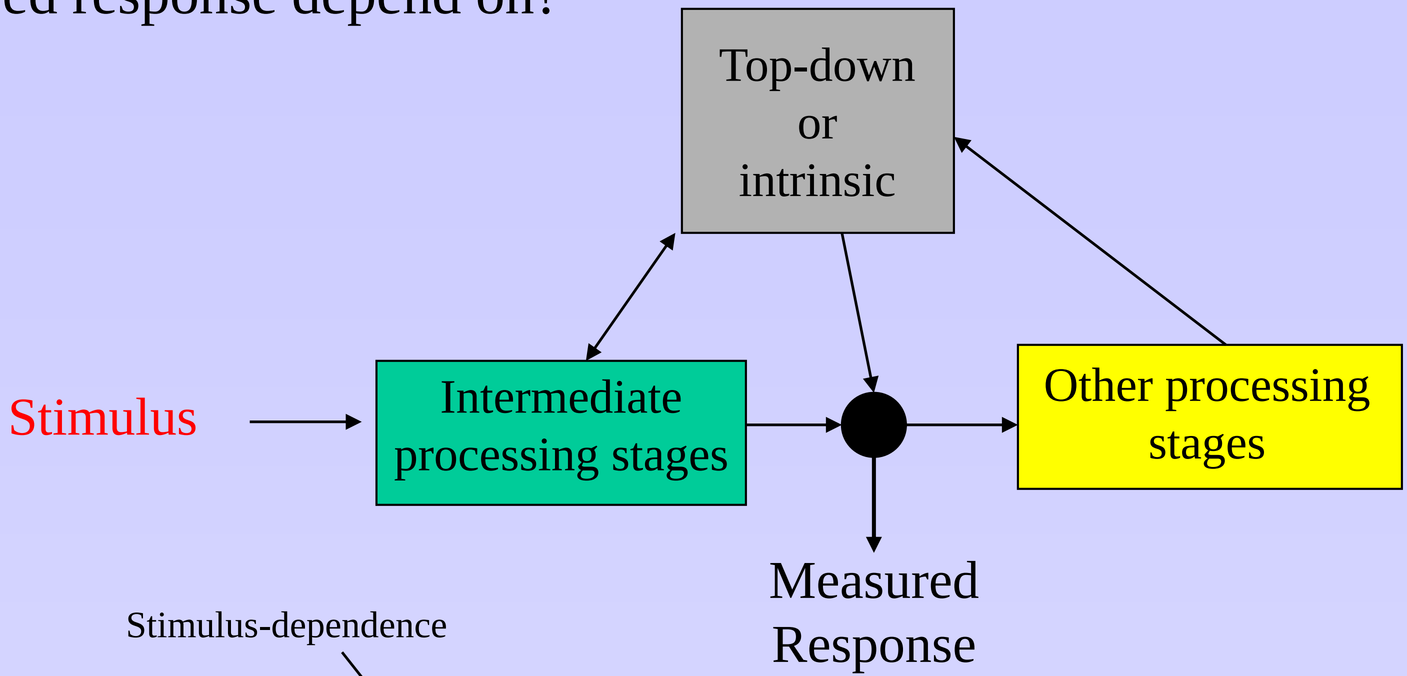
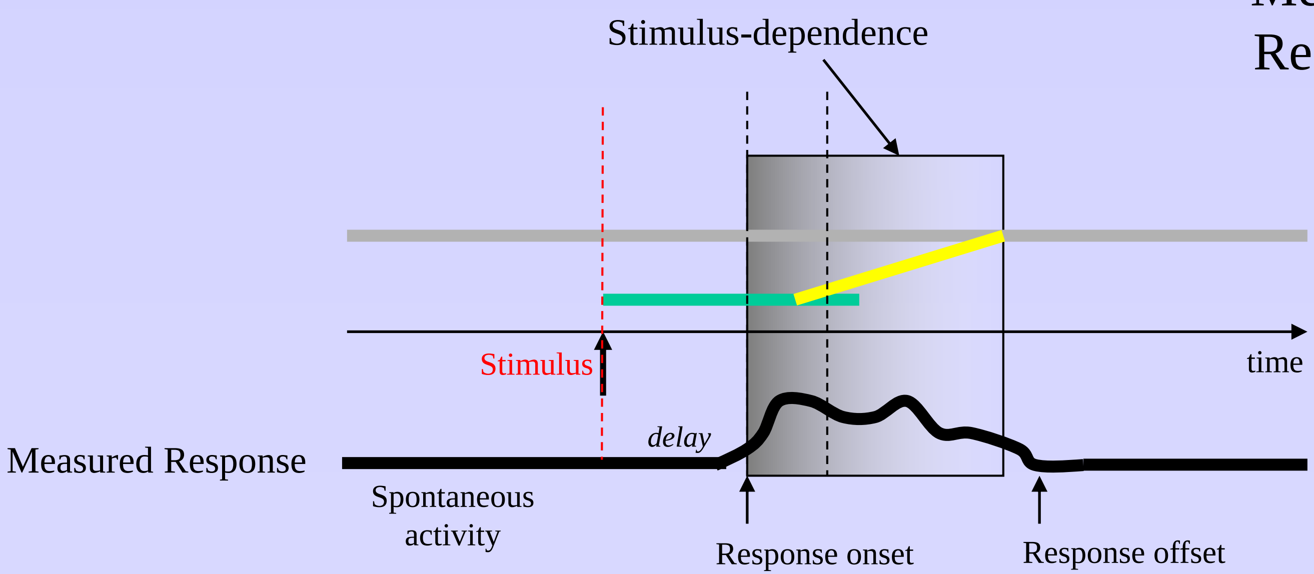
Reverse Correlation

Discriminability

Stimulus-dependence

What does a measured response depend on?



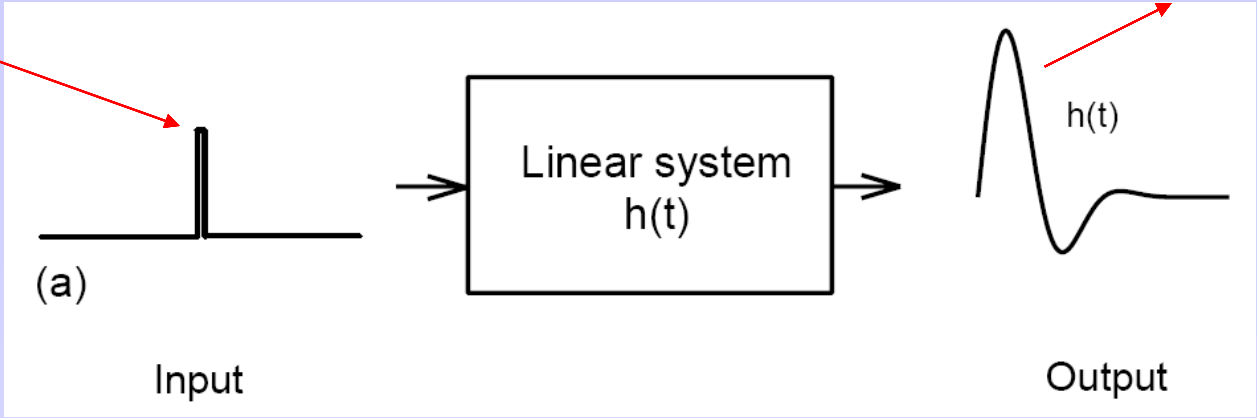


1st order approximation: linear response

- In the area of stimulus dependence, the (sensory) neuron can be understood as a ‘linear transducer’.
- For a single impulse:

