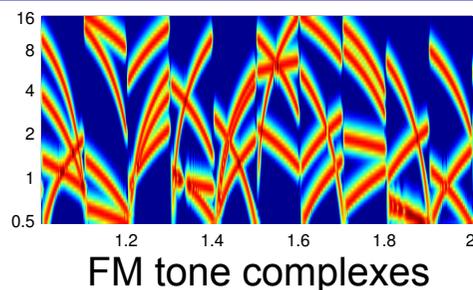


STRF estimation with speech stimuli input

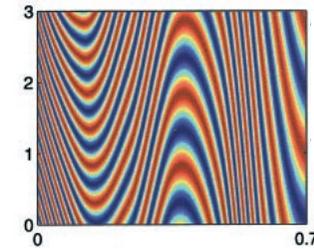
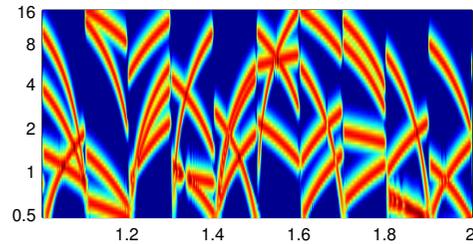


Classification-based method best matches ground-truth

STRF estimation from gerbil IC neurons



Influence of stimulus ensemble on STRF in gerbil IC recordings

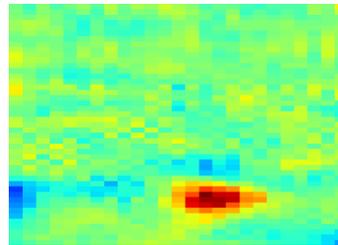
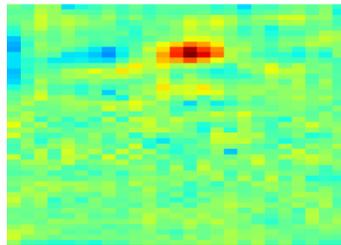


FM tone complexes

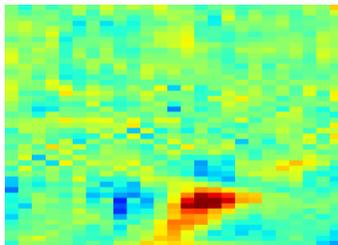
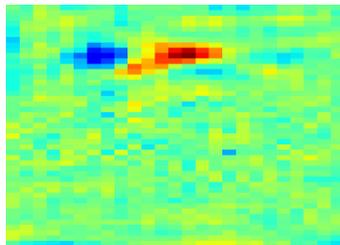
Unit C 

Unit D 

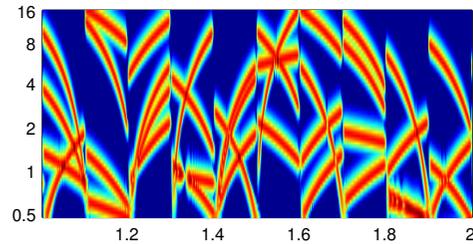
CbRF



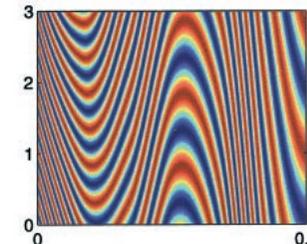
Ridge



Influence of stimulus ensemble on STRF in gerbil IC recordings



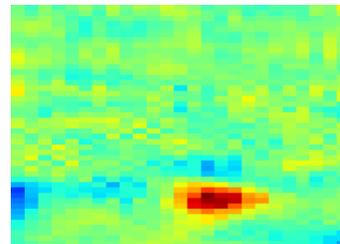
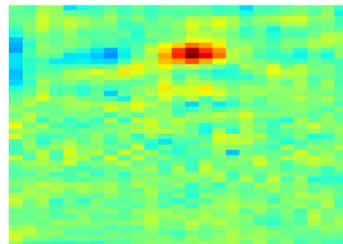
FM tone complexes



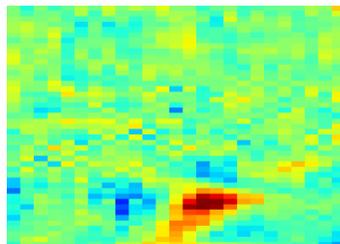
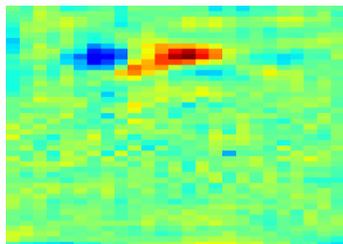
Dynamic moving ripples



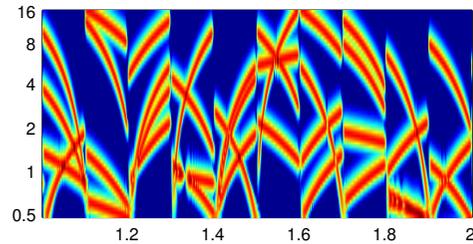
CbRF



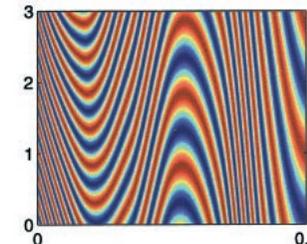
Ridge



Influence of stimulus ensemble on STRF in gerbil IC recordings



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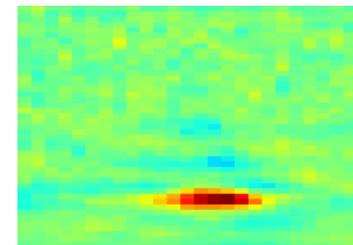
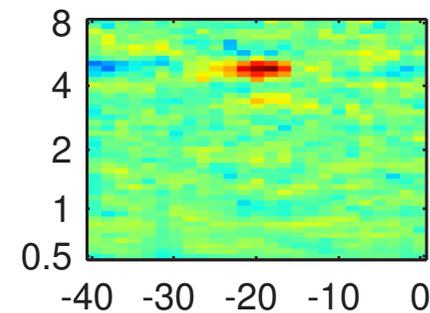
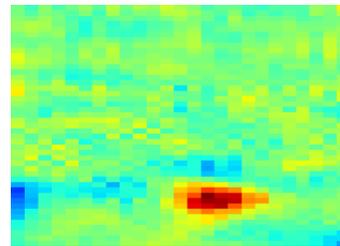
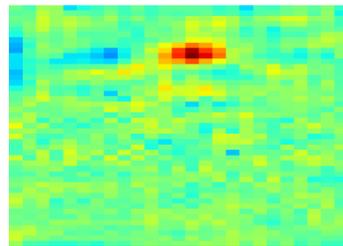
Unit C 

Unit D 

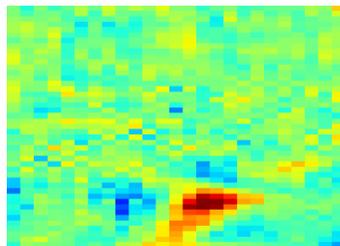
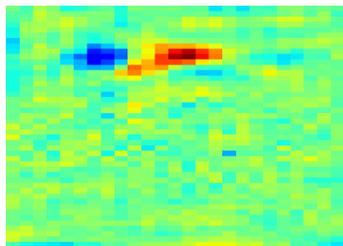
Unit C 

Unit D 

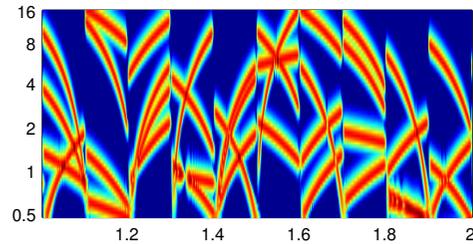
CbRF



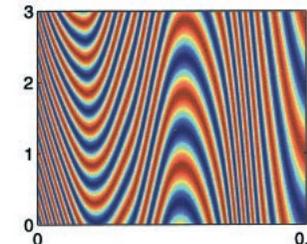
Ridge



Influence of stimulus ensemble on STRF in gerbil IC recordings



FM tone complexes



Dynamic moving ripples

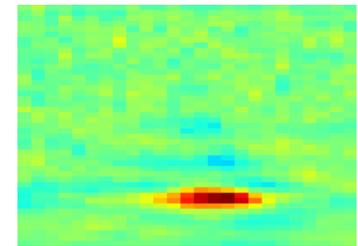
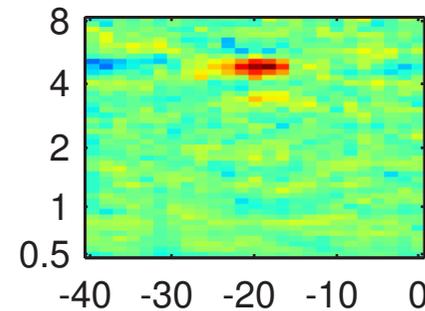
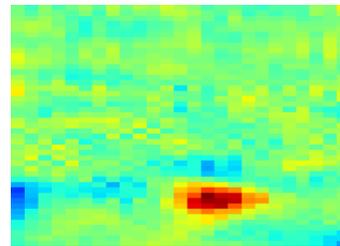
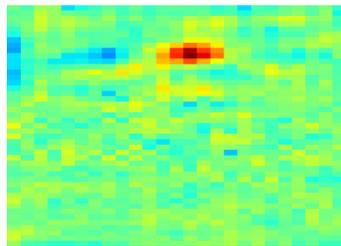
Unit C 

