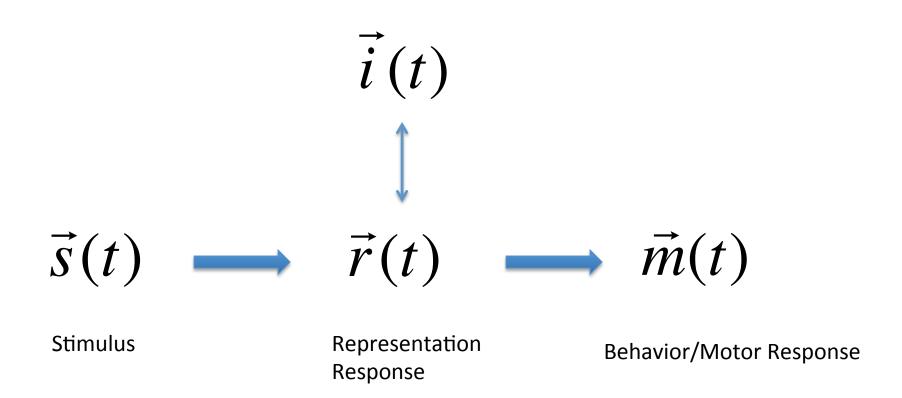
### **Neural Data Analysis**

#### Intro:

Sensory Coding and Computational Neurosciences.

Tutorial 1: Signal and Noise and Coherence

#### The Brain



Highly Dimensional, Dynamic, Recurrent, Multiple time scales,

**Stochastic** 

Dimensionality Reduction, Visualization (modeling)

#### Stochastic Response

 $\vec{r}(t)$  is characterized by a probability distribution

$$E[\vec{r}(t)] = \overline{\vec{r}(t)}$$
 is the expected value or the mean of this distribution

$$\vec{r}(t) \sim N(\vec{r}(t), n)$$

Normal distribution

$$\vec{r}(t) \sim P(\overline{\vec{r}(t)})$$

Poisson distribution

## Probability Distributions (Review) Normal Distribution – 1d

Average across trials

$$p(r(t)) = \frac{1}{\sqrt{2\pi n}} e^{-\frac{1}{2} \frac{(r(t) - \overline{r(t)})^2}{n^2}}$$
Average across trials and time

$$n^2 = \overline{n(t)^2}$$
 Average across trials and time Noise power

$$n = \sqrt{n^2}$$

# Probability Distributions (Review) Poisson Distribution

$$p(r(t)\Delta t = k) = \frac{(\overline{r}\Delta t)^k}{k!}e^{-(\overline{r}\Delta t)}$$

### Stimulus is also probabilistic...

$$\vec{S}(t)$$
 is characterized by a probability distribution

$$p(\vec{s}(t), \vec{r}(t))$$
 fully describes sensory coding

But i) curse of dimensionality and ii) no insight

#### 3 Approaches

Encoding

$$\overline{\overrightarrow{r}(t)} = f(\overrightarrow{s}(t)) \quad \text{Or} \quad \overrightarrow{s}(t) \xrightarrow{f} p(\overrightarrow{r}(t))$$