Impulse

Impulse response

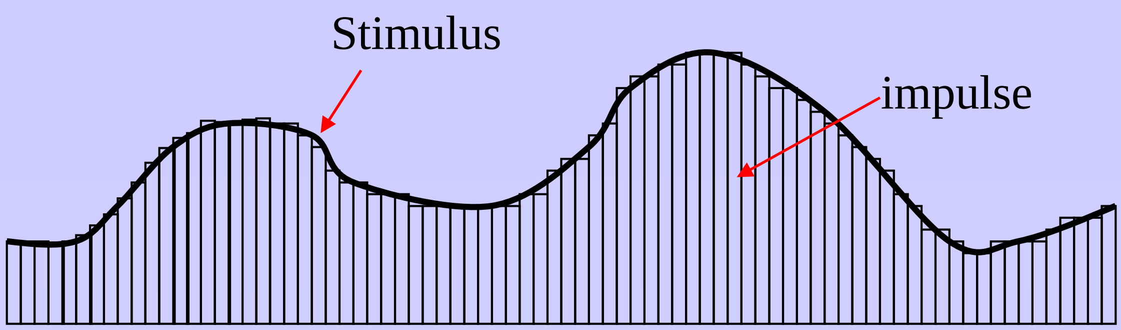


(Ringach Shapley, 2004)

- linearity ➔ 1) $\alpha \times$ input → $\alpha \times$ output
2) input1 + input2 → output1+ output2

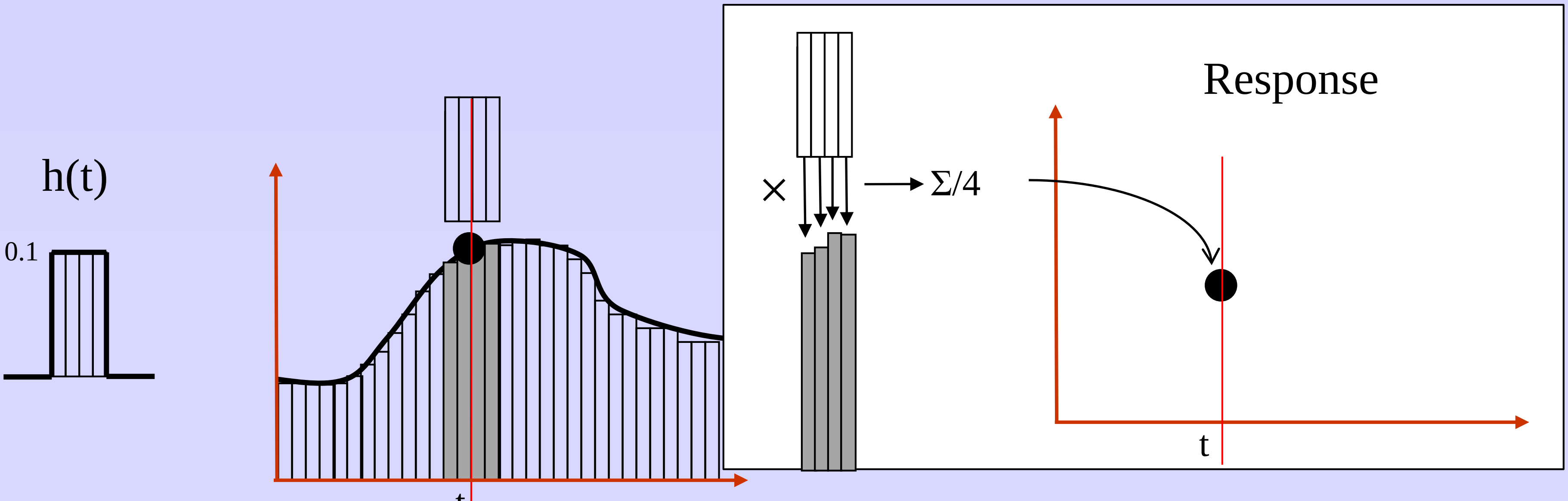
Linear Response

- Any stimulus can be decomposed into a sum of impulses (discretization)



-The response to a stimulus is equivalent to the sum of the individual impulse responses.

- May be the isolated impulse is not a good way to capture the stimulus… What is the response to a 'function of impulses', h()?



Convolution

- Convolution of the stimulus S with a kernel h

$$R(t)=S(t) * h(t)$$

Kernel

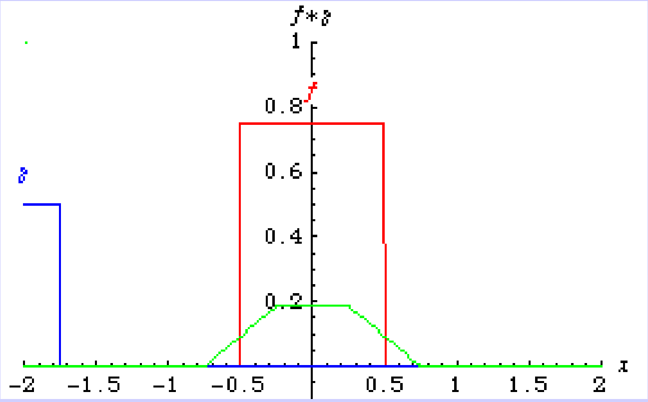
Mathematically:

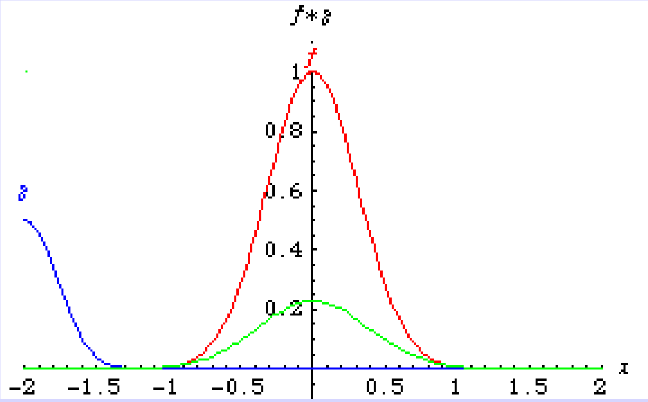
$$S(t)*h(t)=\int_{-\infty}^{+\infty} S(\tau)h(t-\tau)d\tau$$