Unit D 

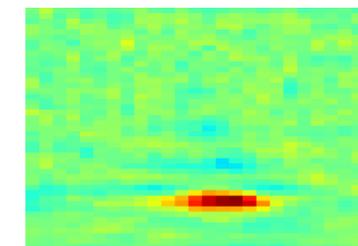
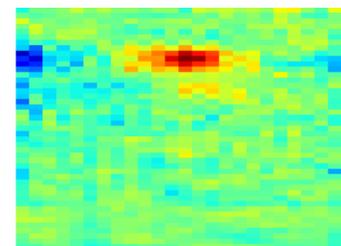
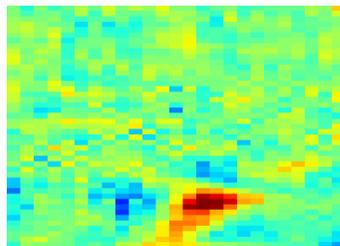
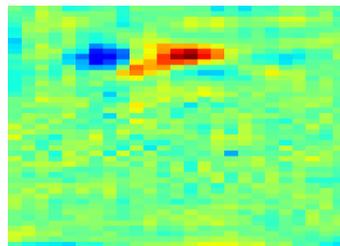
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Unit D 

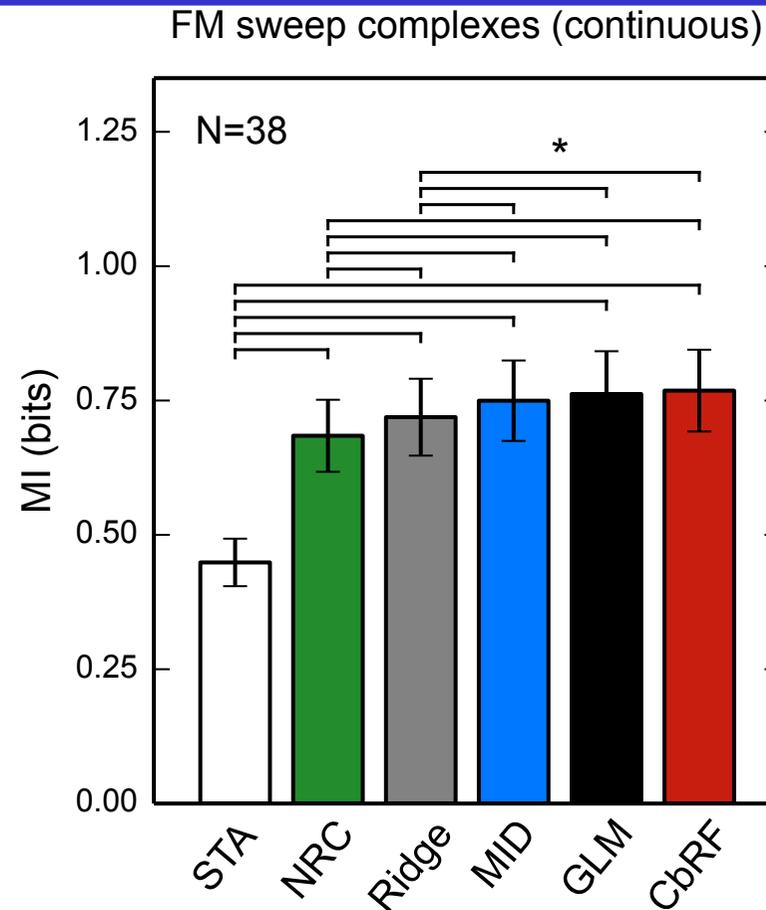
CbRF



Ridge

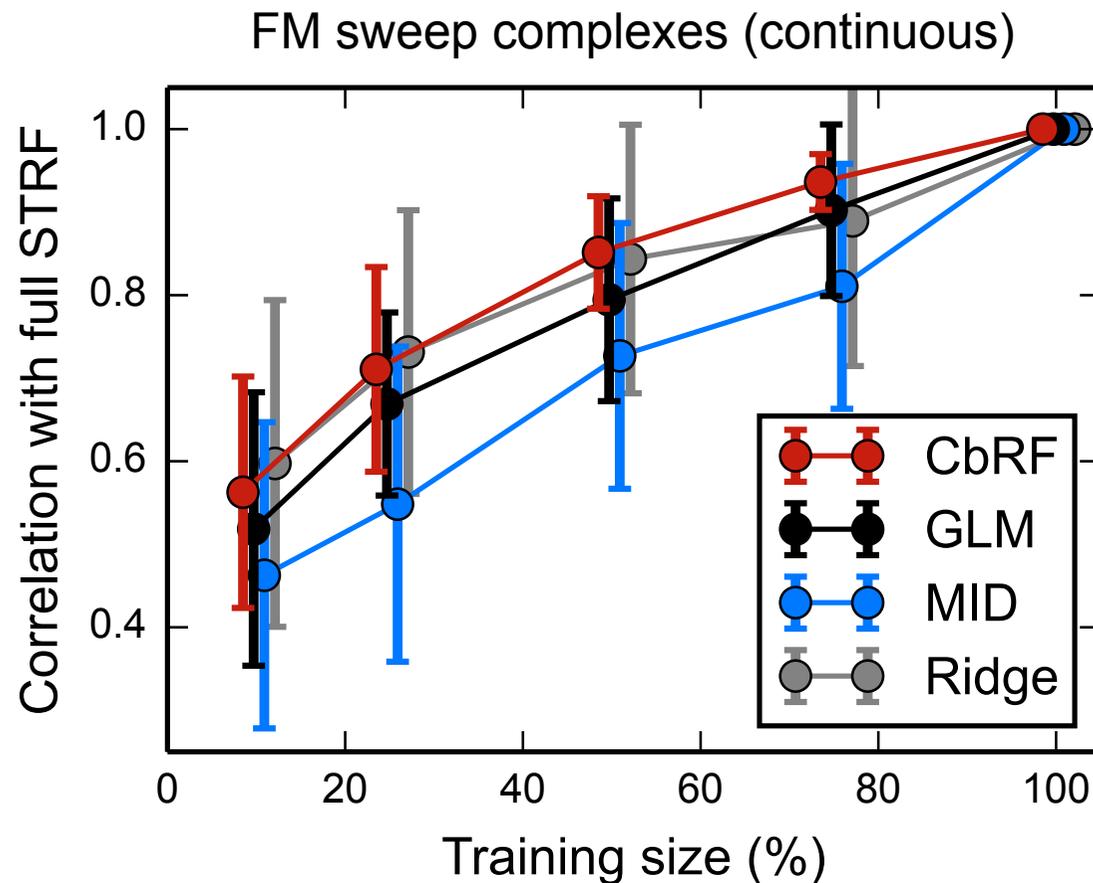


STRF estimation from gerbil IC neurons: Mutual information analysis



Non-linear methods (CbRF, GLM, MID) show highest information-transfer rates for non-Gaussian stimuli

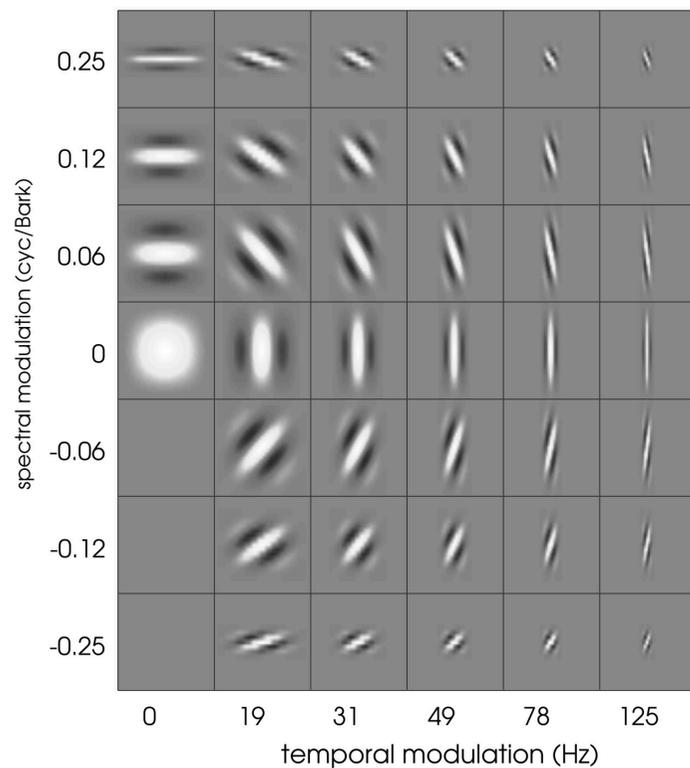
STRF estimation from gerbil IC neurons: speed of convergence