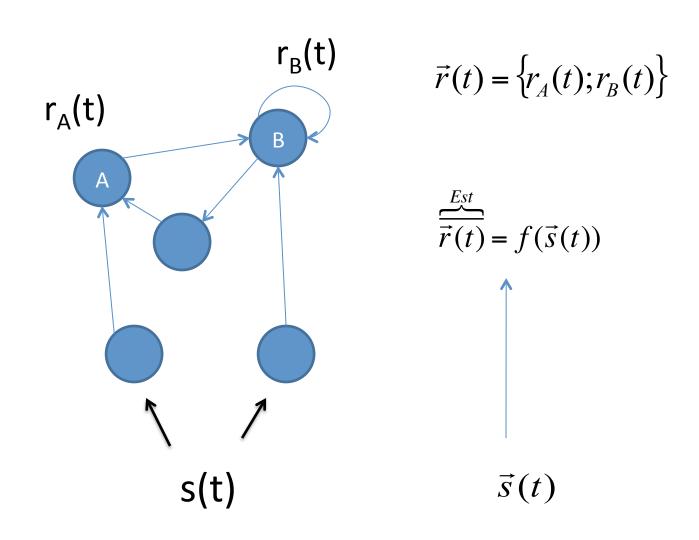
Decoding

$$\frac{\overrightarrow{st}}{\overrightarrow{s}(t)} = g(\overrightarrow{r}(t)) \qquad \text{Or} \quad \overrightarrow{r}(t) \xrightarrow{g} p(\overrightarrow{s}(t))$$

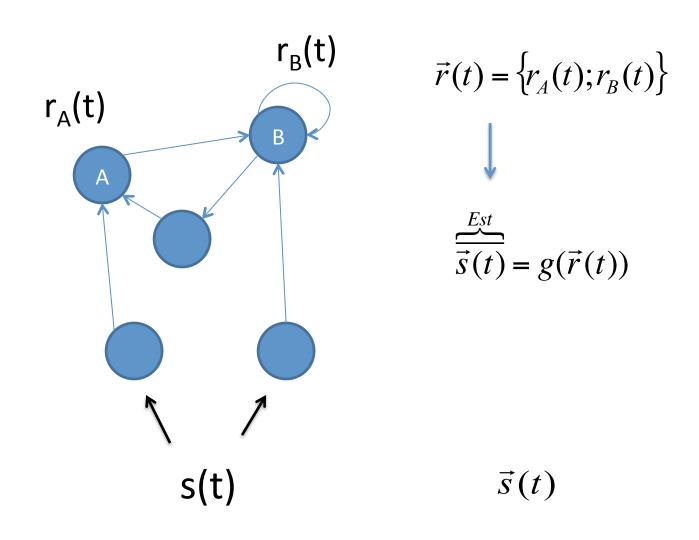
Information/Ceiling Values

$$I(S,R) = \iint p(\vec{s}(t), \vec{r}(t)) \log_2 \frac{p(\vec{s}(t), \vec{r}(t))}{p(\vec{s}(t))p(\vec{r}(t))}$$

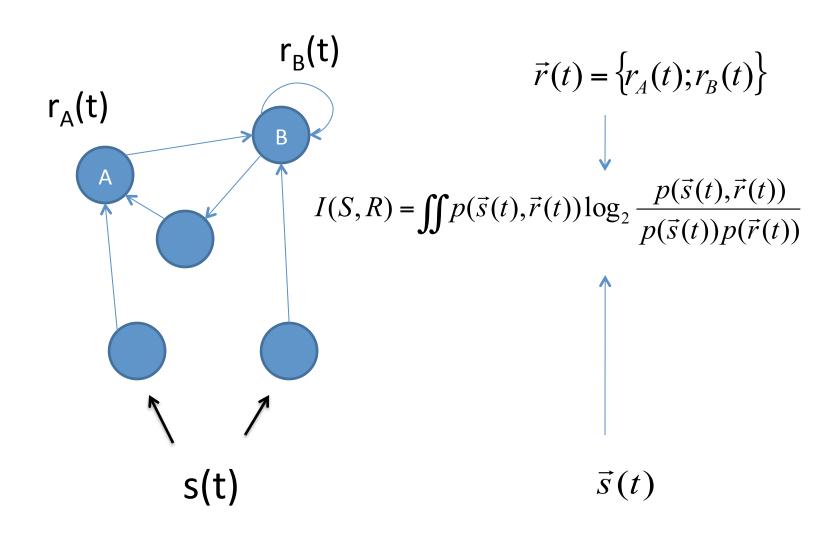
### Sensory Coding: Encoding



#### **Sensory Coding Decoding**



#### Sensory Coding: Mutual Info



#### 3 Approaches

Encoding

Starting this PM

$$\frac{\overrightarrow{r}(t)}{\overrightarrow{r}(t)} = f(\overrightarrow{s}(t)) \quad \text{Or} \quad \overrightarrow{s}(t) \xrightarrow{f} p(\overrightarrow{r}(t))$$