Practically:

$$S(t) * h(t) = FFT^{-1}(FFT(S) \times FFT(h))$$

FFT=Fast Fourier Transform



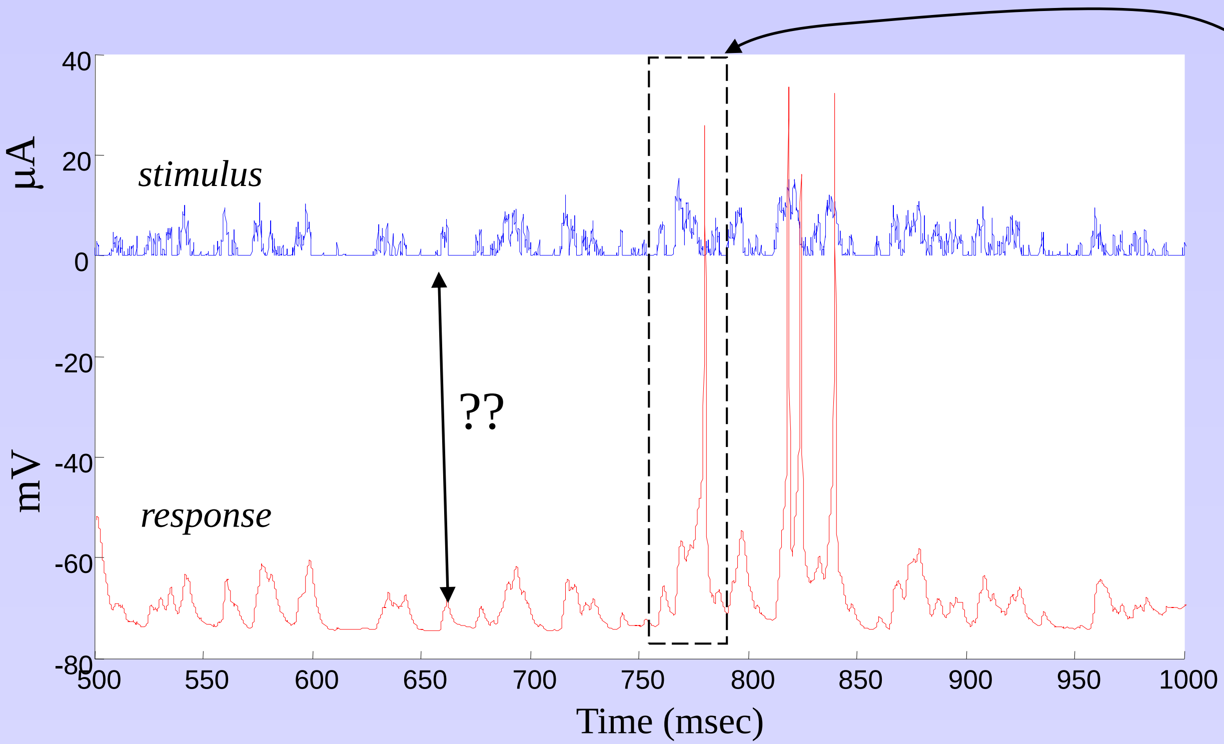


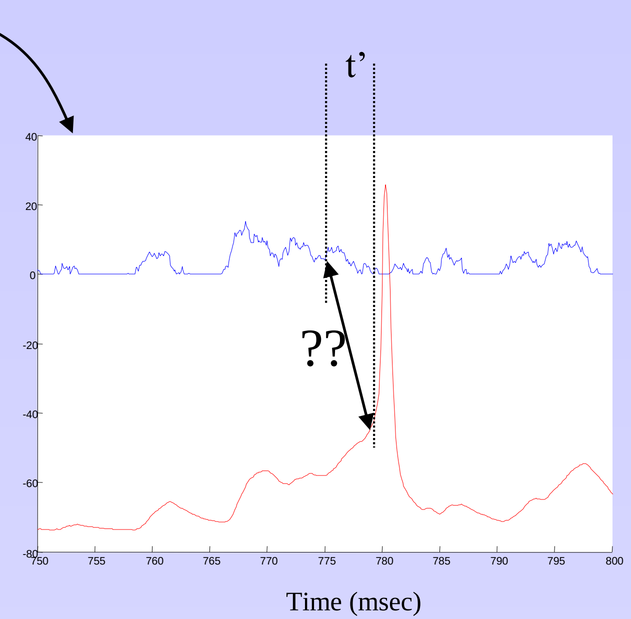
- **Knowing h()** for a particular neuron:

➔ The response R can be predicted for <u>any</u> stimulus S

Reverse Correlation

- What is h(t)? ← → How does the response depends on the stimulus?
- How much does the response of a neuron depends on the stimulus, t' seconds after the stimulus occurred?





t' = 'lag'

$$\langle S(t)R(t+t')\rangle = C(t')$$

➔ C(u)= stimulus-response cross-correlation function

Reverse Correlation

$$\langle S(t)R(t+t')\rangle = C(t')$$

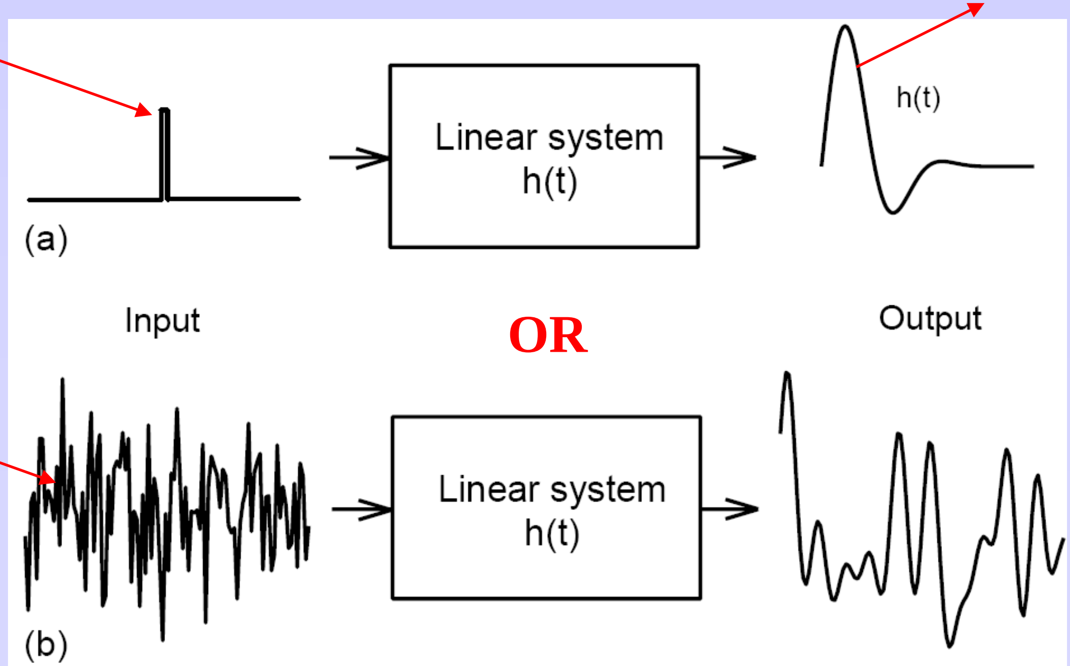
- note: If S(t) is true white noise, then C(t) = h(t) =impulse response.

