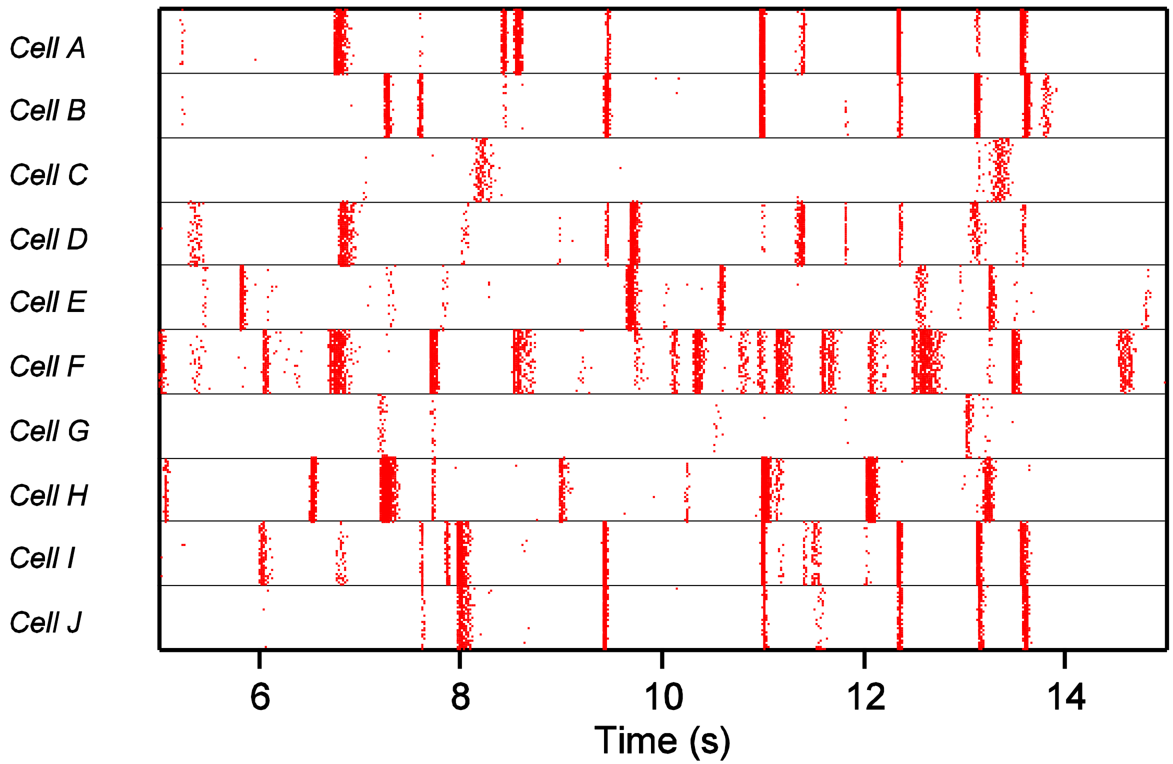
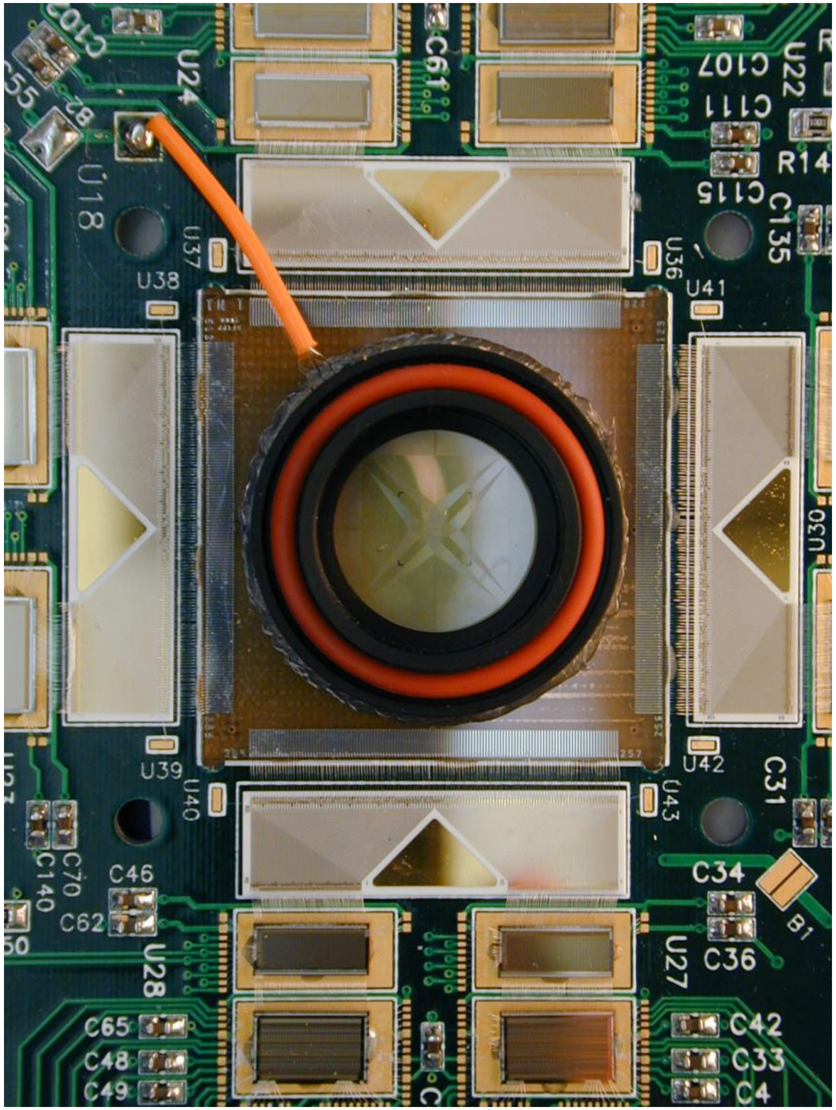
What *is* the neural code?