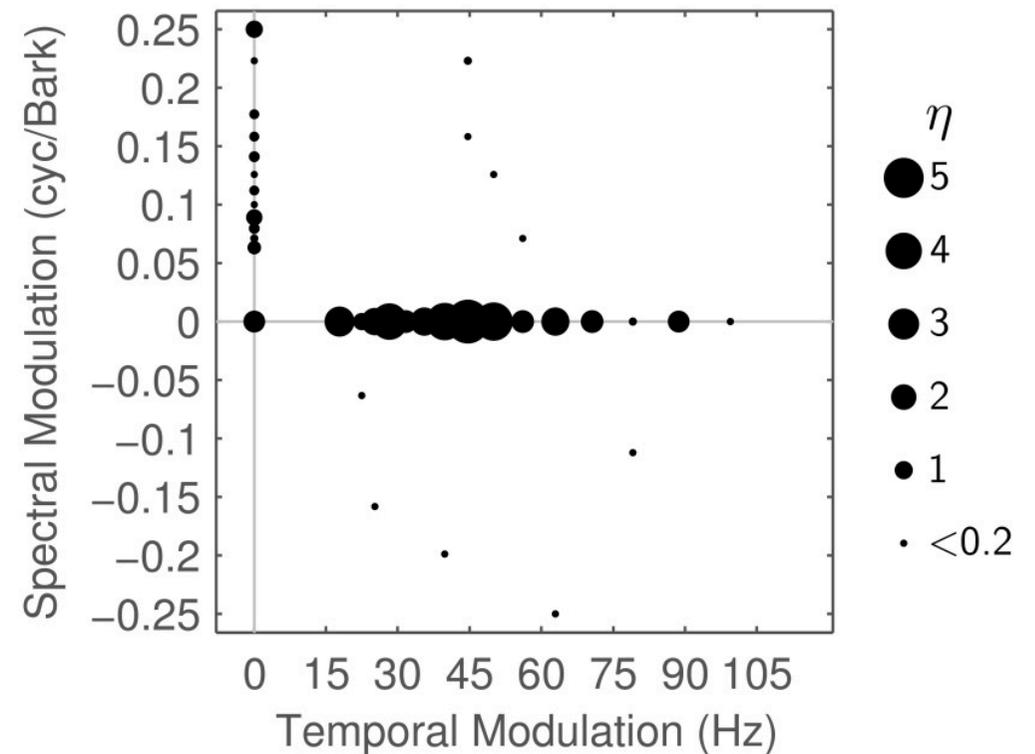
Classification-based method converges quickly and with relatively small estimation variance

Matching pursuit (MP) analysis of spectral, temporal and spectra-temporal characteristics

Gabor basis functions as MP-atoms



Spectro-temporal distribution of MP-selected atoms



Data from Gill, Zhang, Woolley, Fremouw, Theunissen (2006) + ridge regression
Bach, Kollmeier, Anemüller (2017)

Summary STRF estimation

STRF estimation algorithms need to go beyond second order statistics (e.g., GLM, MID, CbRF)

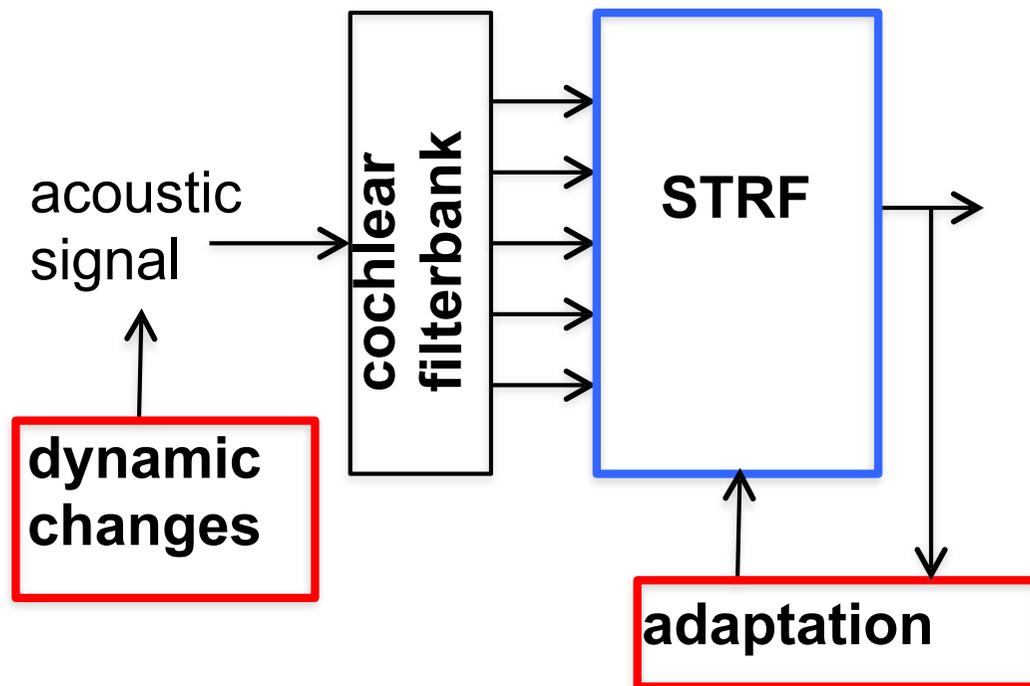
Data show that estimation algorithm influences obtained STRF pattern *qualitatively*

FM-bank stimuli to mimic speech-like t-f-transients

Joint spectra-temporal STRFs appear to be rare, even on FM-bank stimuli

Beyond the linear time-invariant STRF model

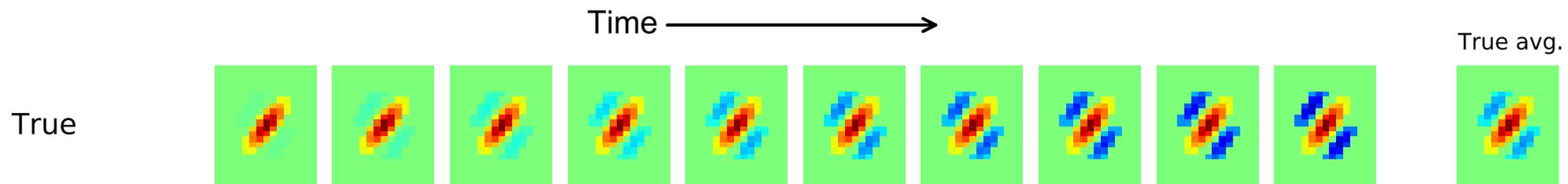
Cue selection under dynamic stimulus changes



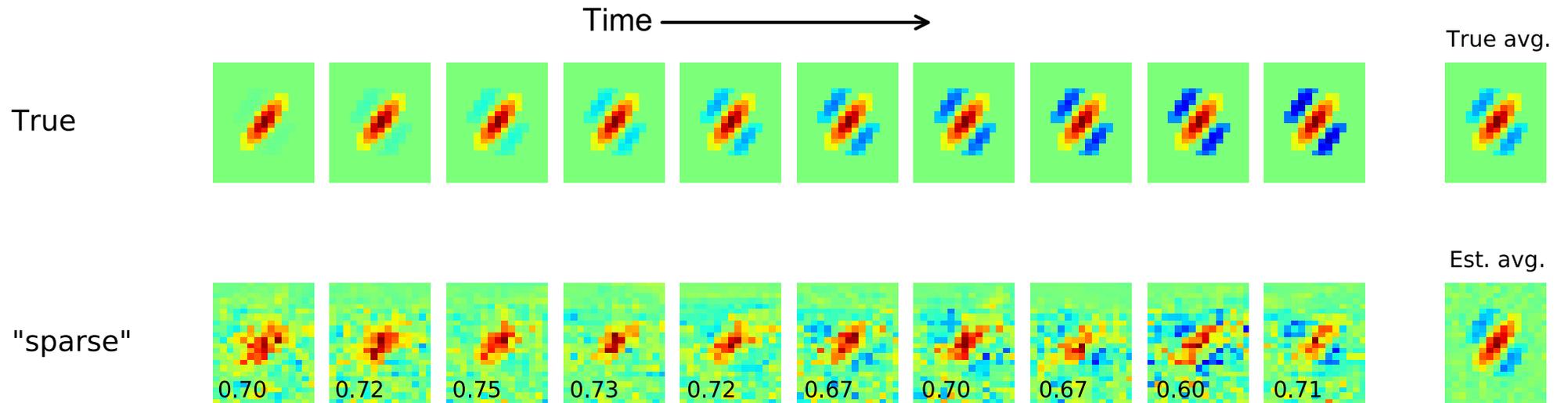
Beyond the linear time-invariant STRF model



Beyond the linear time-invariant STRF model

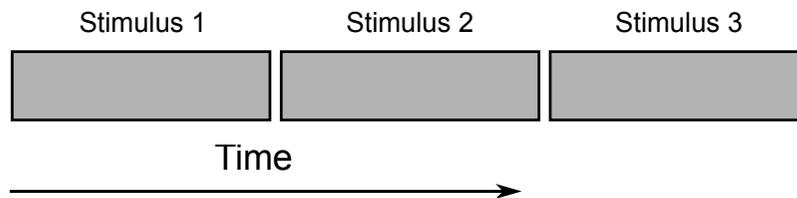


Beyond the linear time-invariant STRF model



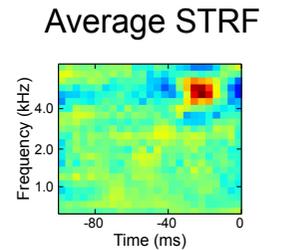
Adaptive STRF estimation model

Step 1 “global”