Decoding

$$\frac{\overrightarrow{\overline{s}t}}{\overrightarrow{\overline{s}(t)}} = g(\overrightarrow{r}(t)) \qquad \text{Or} \quad \overrightarrow{r}(t) \xrightarrow{g} p(\overrightarrow{s}(t))$$

Information/Ceiling Values

NOW

$$I(S,R) = \iint p(\vec{s}(t), \vec{r}(t)) \log_2 \frac{p(\vec{s}(t), \vec{r}(t))}{p(\vec{s}(t))p(\vec{r}(t))}$$

### Combining approaches...

Encoding Model Validation

$$I(f(s),r) \le I(s,r)$$

Neural Code

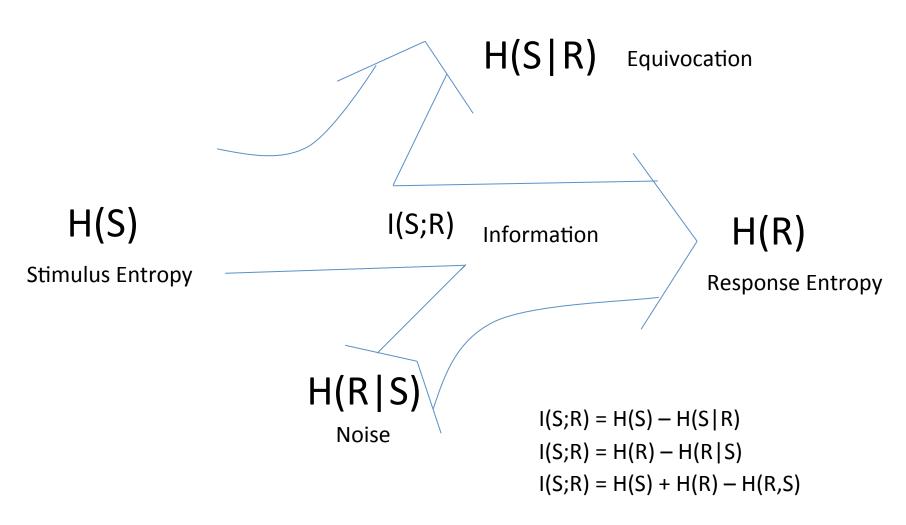
$$I(s, g_1(r)) \le I(s, r)$$

• Efficiency, Redundancy in ensemble responses

$$I(S,r)/H(r)$$
  $\frac{I(S;R_1,R_2,...,R_M)}{\sum_{m=1}^{M}I(S;R_m)}$ 

## Any signal out there??

### Information and Entropies



#### Information and Entropies

$$I(S;R) = H(S) - H(S|R)$$

$$I(S;R) = H(R) - H(R|S)$$

$$I(S;R) = H(S) + H(R) - H(R,S)$$

#### Entropy

- Uncertainty about source.
- Number of items of equal probability.
- Log 2 units or bits.

$$H(S) = \log_2(N)$$

$$H(S) = \sum_{i} p(s_i) \log_2\left(\frac{1}{p(s_i)}\right)$$

$$H(S) = \sum_{i} -p(s_i) \log_2(p(s_i))$$

#### Formulas for Information

$$I(S;R) = H(S) - H(S|R)$$

$$H(S) = \sum_{i} -p(s_i) \log_2(p(s_i))$$

$$H(S | R) = \sum_{j} p(r_{j}) \sum_{i} - p(s_{i} | r_{j}) \log_{2} (p(s_{i} | r_{j}))$$

$$I(S;R) = \sum_{i,j} p(s_i, r_j) \log_2 \left( \frac{p(s_i | r_j)}{p(s_i)} \right)$$