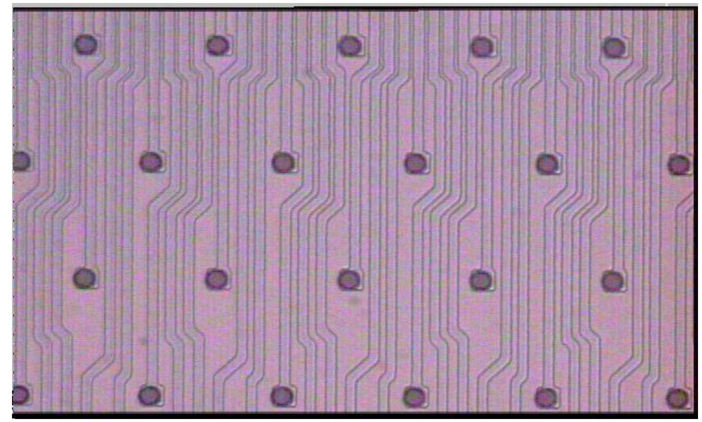
Sekuler lab, Brandeis

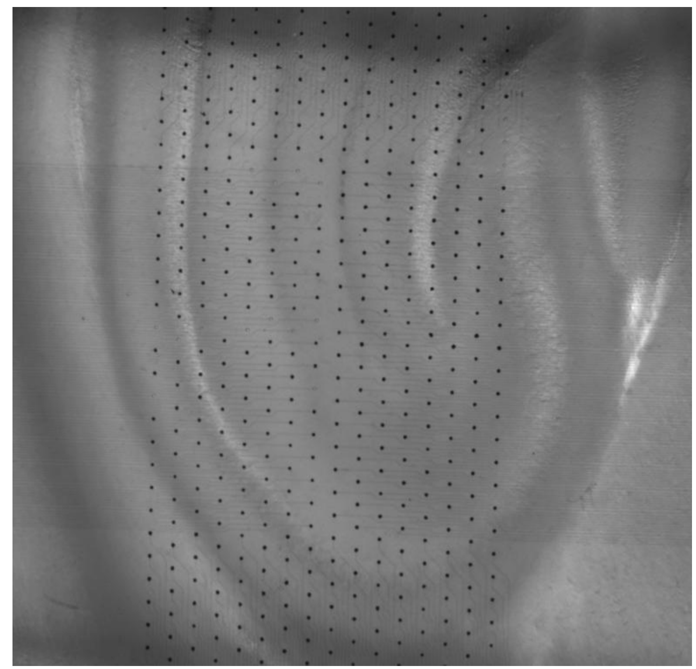
What *is* the neural code?



What *is* the neural code?



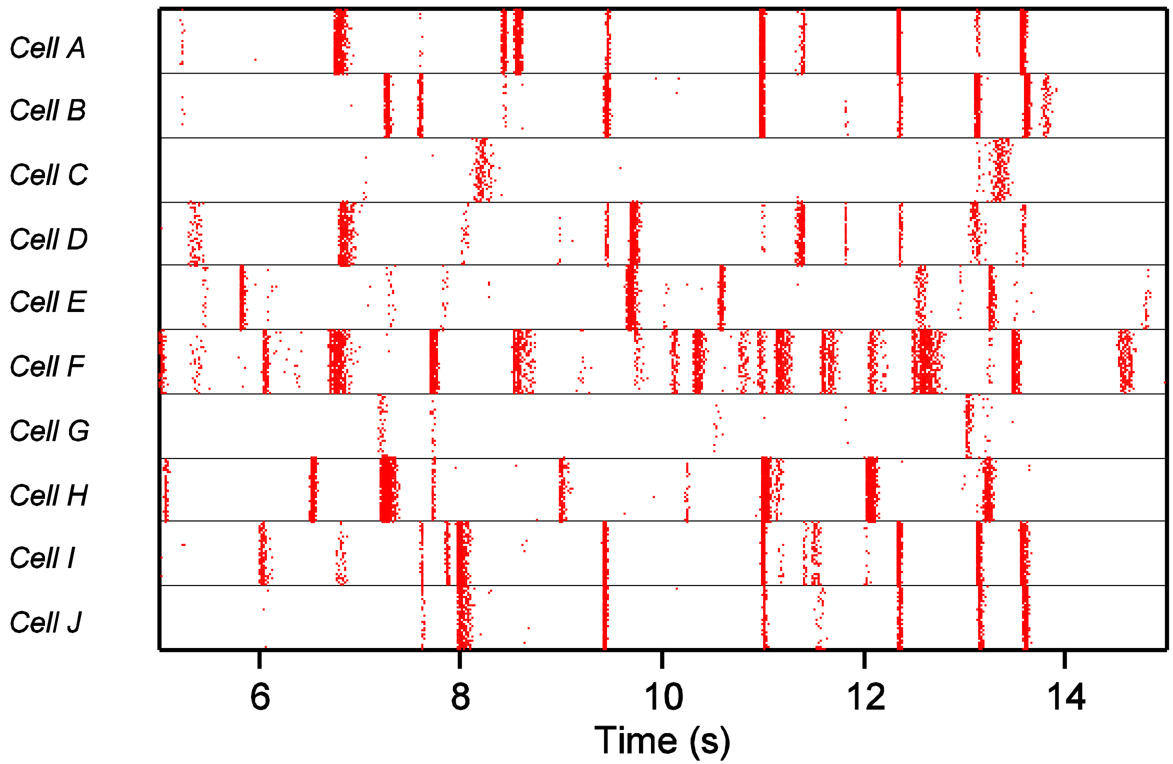




Alan Litke, UCSD

What *is* the neural code?

What *is* the neural code?



What *is* the neural code?