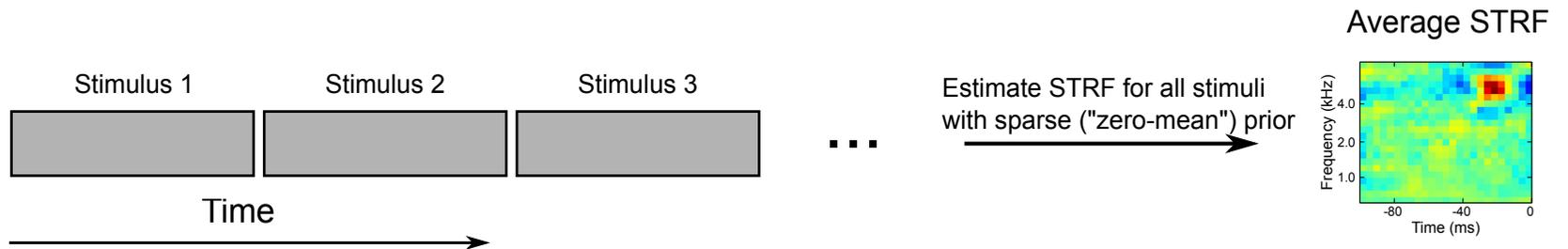
...

Estimate STRF for all stimuli
with sparse ("zero-mean") prior

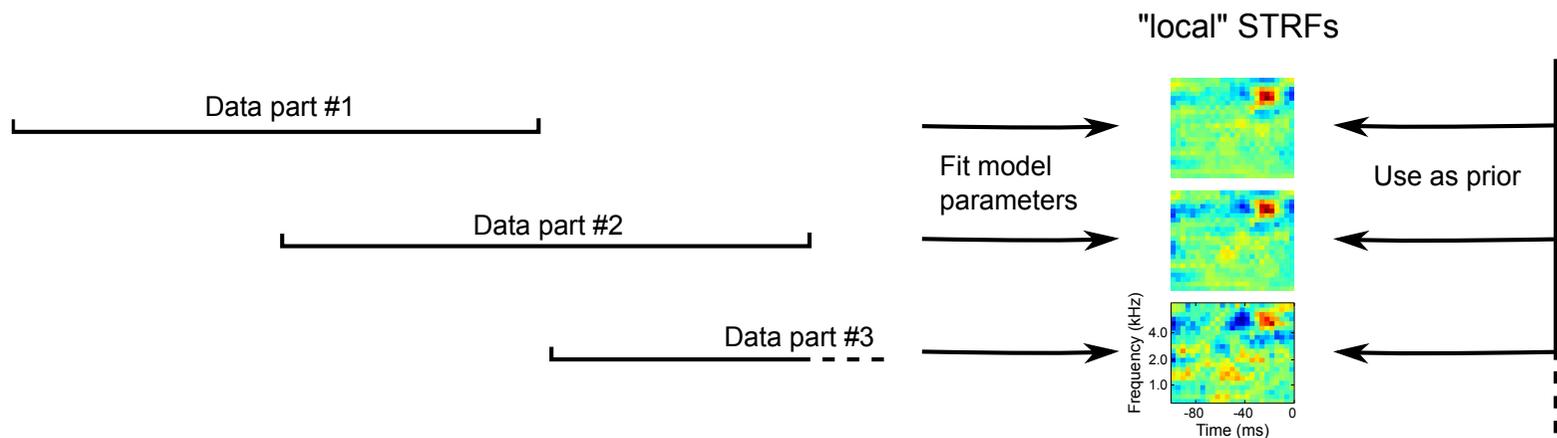


Adaptive STRF estimation model

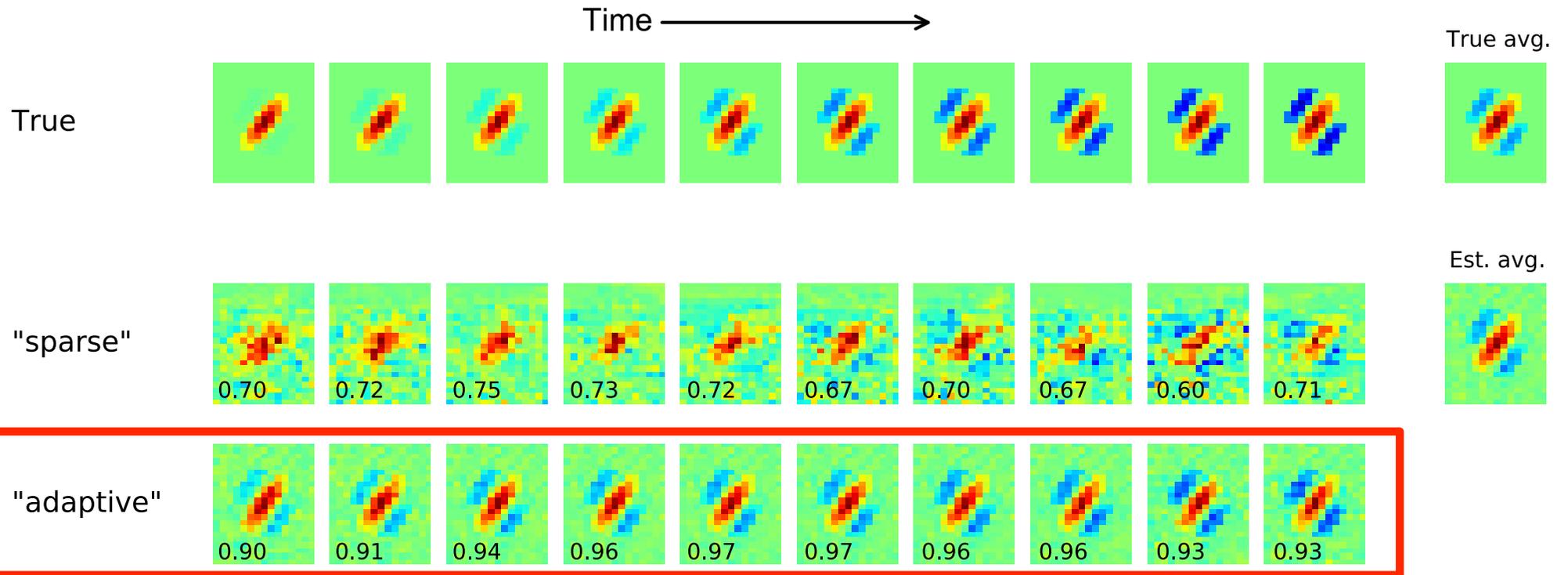
Step 1 “global”



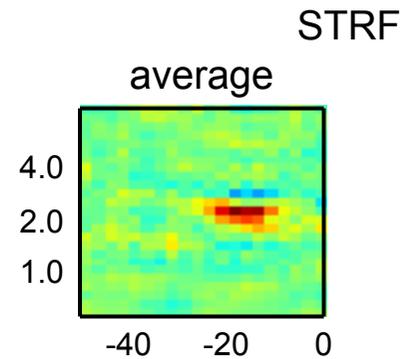
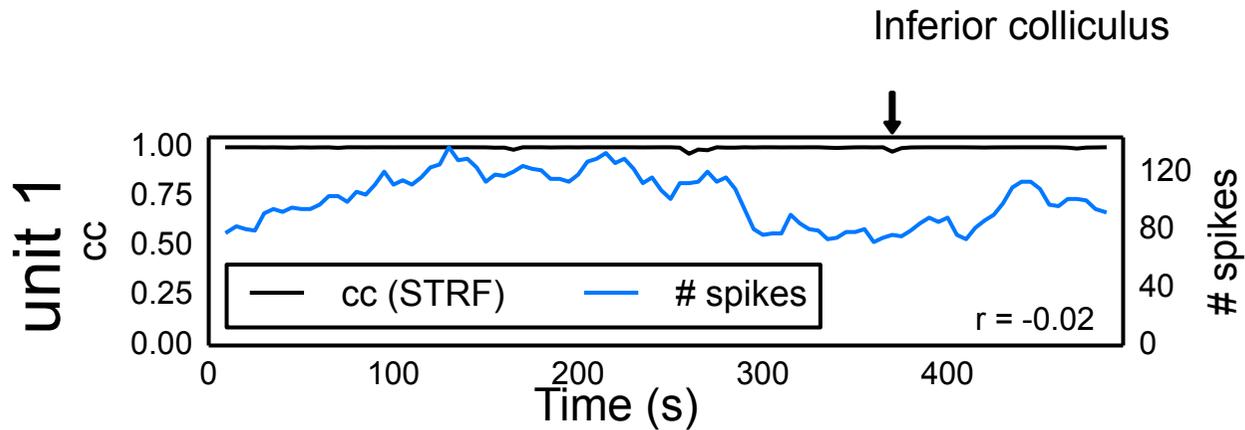
Step 2 “local”