#### Formulas for Information

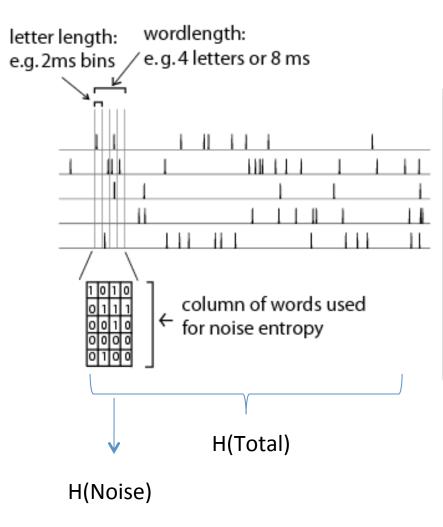
$$I(S;R) = H(S) - H(S|R) \longrightarrow I(S;R) = \sum_{i,j} p(s_i, r_j) \log_2 \left(\frac{p(s_i|r_j)}{p(s_i)}\right)$$

$$I(R;S) = H(R) - H(R|S) \longrightarrow I(S;R) = \sum_{i,j} p(s_i, r_j) \log_2 \left(\frac{p(r_j \mid s_i)}{p(r_j)}\right)$$

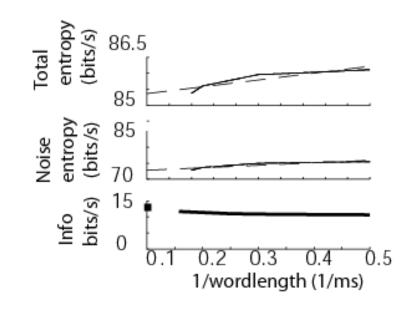
$$I(R;S) = H(S) + H(R) - \longrightarrow I(S;R) = \sum_{i,j} p(s_i, r_j) \log_2 \left( \frac{p(r_j, s_i)}{p(s_i)p(r_j)} \right)$$

$$H(R,S)$$

#### Direct Method for estimating MI



Total minus noise entropy from data
 Info extrapolated to infinite wordlength
 Entropy estimated from data
 Linear extrapolation to infinite wordlength



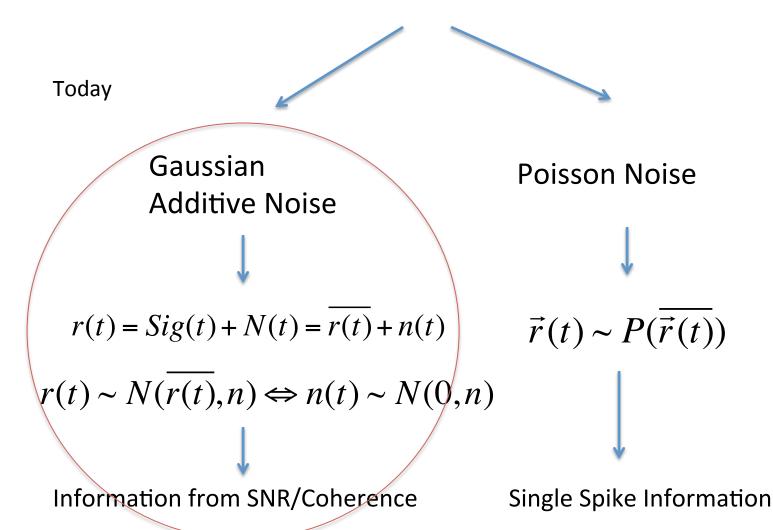
I=H(Total)-H(Noise)

$$I(s,r) = H(r) - H(r \mid s)$$

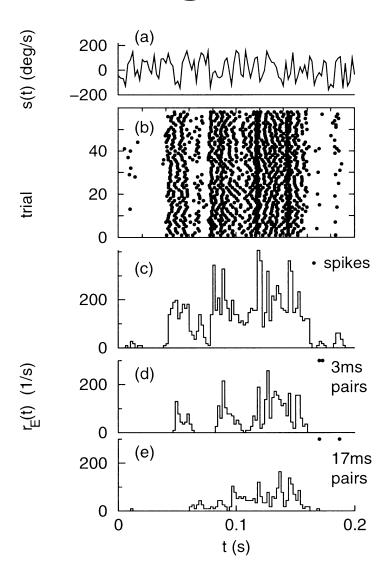
 $I_{LB}$ =64 bits/s  $\rightarrow$  I=75 bits/s