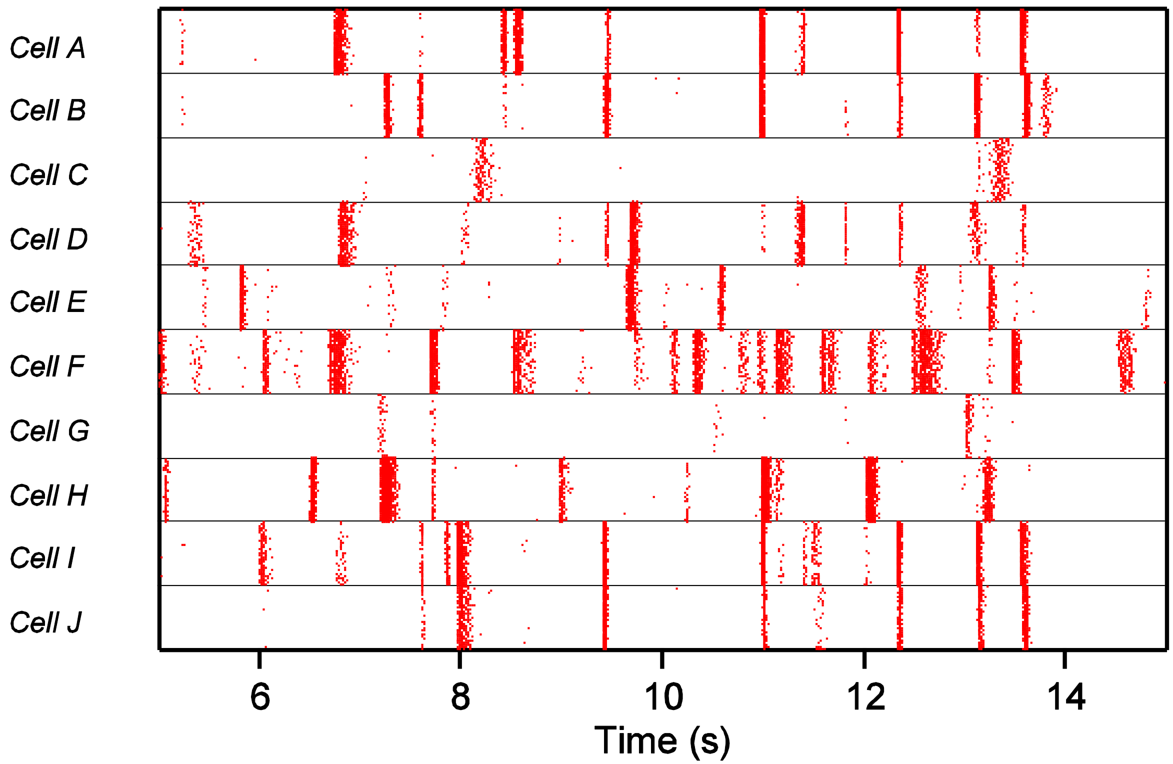
Encoding: how does a stimulus cause a pattern of responses?

- what are the responses and what are their characteristics?
- neural models:
  what takes us from stimulus to response;
  descriptive and mechanistic models, and the relation between them.

Decoding: what do these responses tell us about the stimulus?

- Implies some kind of decoding algorithm
- How to evaluate how good our algorithm is?

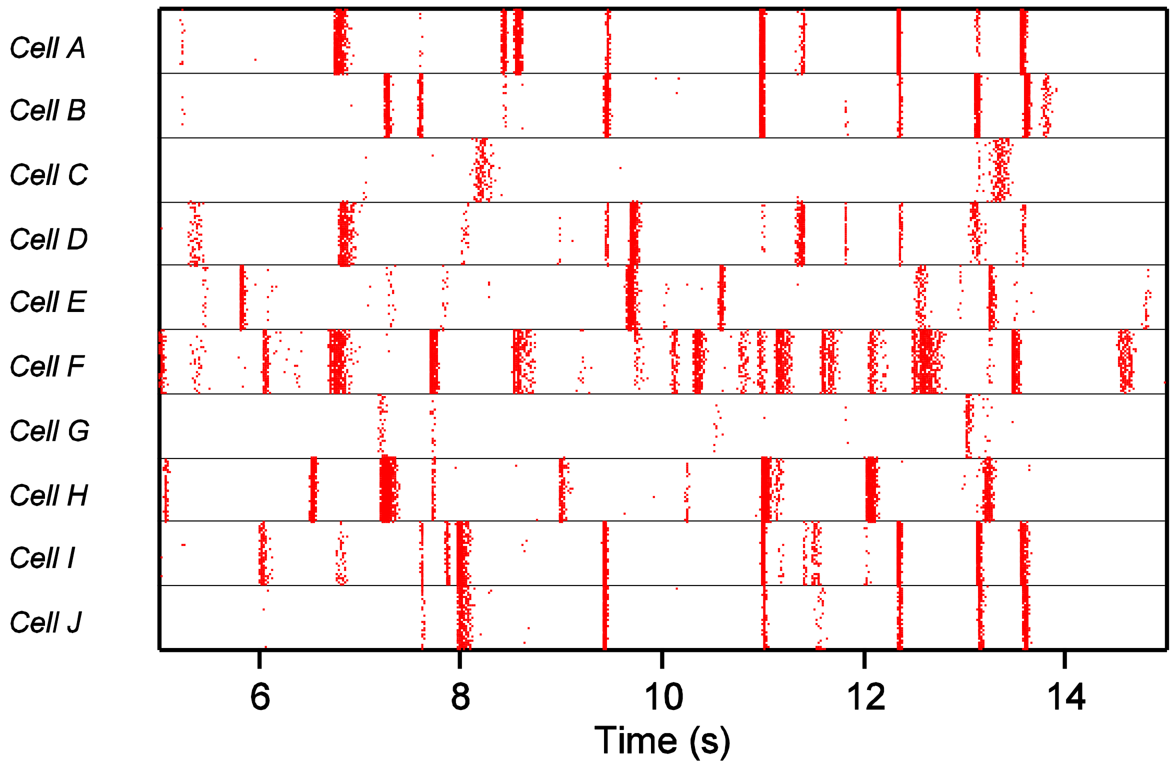
What *is* the neural code?