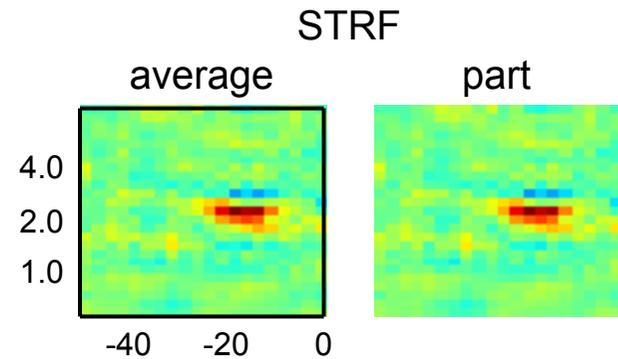
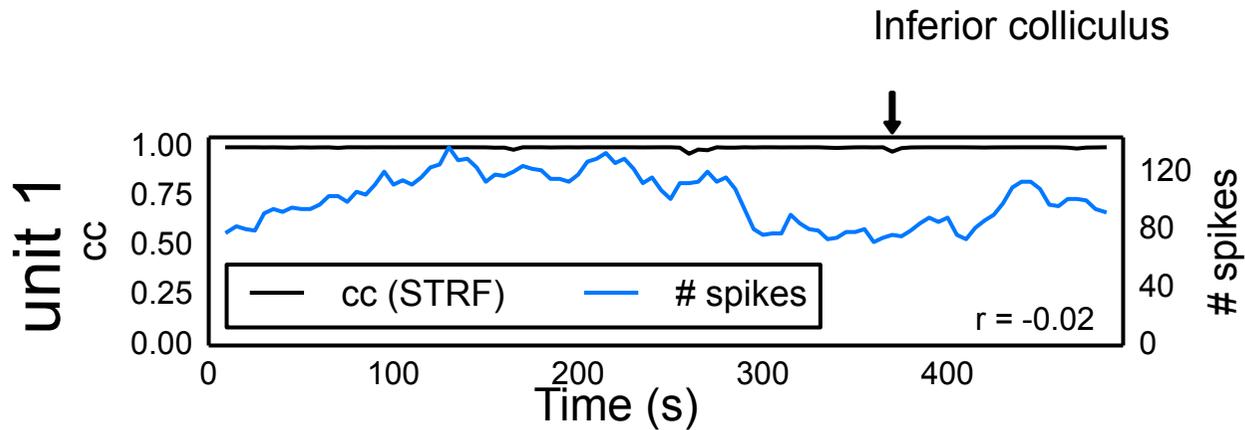
Adaptive STRF estimation model



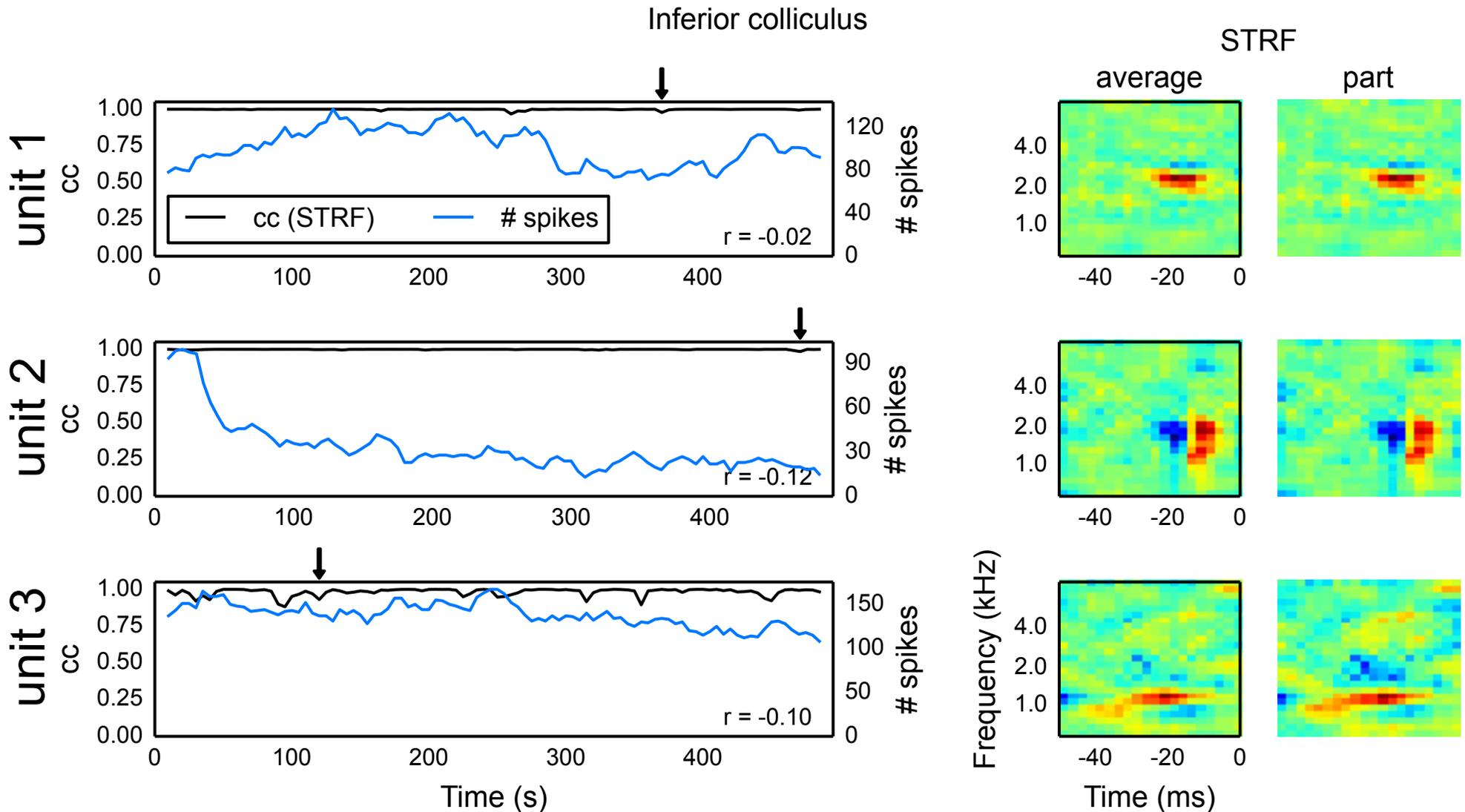
STRF variability across time: Gerbil inferior colliculus



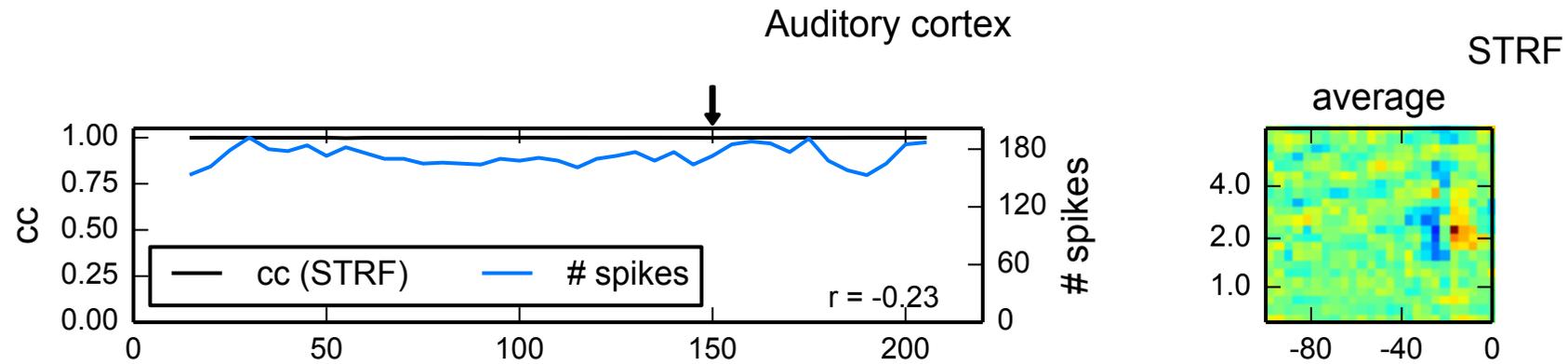
STRF variability across time: Gerbil inferior colliculus