→ A second (easy) way to estimate h(t)!

Impulse

Impulse response = **h(t)**

White noise



(Ringach Shapley, 2004)

h(t)=CrossCorrelation: <input, output>

Reverse Correlation

Fact: How much does the response of a neuron depend on the stimulus, t' seconds *after* the stimulus occurred? $\langle S(t)R(t+t')\rangle = C(t')$

⟵ (time-invariant) ⟶

How much does the response of a neuron depend on the stimulus t' seconds *before* the response?

$$\langle S(t-t')R(t)\rangle = C(t')$$

⟶ **Reverse** correlation

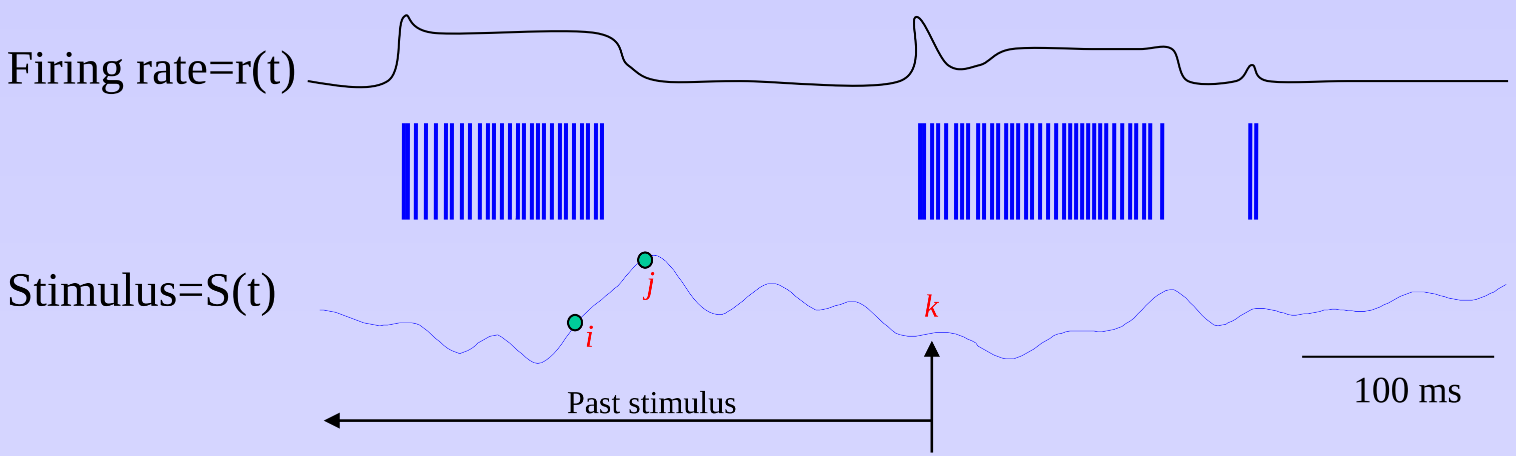
- In most cases, R is discrete (0 or 1 = spike). Reverse correlation need only be calculated when the cell spikes.

⟶ C(t')=stimulus **S**pike**T**triggered**A**verage

- In most other cases, R(t) is the firing rate

Predicting the firing rate

- Understand the response: Linear Vs Non linear
- Knowing the stimulus, can we estimate the firing rate (= response)?
    - method1: Build a model of the neuron (highly non linear)
    - method2: Get responses, and ‘infer’ the stimulus-response relationship



Firing rate estimate R(t) of r(t) ?

(Assumption: R(t) only depends on the past stimulus)

R(t)=f(S(t))

$$R_k = a_0^k + \sum_i a_i^k S_i + \sum_i \sum_j a_i^k a_j^k S_i S_j + \cdots$$

i,j = ‘distances’ in the past

Predicting the firing rate

$$R_k = a_0^k + \sum_i a_i^k S_i + \sum_i \sum_j a_i^k a_j^k S_i S_j + \cdots$$

With the constraint: ‘R depends only on the *past* stimulus’

→ $S_i = S(t - i.dt)$ with i in [0 ∞]. Since t continuous → use the integral

→ Volterra expansion

$$R(t) = R_0 + \int_0^\infty D(\tau) S(t-\tau) d\tau + \int_0^\infty D_2(\tau_1, \tau_2) S(t-\tau_1) S(t-\tau_2) d\tau_1 d\tau_2 + \cdots$$

- Assume that the firing rate at t depends *linearly* on the stimulus at times < t

a.k.a: 1st Wiener Kernel

$$R(t) = R_o + \int_0^\infty D(\tau) S(t-\tau) d\tau$$

Predicting the firing rate

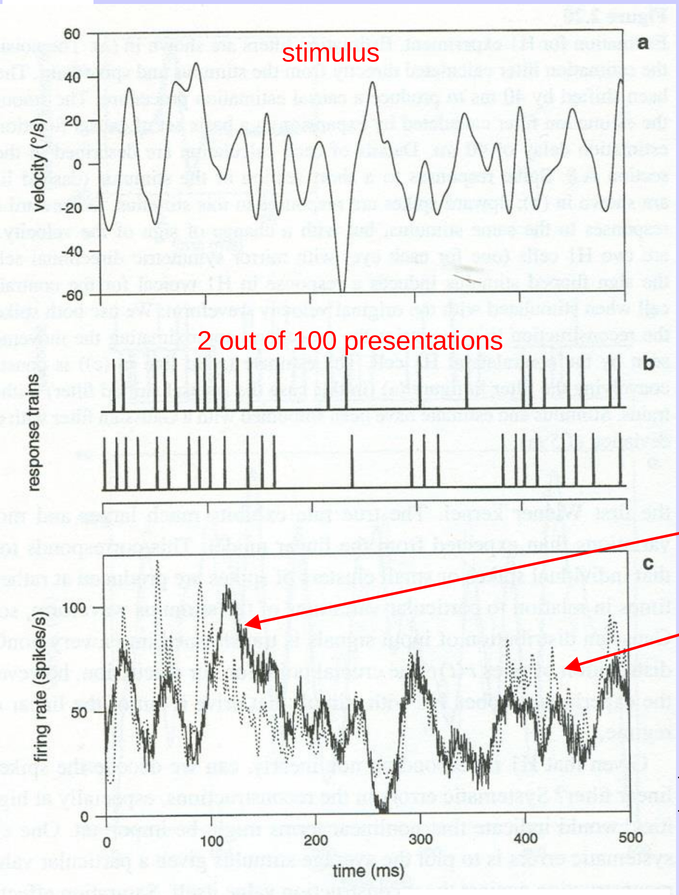
- Fact: For white noise stimulus:

$$D(\tau) = \frac{\mu . C(\tau)}{\sigma_S^2}$$

Where C() is the **spike triggered average**

$$R(t) = R_o + \int_0^\infty D(\tau) S(t-\tau) d\tau$$

H1



(Rieke et al 1997)