Single cells:

- spike rate
- spike times
- spike intervals

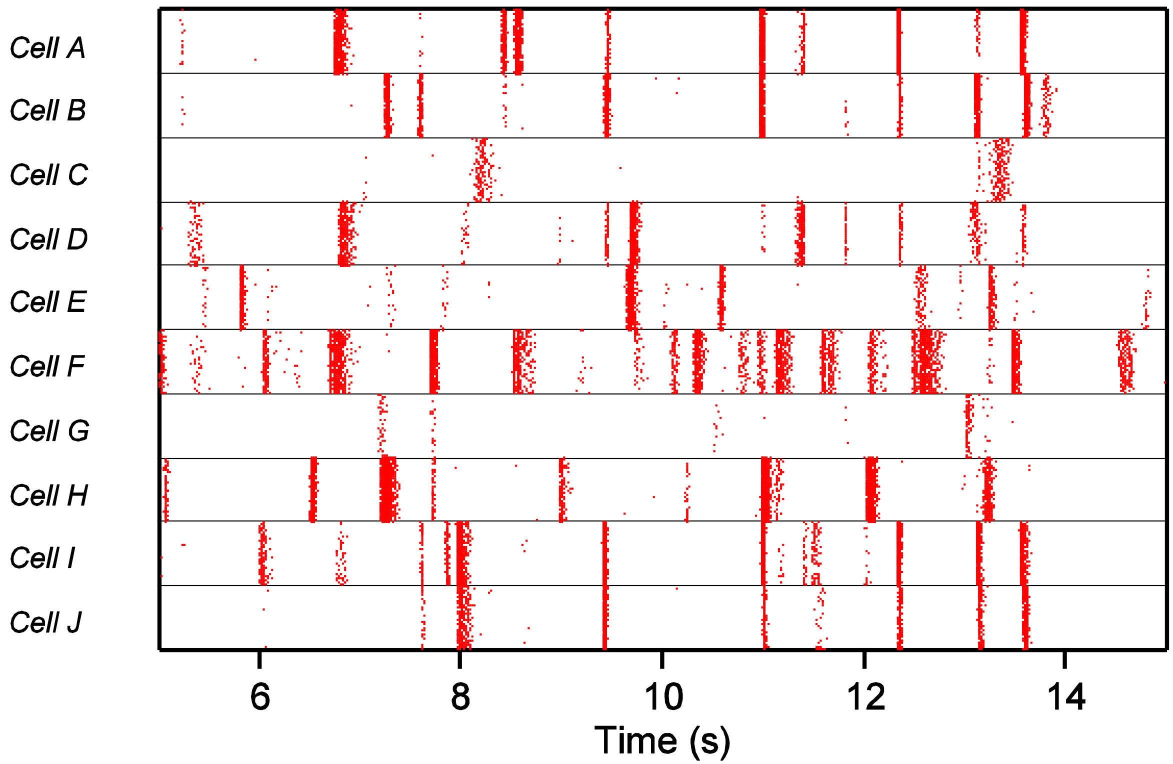
What *is* the neural code?



Single cells:

spike rate: what does the firing rate correspond to?
spike times: what in the stimulus triggers a spike?
spike intervals: can patterns of spikes convey extra information?

What *is* the neural code?

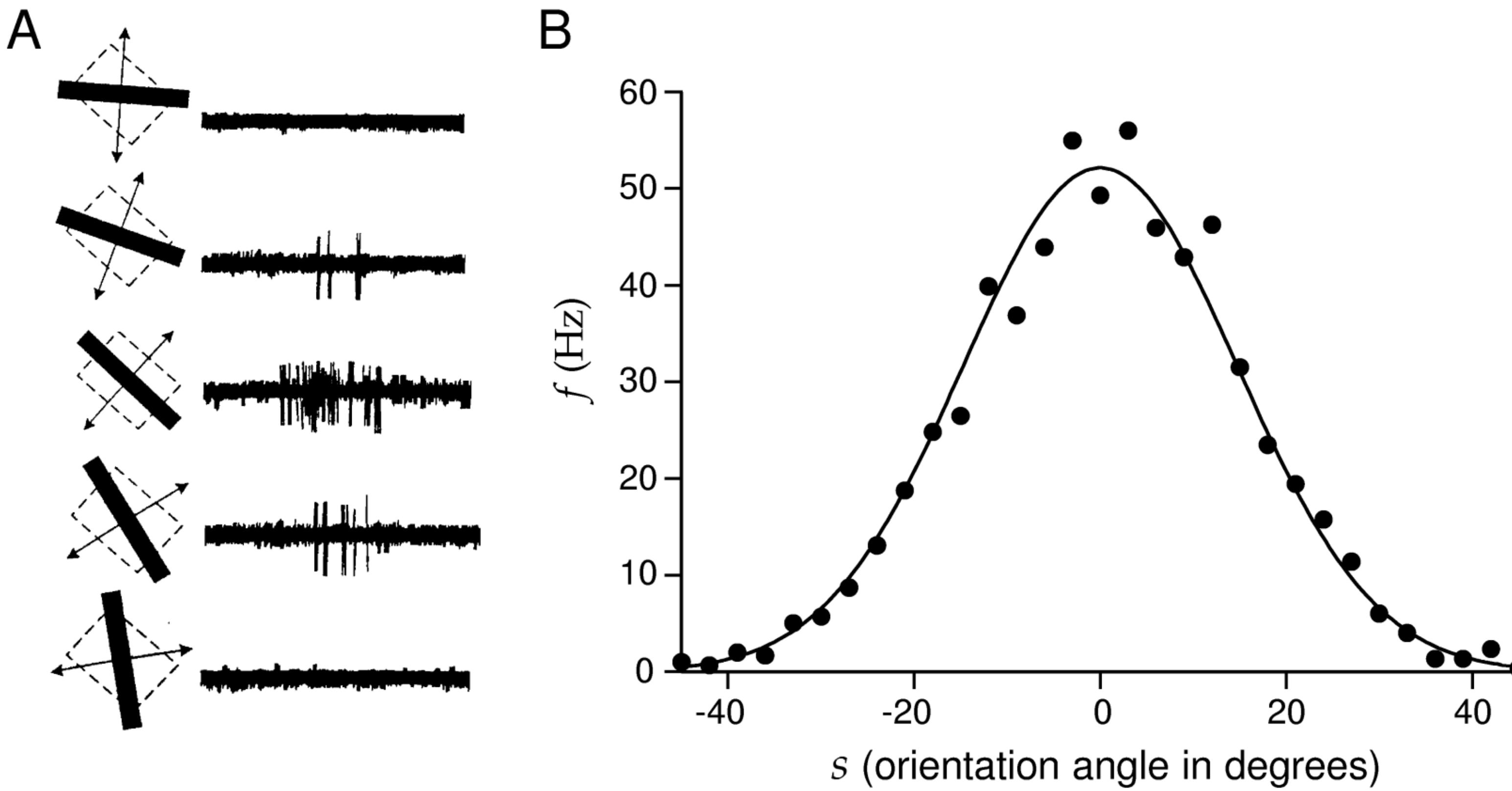


Populations of cells:

population coding
correlations between responses
synergy and redundancy

Receptive fields and tuning curves

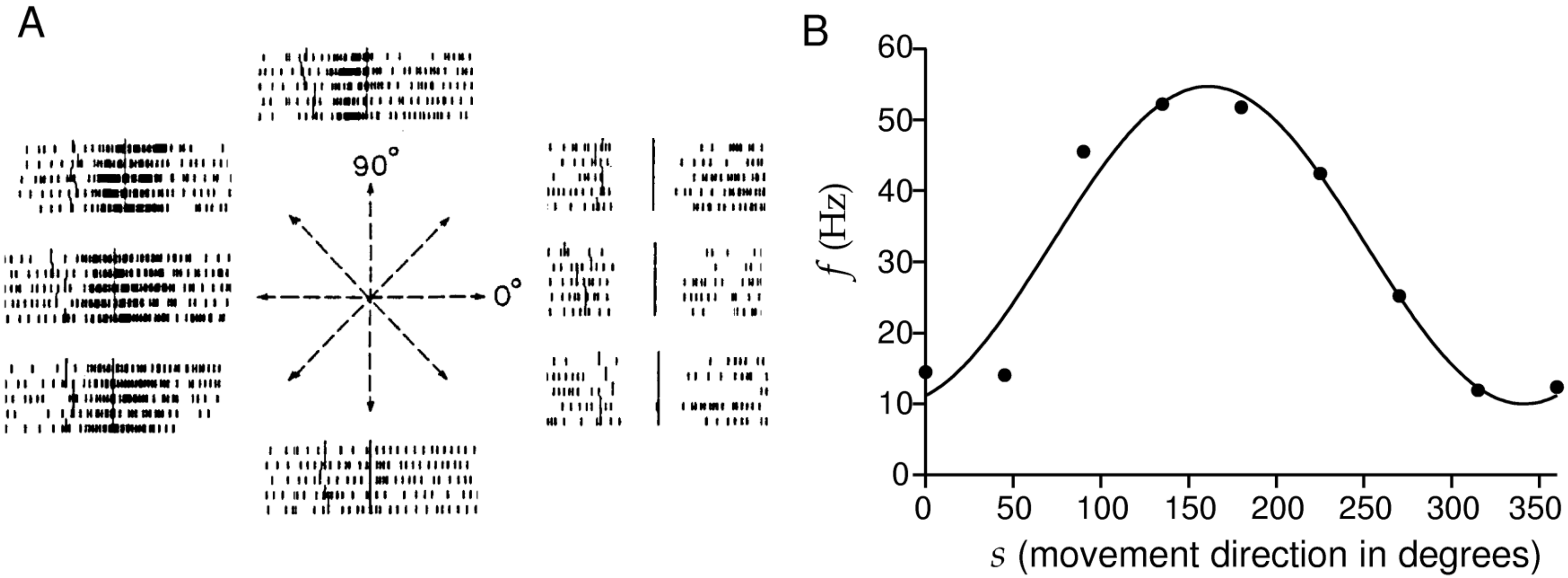
Tuning curve: r = f(s)



Gaussian tuning curve of a cortical (V1) neuron

Receptive fields and tuning curves

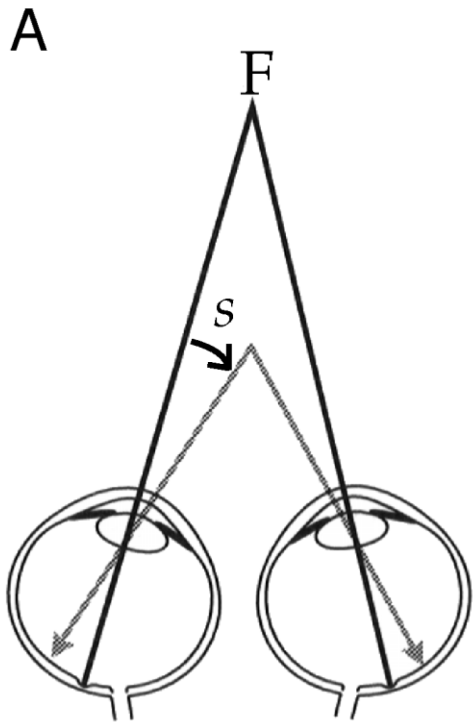
Tuning curve: r = f(s)