Strong et al. Phys Rev Letters 1998

#### Dimensionality Reduction for Information Calculation

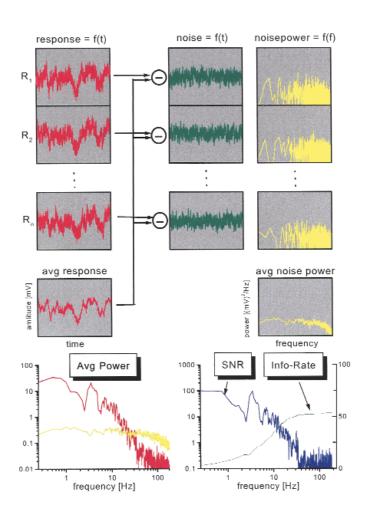


#### Single Event Information



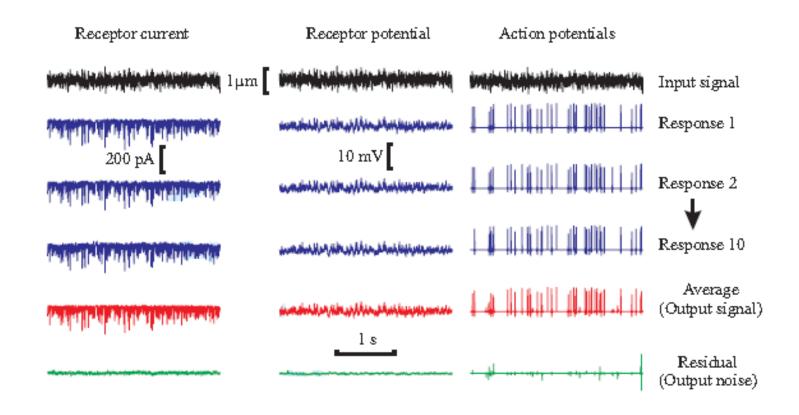
$$I(E,s) = \frac{1}{T} \int_{0}^{T} dt \left( \frac{r_{E}(t)}{\bar{r}_{E}} \right) \log_{2} \left( \frac{r_{E}(t)}{\bar{r}_{E}} \right)$$

### Getting the "signal" by averaging...



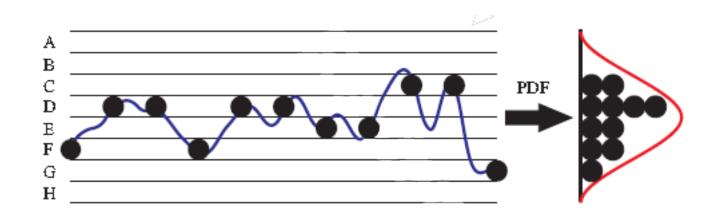
From Borst and Theunissen: Fly visual neurons

### Getting the signal by "averaging"



From Andrew French: Spider Mechanoreceptors

#### Is the noise Gaussian?



#### From SNR to Info

$$I = \int \log_2 \left( 1 + \frac{\left\langle Sig(f)^2 \right\rangle}{\left\langle N(f)^2 \right\rangle} \right) df$$

This is the Channel Capacity or Information Upper Bound.

It is an upper bound is Noise is Gaussian.