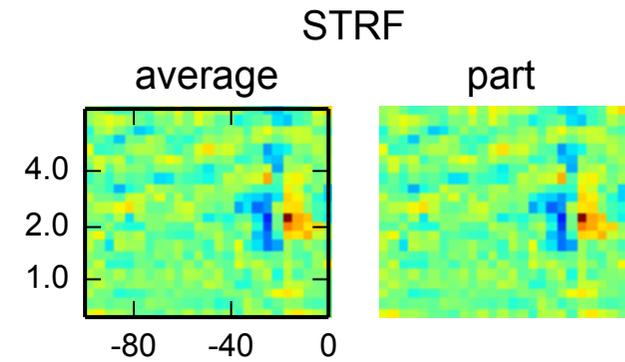
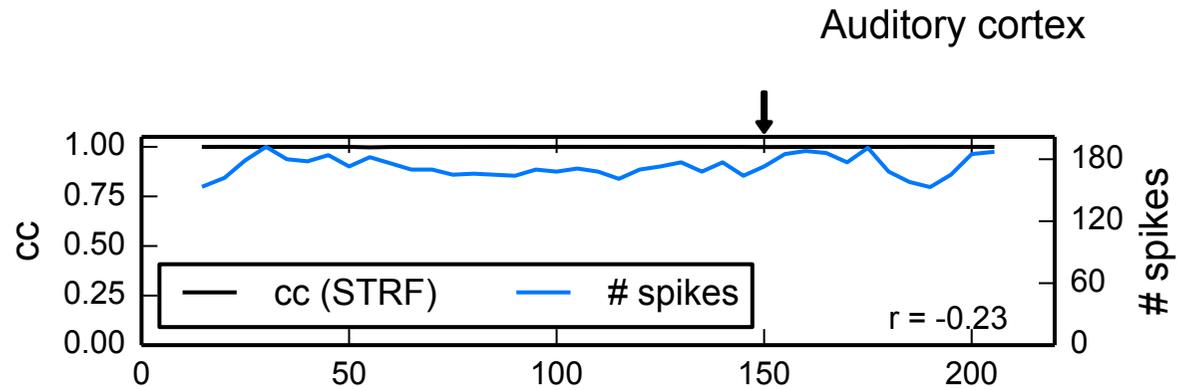
STRF variability across time: Gerbil inferior colliculus



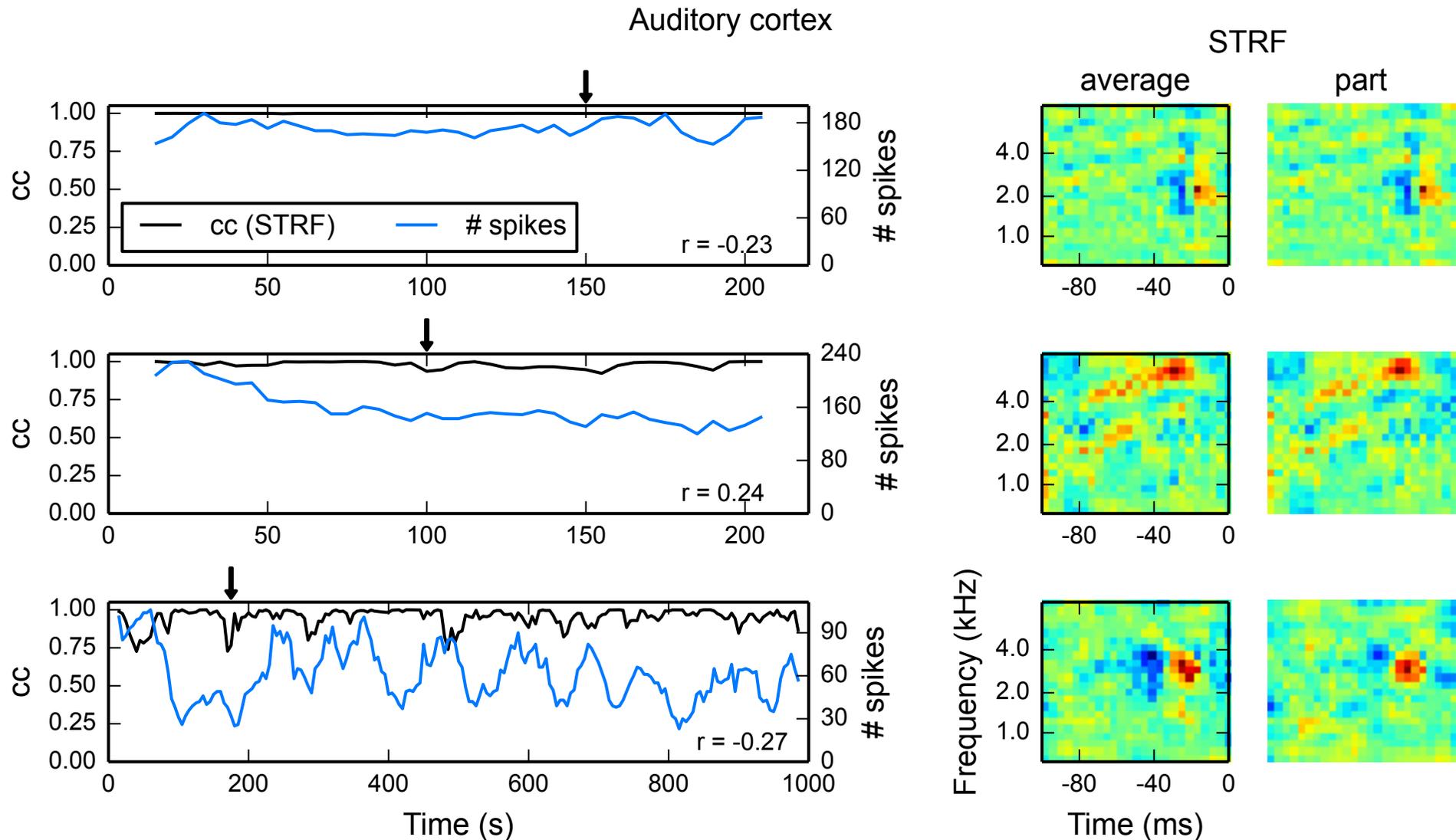
STRF variability across time: Gerbil auditory cortex



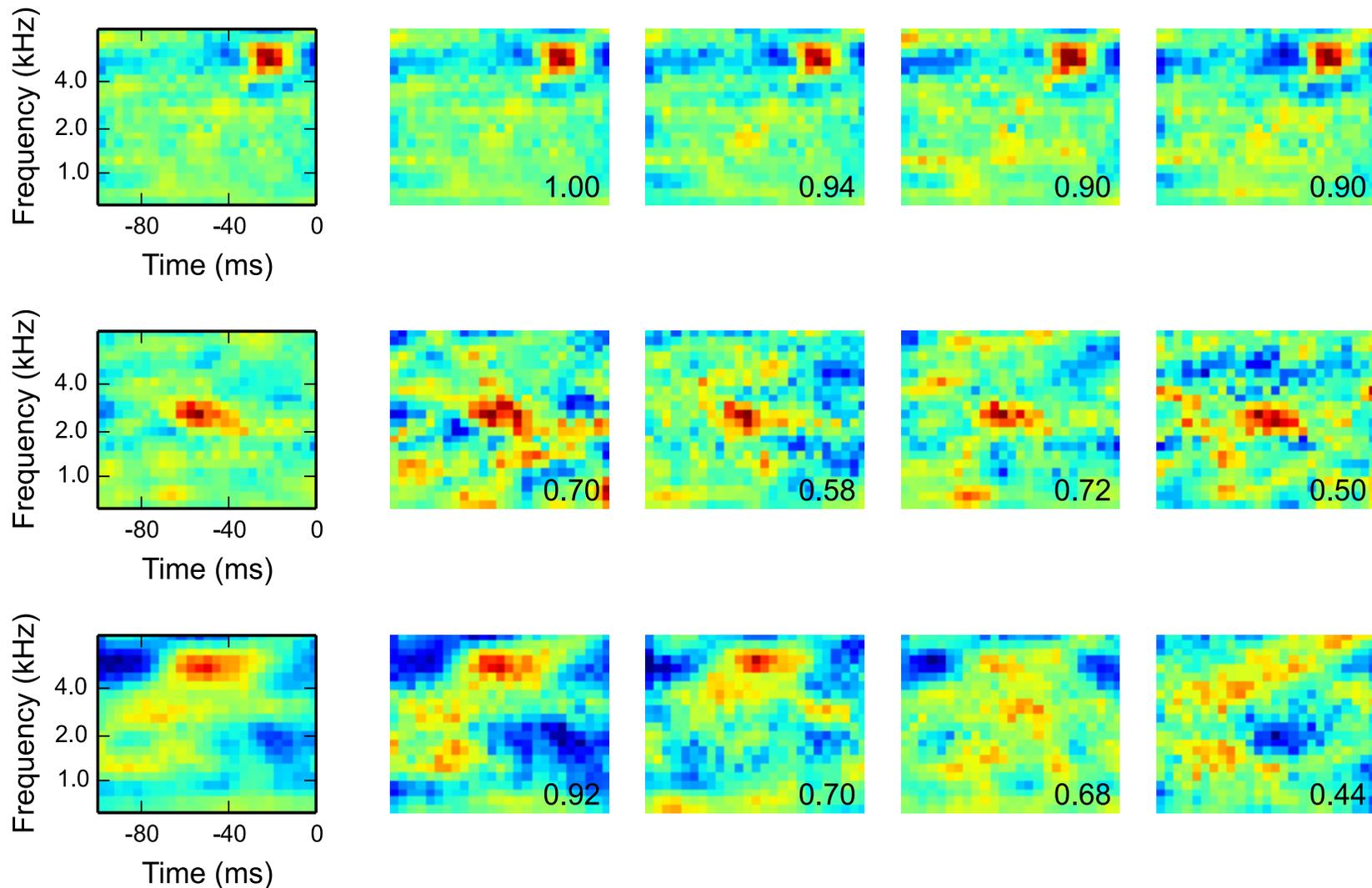
STRF variability across time: Gerbil auditory cortex