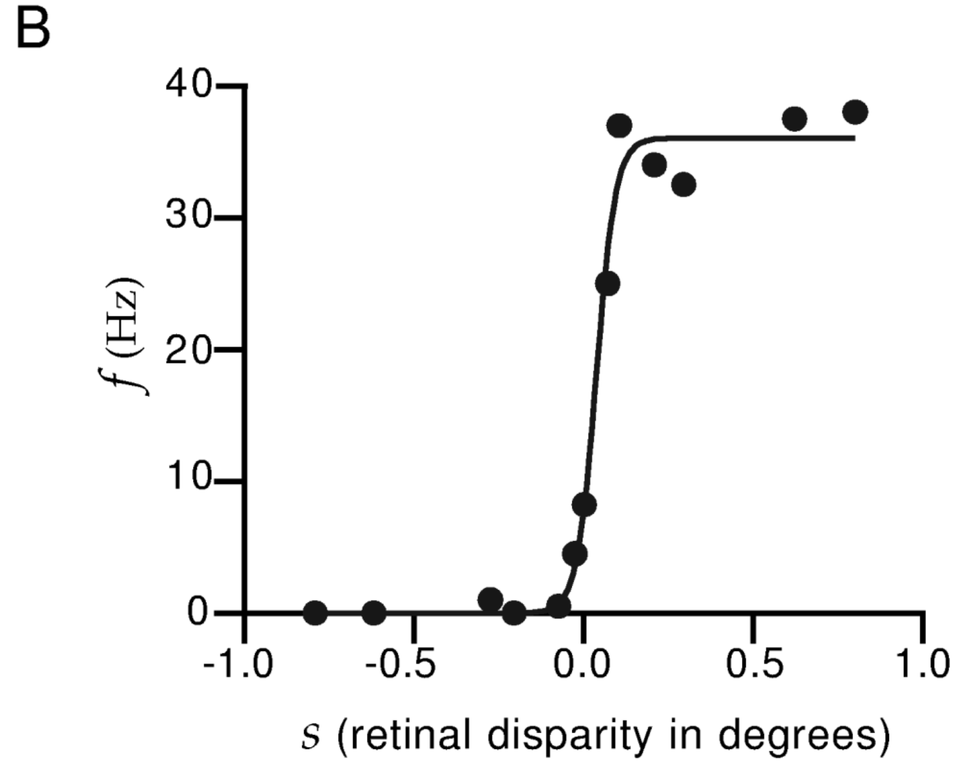
Hand reaching direction

Cosine tuning curve of a motor cortical neuron

Receptive fields and tuning curves

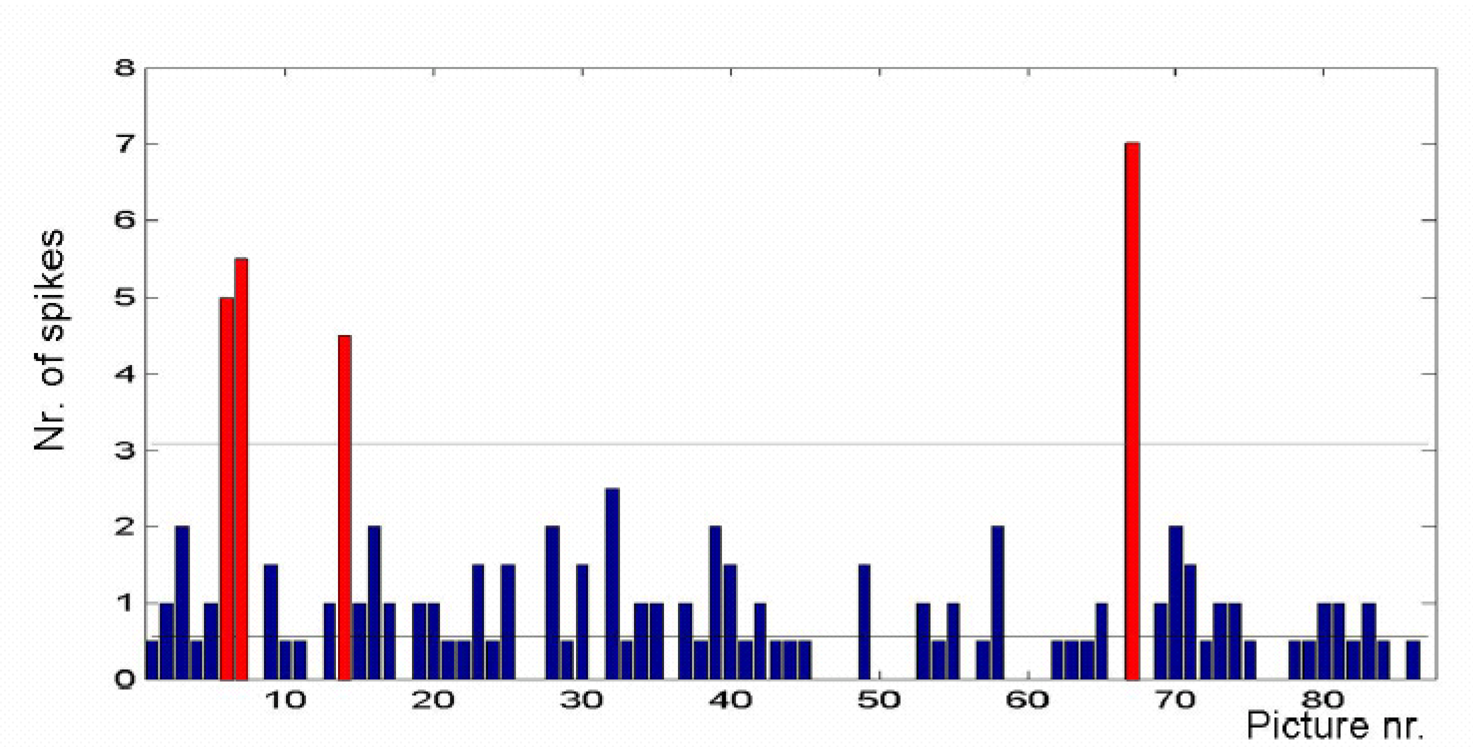


Retinal disparity for a "near" object