#### The coherency and the coherence

$$S_{xy}(f) = \langle \overline{x}(f)y(f) \rangle = FT \left\{ \frac{1}{T} \int_{0}^{T} \overline{x}(t)y(t+\tau)dt \right\}$$

$$\gamma(f) = \frac{S_{xy}(f)}{|S_{xx}(f)S_{yy}(f)|^{1/2}}$$

$$\gamma^{2}(f) = \frac{\left|S_{xy}(f)\right|^{2}}{\left|S_{xx}(f)S_{yy}(f)\right|}$$

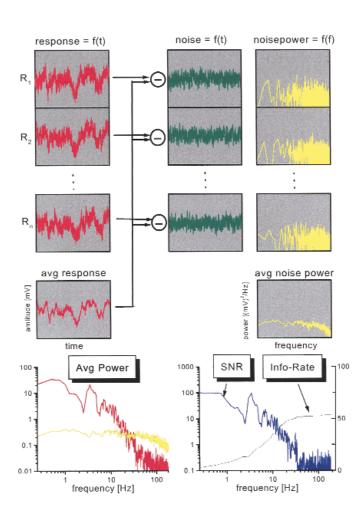
# The coherence between a signal and signal+ noise

$$\gamma_{s,s+n}^2 = \frac{\left\langle S^2(f) \right\rangle}{\left\langle S^2(f) \right\rangle + \left\langle N^2(f) \right\rangle}$$

$$\frac{S^2}{N^2} = \frac{\gamma^2}{1 - \gamma^2}$$

$$I = \int \log_2 \left( 1 + \frac{\left\langle S(f)^2 \right\rangle}{\left\langle N(f)^2 \right\rangle} \right) df = \int -\log_2 (1 - \gamma^2(f)) df$$

### From SNR to info capacity...



#### Signal Averaging

**Neural Responses are noisy** 

$$R^{2}(\omega) = Sig^{2}(\omega) + N^{2}(\omega)$$

An average response obtained from M trials is still noisy

$$\overline{R}_M^2(\omega) = Sig^2(\omega) + N^2(\omega) / M$$

Actual signal (S) is unknown and we are overestimating signal power...

## **Noise Estimation** (note here Sig=S)

• If we estimate noise with  $N_{ast} = R - R$ 

$$N_{est} = R - \bar{R}$$

$$N_{est}^2 = |S - S|^2 + |N(1 - \frac{1}{M})|^2 + \frac{M - 1}{M^2}|N|^2$$

We can recover the unbiased noise power by

$$N_{est}^2 = \frac{M-1}{M} |N|^2 \Longrightarrow |N|^2 = \frac{M}{M-1} N_{est}$$

We can recover the unbiased signal power by:

$$|S|^2 = |\bar{R}|^2 - \frac{|N|^2}{M} = |\bar{R}|^2 - \frac{N_{Est}}{M-1}$$

#### Validation

Solution: Compare the coherence function between a single spike train, R, and the actual rate, A, with the coherence function between a single spike train, R, and the predicted rate, B.

Coherence between R and A is estimated by resampling:

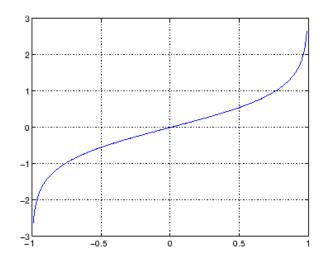
$$\frac{1}{\gamma_{AR}^2} - 1 = \frac{-M + M\sqrt{\left(\frac{1}{\gamma_{\overline{R}_{1,M/2}}^2 \overline{R}_{2,M/2}}\right)}}{2}$$
 Equation 8 in Hsu et al