Predicted

Actual

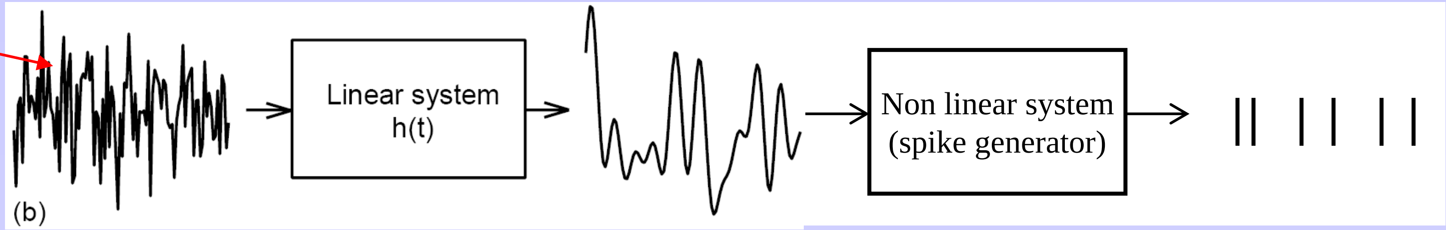
→ Slow fluctuations only…

Discrepancy ➔ How much non-linearity exist in the data

From temporal to Spatio-temporal domains

- Temporal domain (e.g. audition)

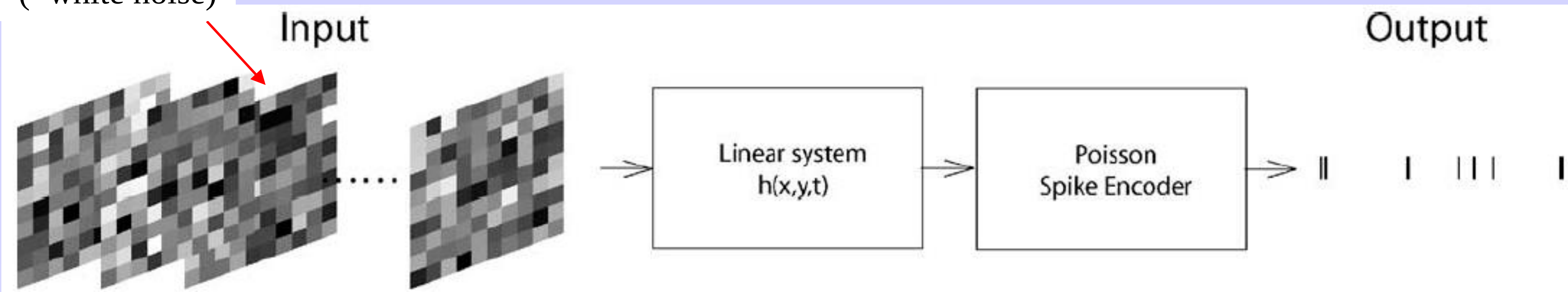
White noise



Auditory cell

- Spatio-Temporal (e.g. vision, place cells?)

m-sequence
(~white noise)



(Ringach Shapley, 2004)

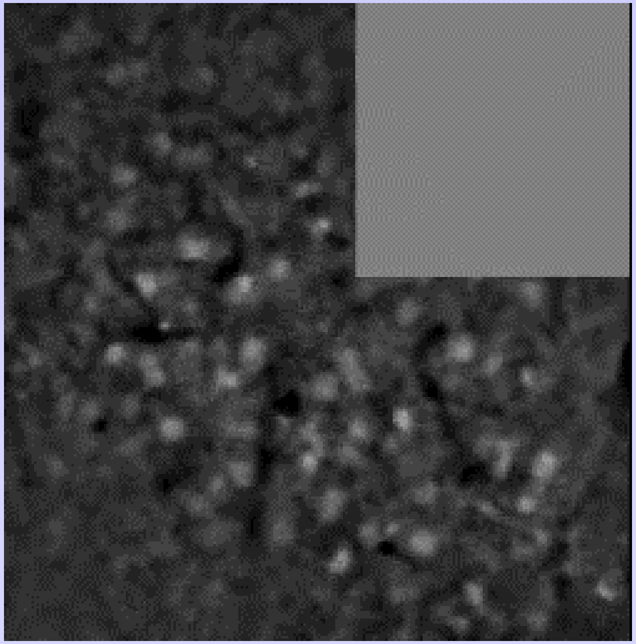
V1 cell

- Useful when nothing is known a priori about the response properties of the cell.

V1: Oriented responses

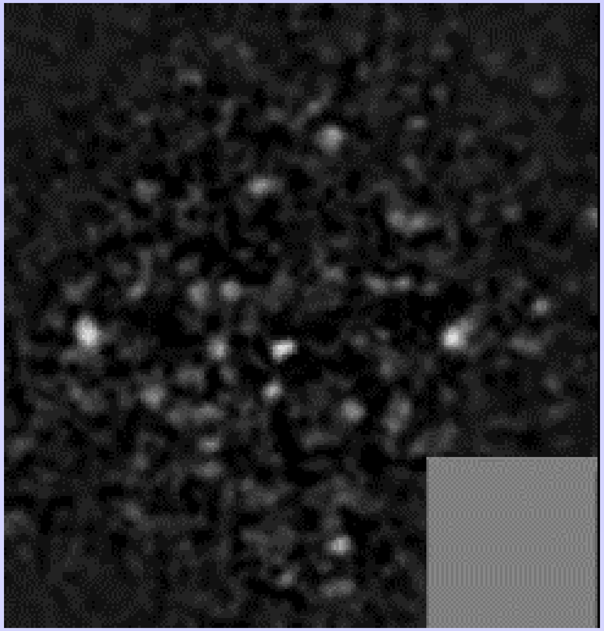
- Basic fact: V1 responses are selective to Orientation
- In vivo imaging. Area: 300 x 300 μm. Calcium sensitive indicator

Cat V1



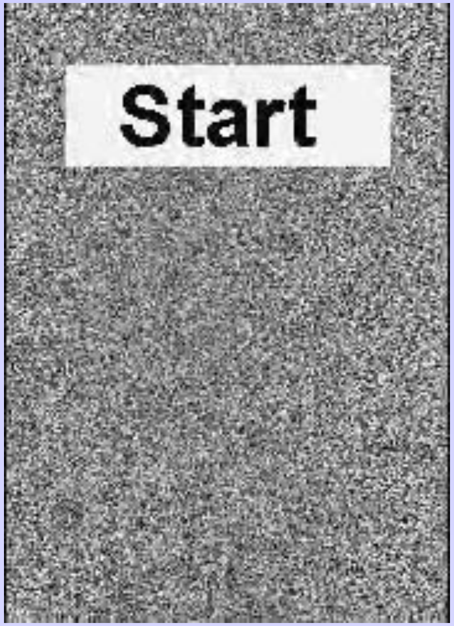
Vs.