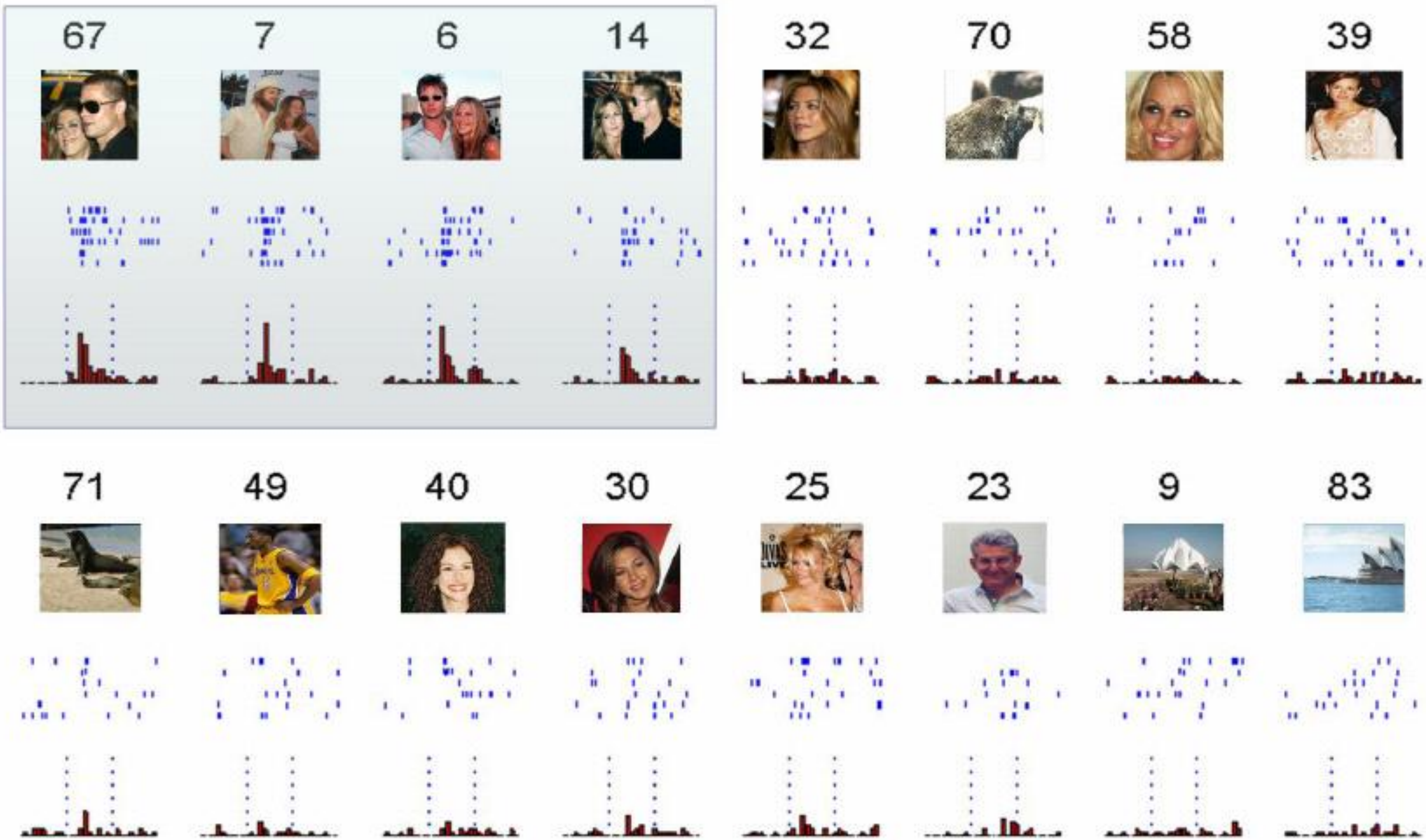


Sigmoid/logistic tuning curve of a "stereo" V1 neuron

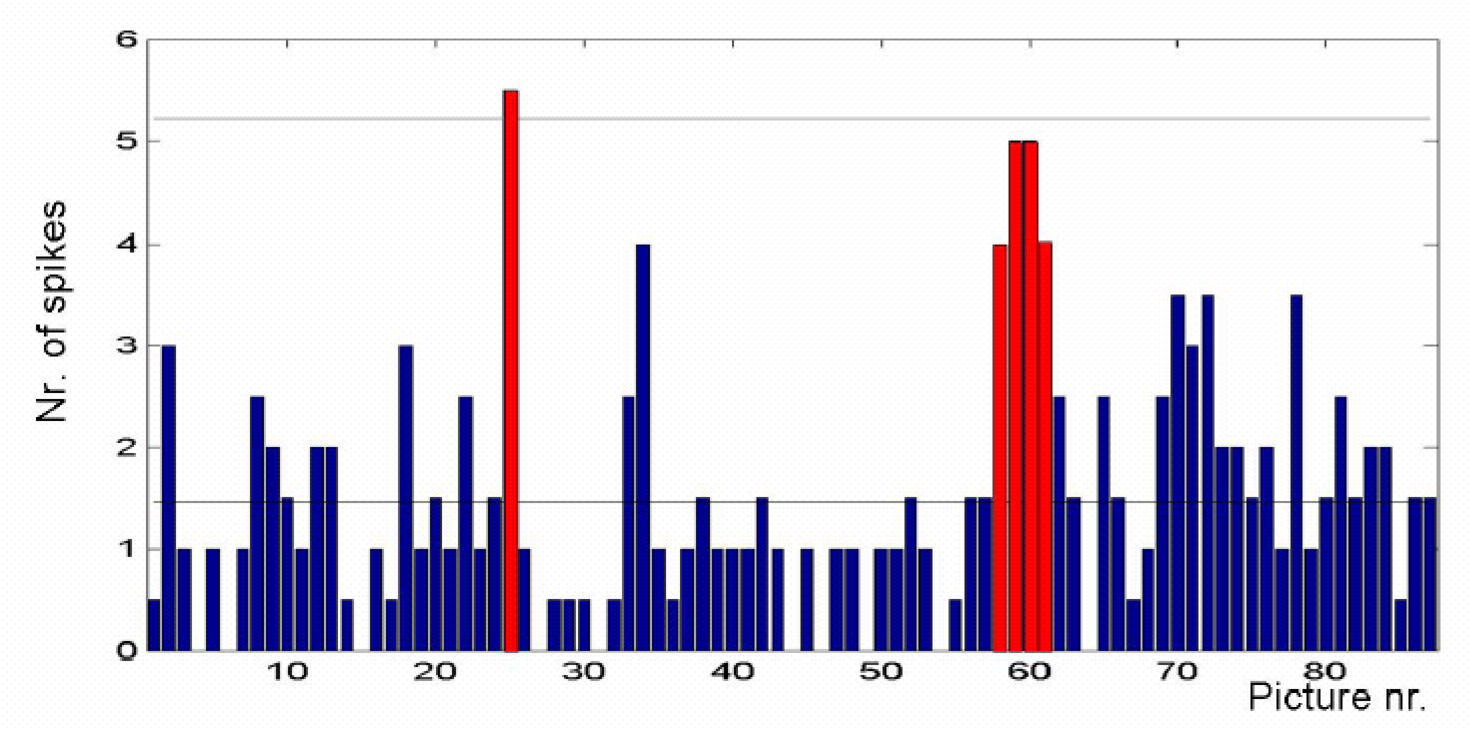
Higher brain areas represent increasingly complex features