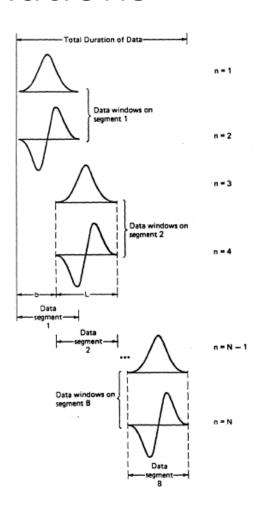
Coherence between R and B can be estimated from the coherence between the PSTH and B:

$$\frac{\gamma_{BR}^{2}}{\gamma_{B\overline{R}}^{2}} = \frac{\gamma_{AR}^{2}}{\gamma_{A\overline{R}}^{2}} = \frac{1 + \sqrt{\left(\frac{1}{\gamma_{\overline{R}_{1,M/2}\overline{R}_{2,M/2}}}\right)}}{-M + M\sqrt{\left(\frac{1}{\gamma_{\overline{R}_{1,M/2}\overline{R}_{2,M/2}}}\right)} + 2}$$
 Equation 11 in Hsu et al

# Jack-knifing, Multi-taper methods, Data Transformations

$$p_i = N \vartheta_{All} - (N-1) \vartheta_{\hat{i}}$$





## How about methods for non-Gaussian noise?

- Spike trains can be modeled as nonhomogeneous Poisson or Gamma Processes.
- Time-rescaling can be used to assess order of Gamma model.
- Information rates can be calculated numerically.
- Direct Information Theoretic Measures.
- Robert Kass' Lectures

#### Maximum Entropy Rate for Spikes

$$E \approx \bar{r} \log_2 \left(\frac{e}{\bar{r}\Delta t}\right)$$

$$\bar{r}\Delta t << 1$$

From Spikes (Rieke et al.) Ch 3.

#### Reducing the dimensions...

Encoding Analysis

$$\frac{\overrightarrow{r}(t)}{\overrightarrow{r}(t)} = f(\overrightarrow{s}(t)) \Rightarrow \frac{\overrightarrow{r}(t)}{\overrightarrow{r}(t)} = f_{Static}(\overrightarrow{h} \cdot \overrightarrow{\phi}(\overrightarrow{s}(t))) \Rightarrow \frac{\overrightarrow{r}(t)}{\overrightarrow{r}(t)} = \overrightarrow{h} \cdot \overrightarrow{s}(t)$$

Mutual information

$$I(s,r) = H(r) - H(r \mid s)$$



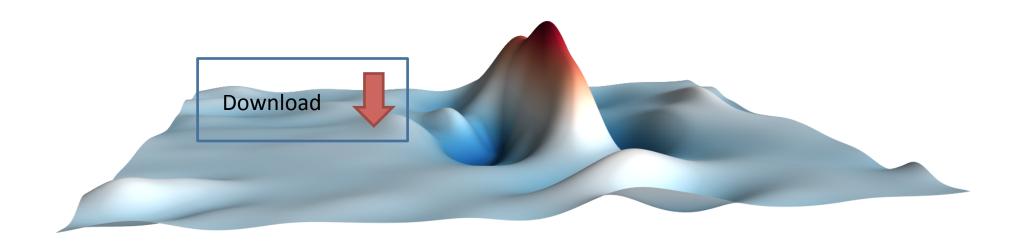
Gaussian Channel Single Spike

Extrapolation (Direct)

- + Bounds
- + Methods for estimating H

#### Tutorials inspired by STRFLab

STRFPAK 5.3 STRFLab 1.0



http://strflab.berkeley.edu

#### Key References

- **Direct Estimation**: Strong, S. P., R. Koberle, R. de Ruyter van Steveninck and W. Bialek (1998). "Entropy and information in neural spike trains." Phys Rev Letters **80**(1): 197-200.
- *Single Spike Information*: Brenner, N., S. P. Strong, R. Koberle, W. Bialek and R. R. de Ruyter van Steveninck (2000). "Synergy in a neural code." <u>Neural Comput</u> **12**(7): 1531-1552.
- Review+Gaussian Channel Information: Borst, A. and F. E. Theunissen (1999). "Information theory and neural coding." Nat Neurosci 2(11): 947-957.
- Gaussian Channel, Coherence and Model Validation: Hsu, A., A. Borst and F. E. Theunissen (2004). "Quantifying variability in neural responses and its application for the validation of model predictions." Network 15(2): 91-109.

### Assignment

• coherence\_tutorial.m