Rat V1



(K. Ohki, S. Chung, Y. Ch'ng, P. Kara, R.C. Reid)

Cat V1



Orientation map

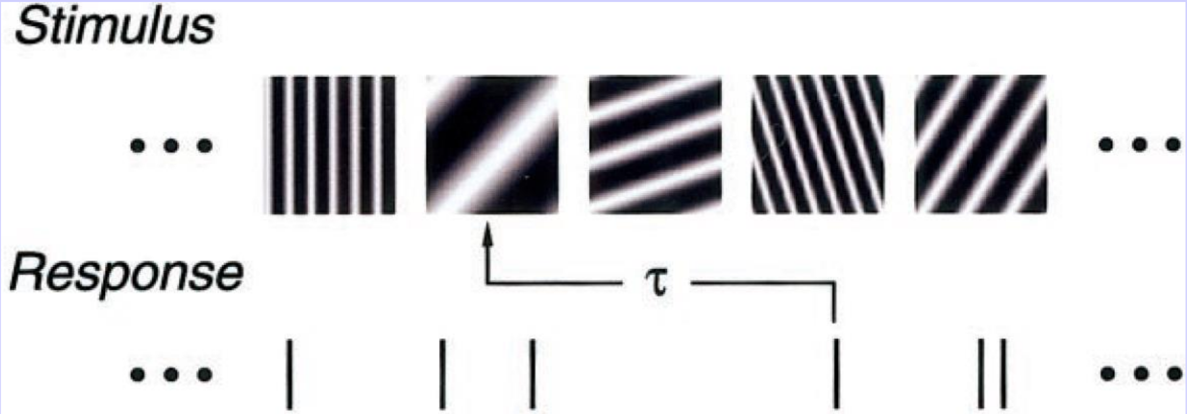
- Can the spatio-temporal impulse function of V1 cell ‘explain’/’predict’ their orientation preference?

Subspace reverse correlation

- Using a priori knowledge about 'preferred stimuli'

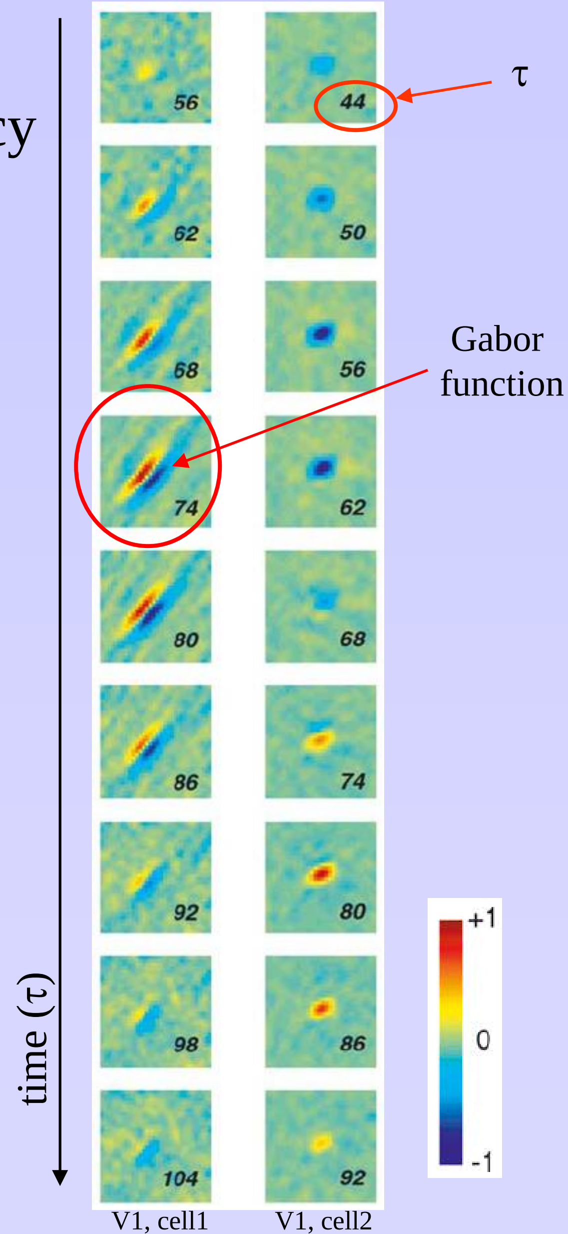
→ Hartley basis functions: Orientation, spatial frequency

→ Fast determination of impulse response function



(Ringach Shapley, 2004)

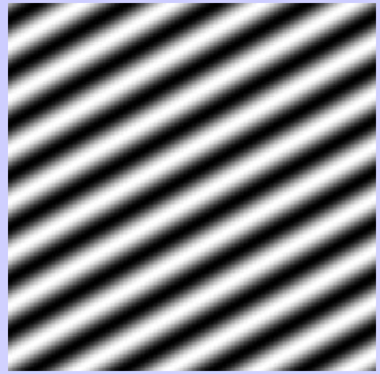
Impulse response h(x,y,t)



Gabor Kernel

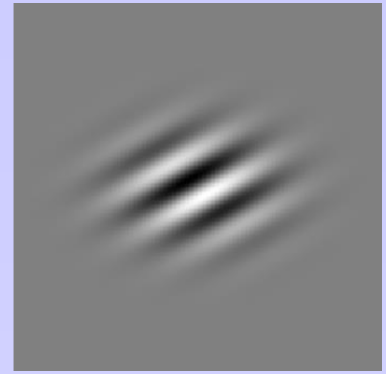
gaussian

X



Oriented sine wave
Spatial frequency

=



Gabor wavelet

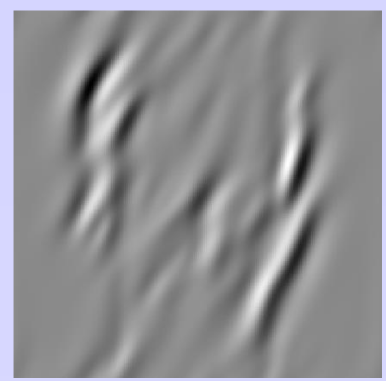
convolution!