STRF variability across time: Gerbil auditory cortex

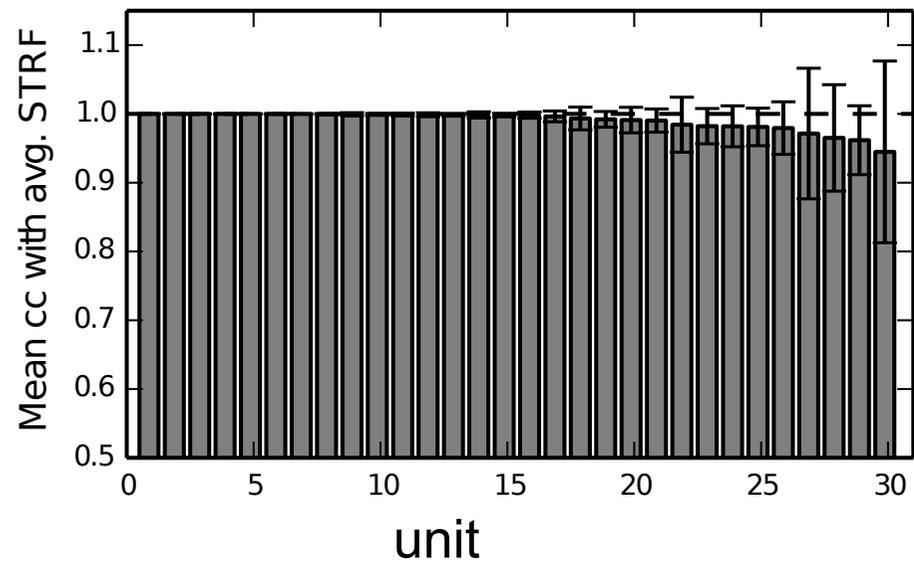


STRF variability across time: 3 units, moderate to strong fluctuation



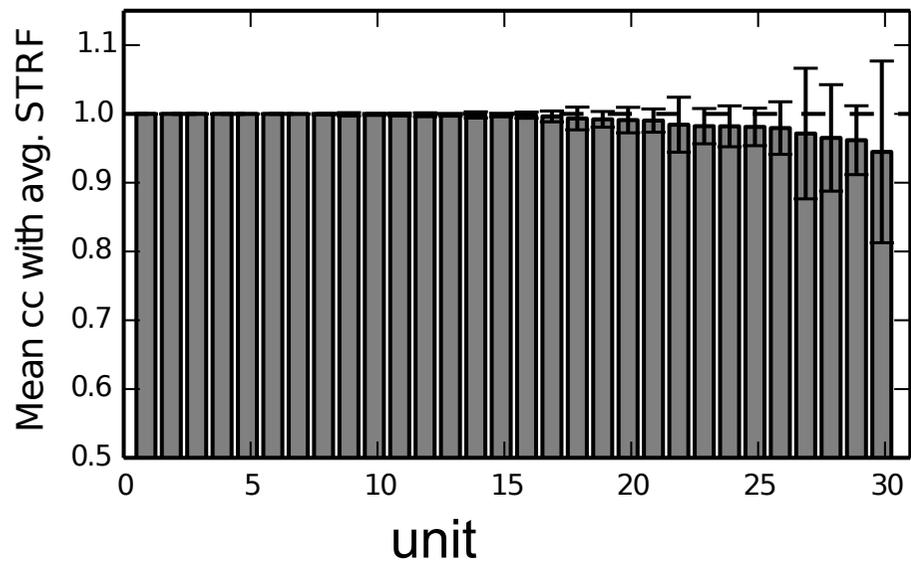
STRF variability across time: Summary statistics