Stimulus

*

V1 impulse function

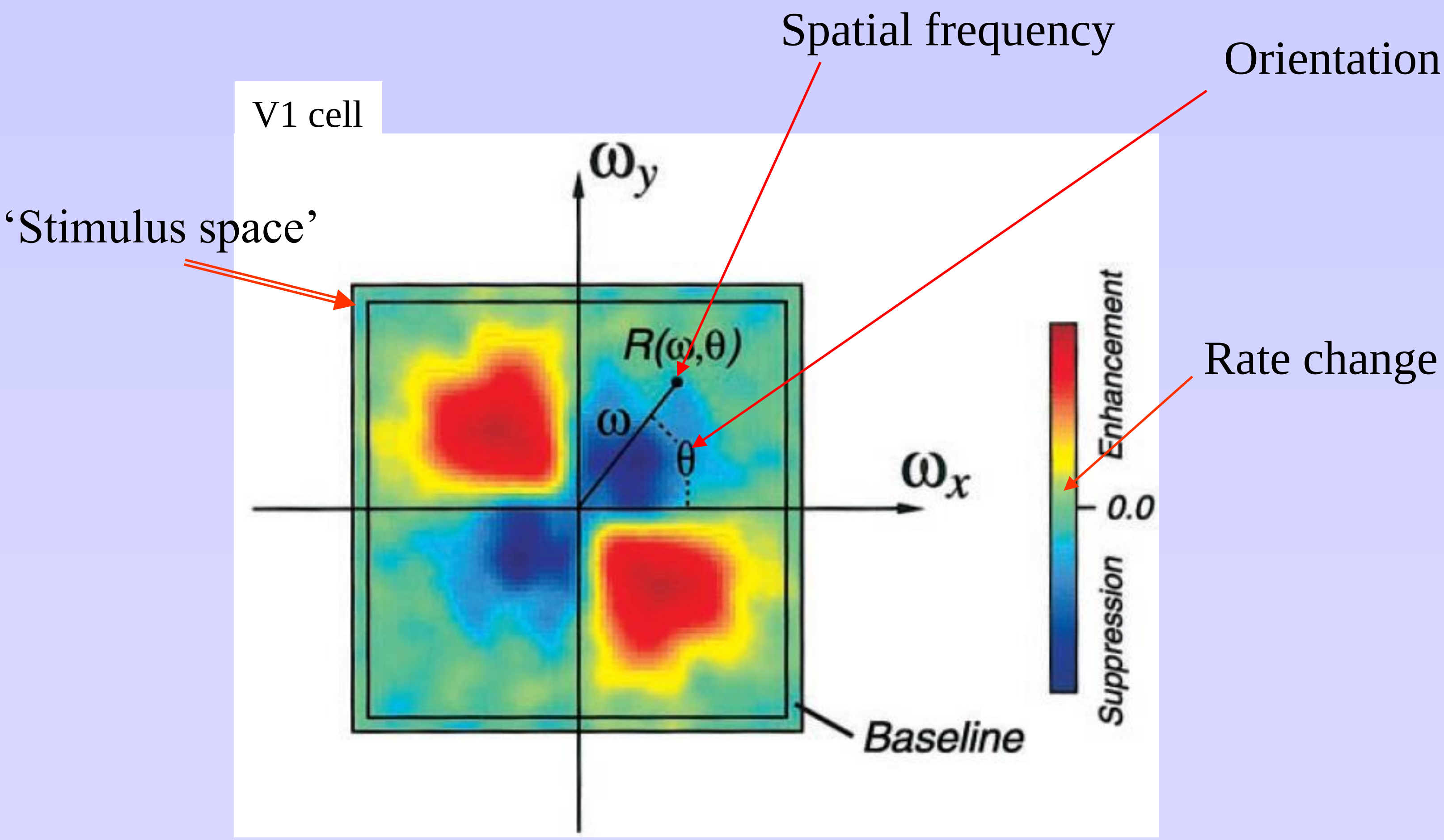
=



V1 estimated firing rate

Subspace reverse correlation

- Parametrized stimulus space: Orientation -- Spatial Frequency
- Probability of observing a specific (ω,θ) pair, 50 ms before a spike:



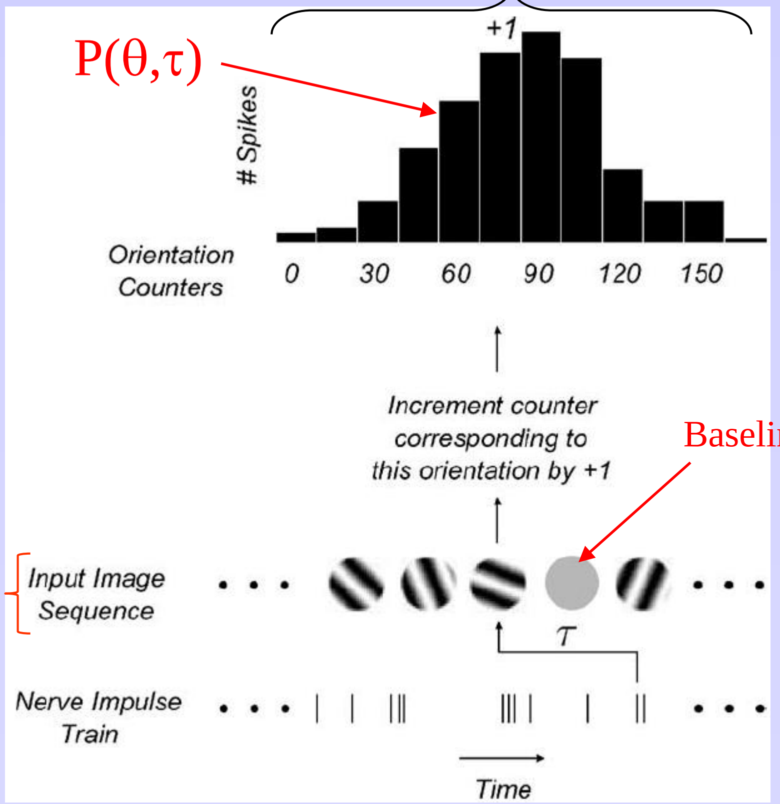
(Ringach and Shapley, 2004)

Subspace reverse correlation

- Tuning curve and modulation depth

$$R(\theta,\tau) = \log\left(\frac{p(\theta,\tau)}{p(Blank,\tau)}\right)$$

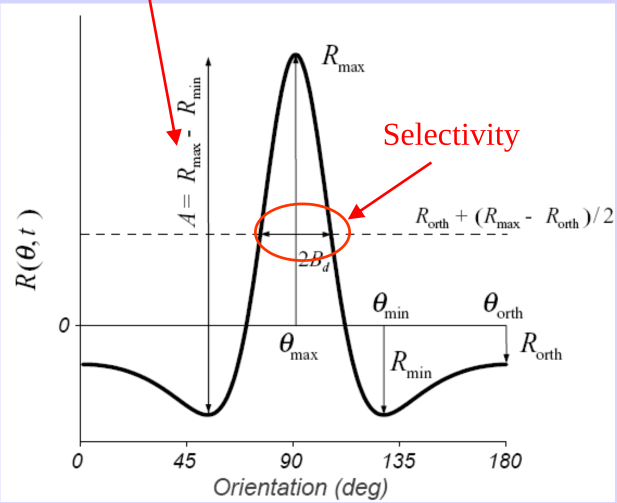
For each τ



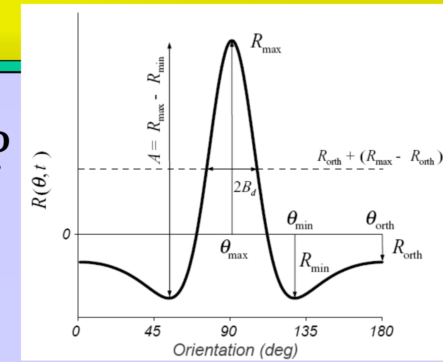
(Ringach and Shapley, 2004)

Tuning Curve

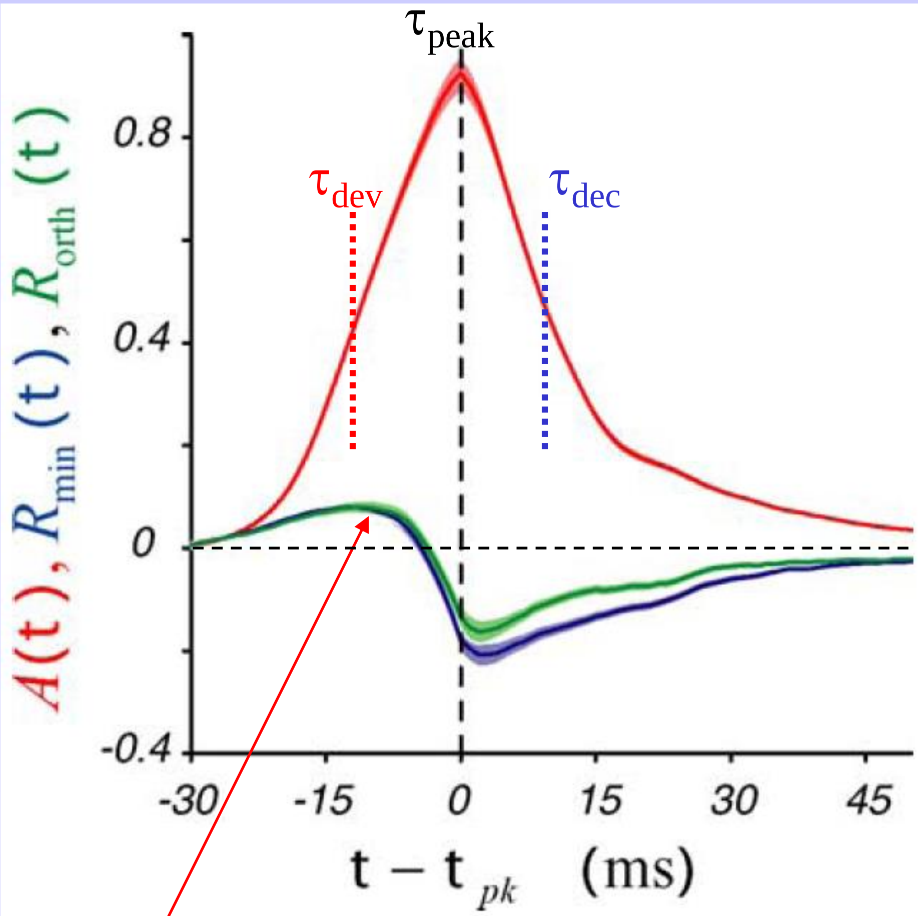
Modulation depth A(τ)



Subspace reverse correlation



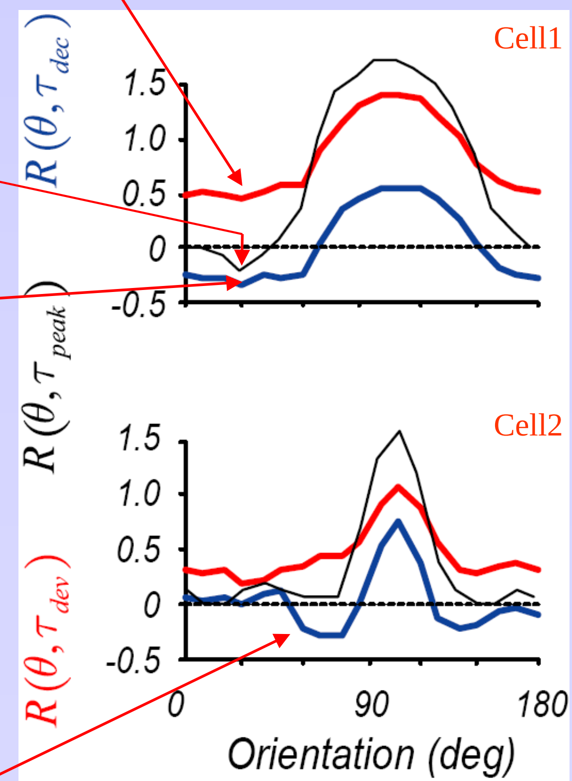
- Time evolution of orientation selectivity: What do we learn?



1) Initial
global 'excitation'
(i.e. feedforward signal)

2) Inhibition of non-preferred orientations

3) Late
global inhibition



R_{min} >0: V1 cells respond to all orientations
early after the stimulus

3') Late
Tuned/specific inhibition

Where are we?

- General introduction:
  - Neurons and synapses; Basic neuroanatomy; Basic neurophysiology; (action potential, E/IPSPs, integration); Methods in brain Research.

- General Issues in Neural Data Analyses
  - Quantitative Vs Qualitative Analyses; Breadth-first Vs Depth-first Analyses; Data Representations.

- Surrogate Datasets
  - Simulation data (NEURON models); Point processes; Refractory period and stationarity; Distribution of ISIs (Gaussian, Poisson, Gamma); Comparing Neural responses.

- Spontaneous activity: membrane potential, FR, CV/2, ISI return maps, FF.

- Stimulus-dependent activity: ex. Vision (RGC-LGN-V1, and H1) FF, STA, PSTH.

Where are we?

- Estimate the neuron response, given a stimulus. The impulse response h(t).

- Case of discrete response: use STA, case of continuous response use Wiener kernel/linear approximation. If white noise stimulus, use STA.

- Example of V1 (Ringach & Shapley, 2004). h(x,y,t) by subspace reverse correlation. Gabor kernel. Use h(t) to study the orientation selectivity of V1 cells, and its time course.

- Next: Example of V1 (Usrey, Sceniak and Chapman, 2003)

h(x,y,t) → $\langle h() \rangle_{x,y}$ Impulse response

h(x,y,t) → $\langle h() \rangle_{t}$ Receptive field