Inferior colliculus

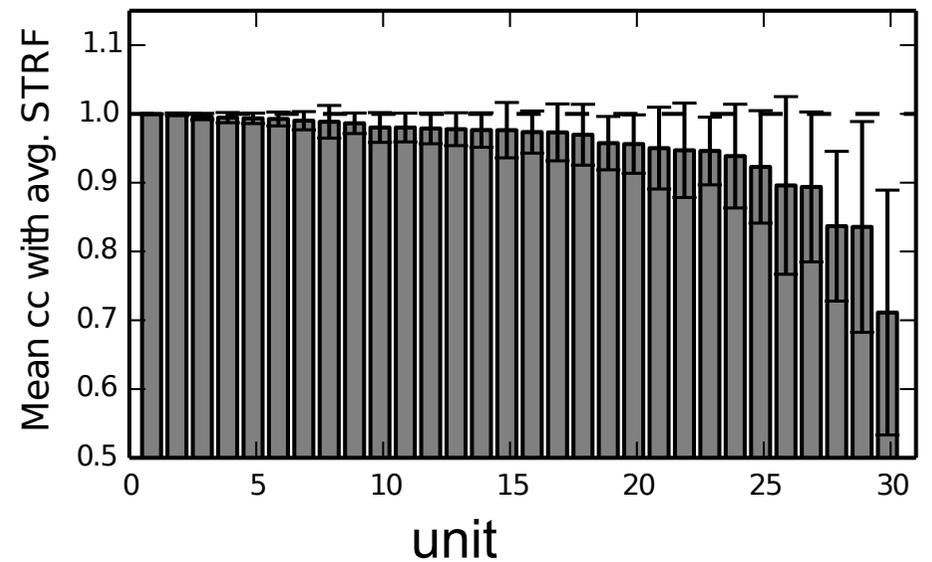


STRF variability across time: Summary statistics

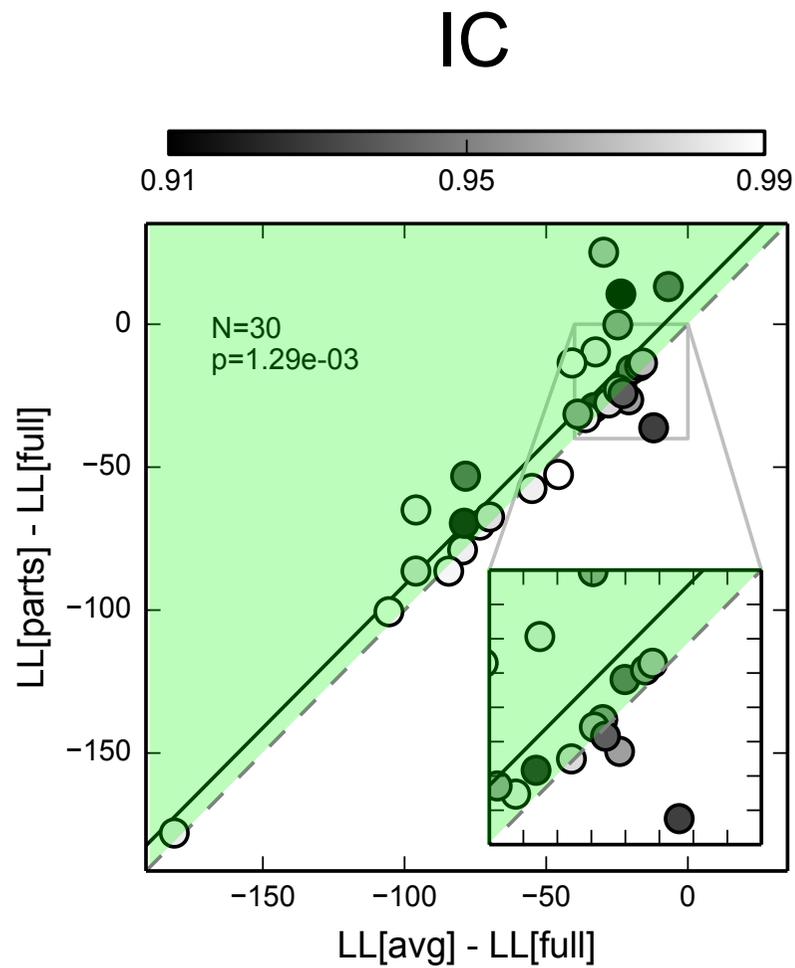
Inferior colliculus



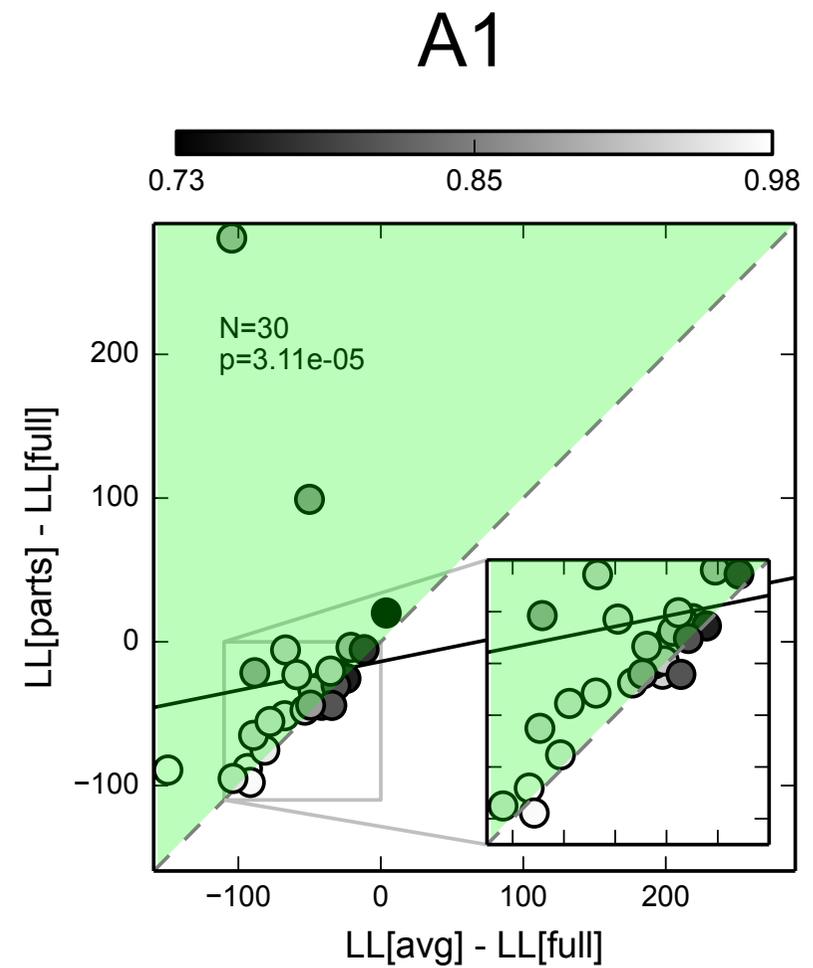
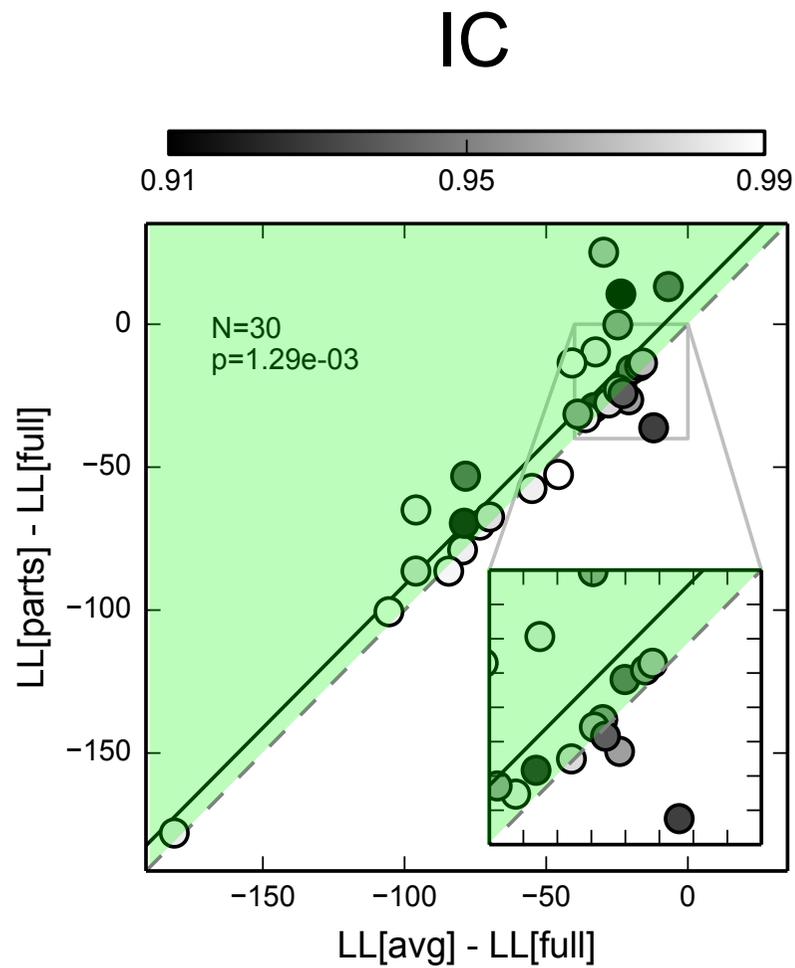
Auditory cortex



Likelihood evidence of static vs. adaptive STRF model

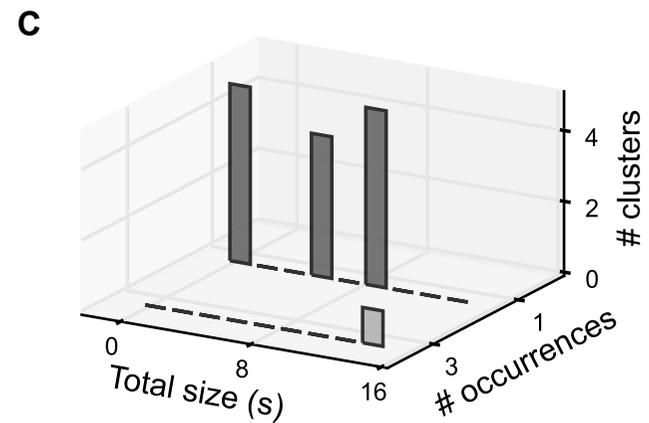
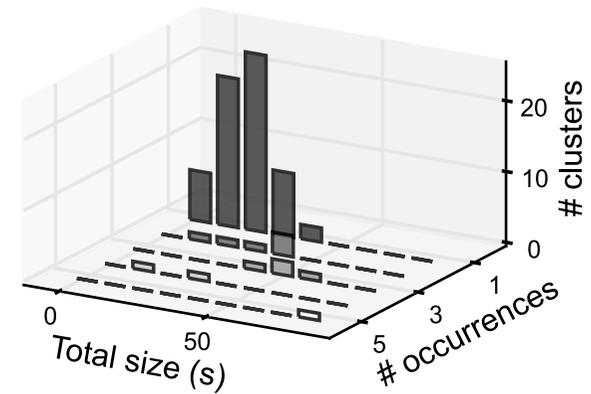
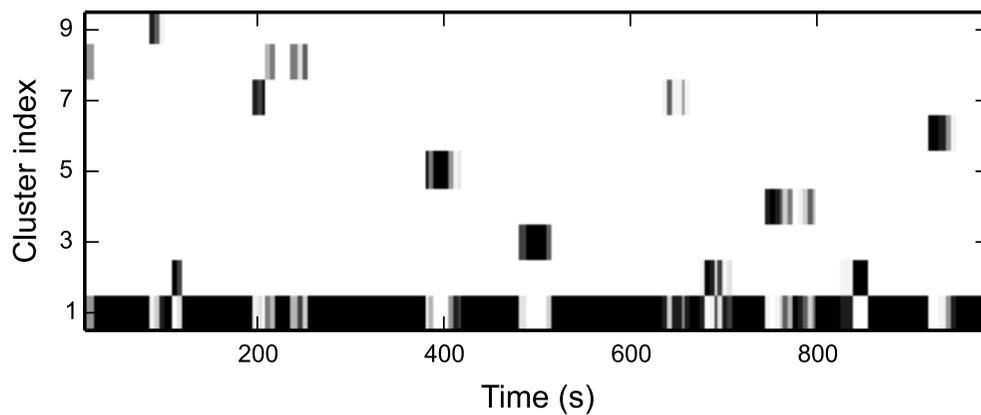
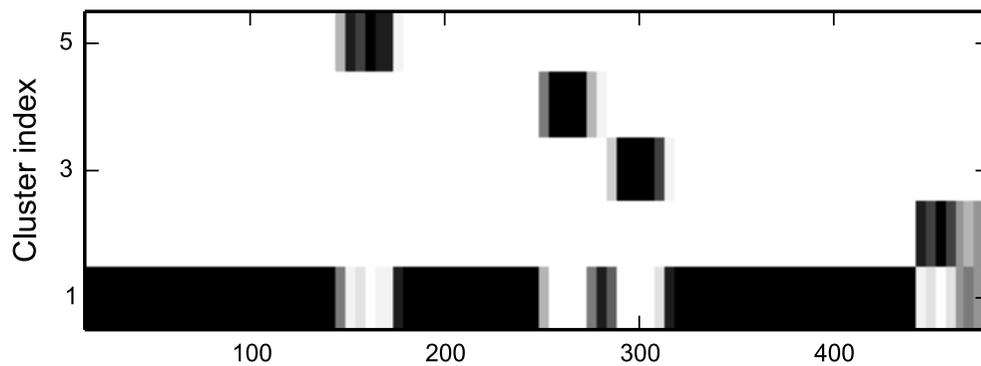


Likelihood evidence of static vs. adaptive STRF model



Cluster analysis: Do the neurons “revisit” discrete states?

Cluster analysis of two A1 units



Summary dynamic STRF model

- dynamic variability in STRF seems unrelated to spike count
- STRF variability higher in A1 than IC (shown quantitatively)
- quality of STRF variability:
 - parts of STRF change dynamically
 - even spectral BF changes in some cases
- dynamic STRF model supported by higher likelihood than static model
- Origin of fluctuations unclear. Randomly on timescale ~10s? Linked to stimuli?