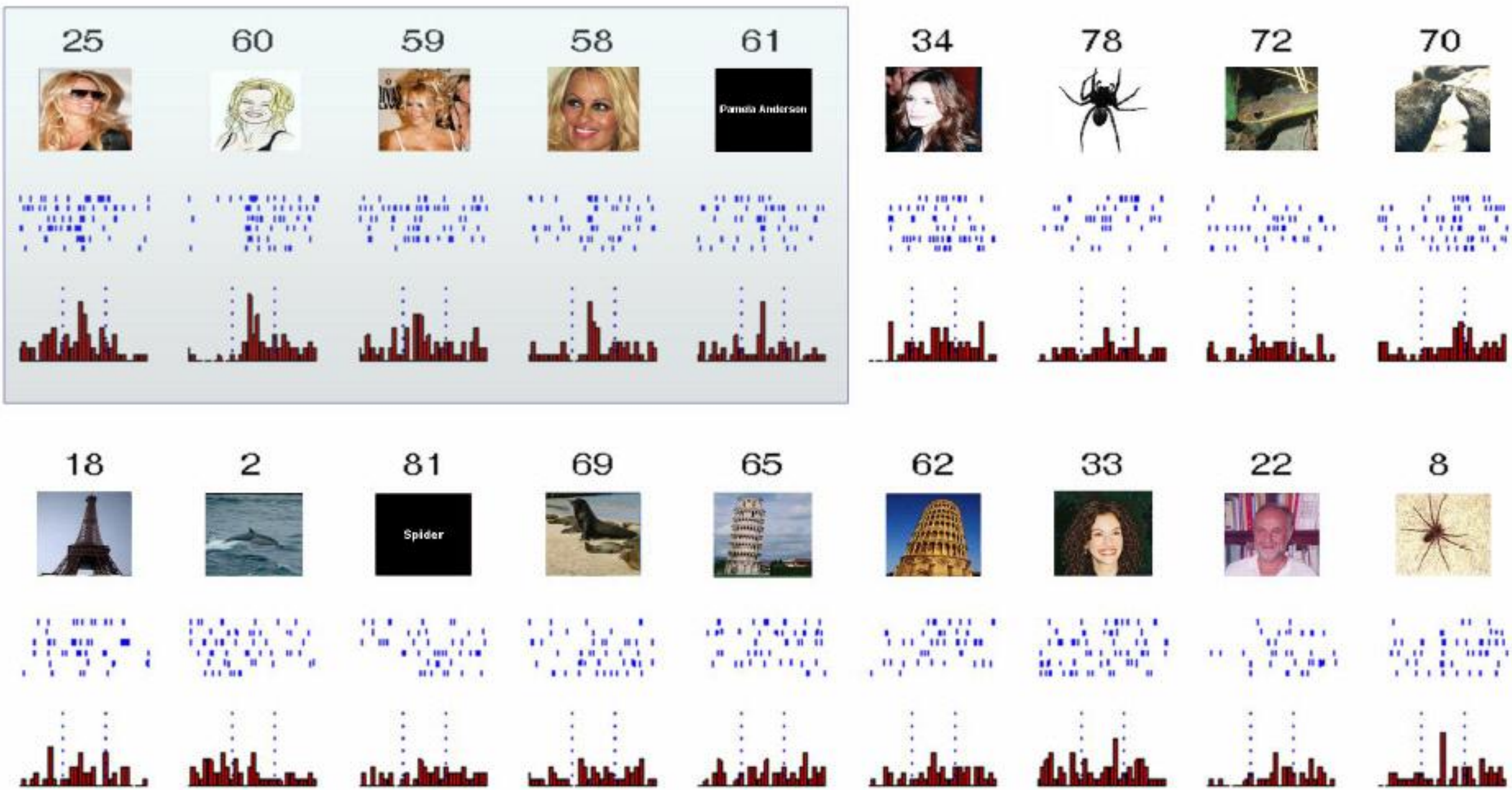
Quian Quiroga, Reddy, Kreiman, Koch and Fried, *Nature* (2005)



67
7
6
14
32
70
58
39
71
49
40
30
25
23
9
83



6
5
4
3
2
1
0
Nr. of spikes
10
20
30
40
50
60
70
80
Picture nr.



25
60
59
58
61
Pamela Anderson
34
78
72
70
18
2
81
Spider
69
65
62
33
22
8

More generally, we are interested in determining the relationship:

P(response | stimulus) *encoding*

P(stimulus | response) *decoding*

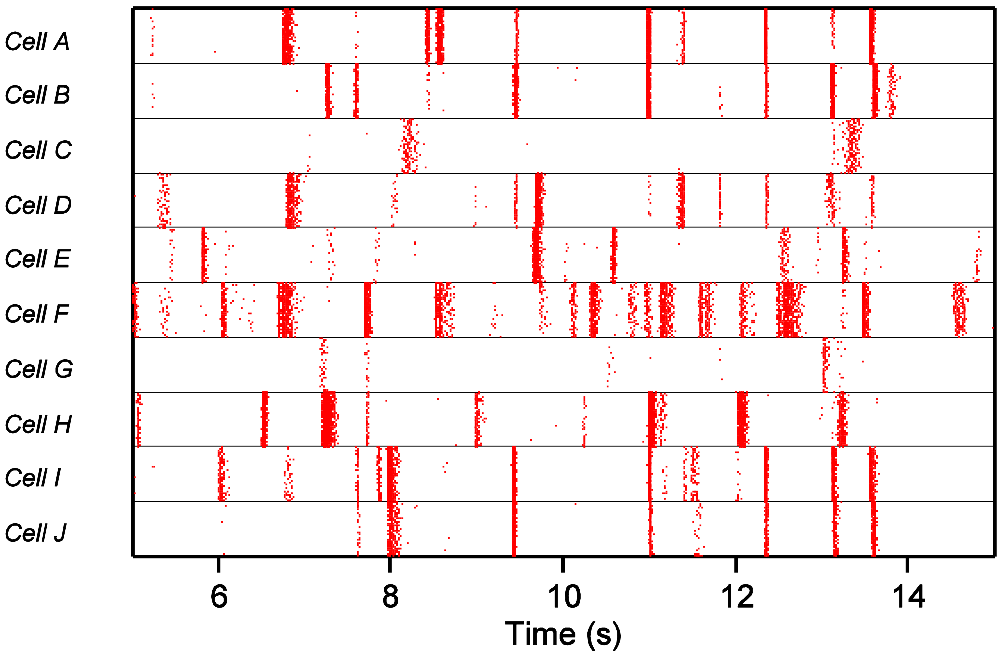
Due to noise, this is a stochastic description.

Problem of dimensionality, both in response and in stimulus

Reverse correlation

Fast modulation of firing by dynamic stimuli

Feature extraction



Use reverse correlation to decide what each of these spiking events stands for, and so to either:

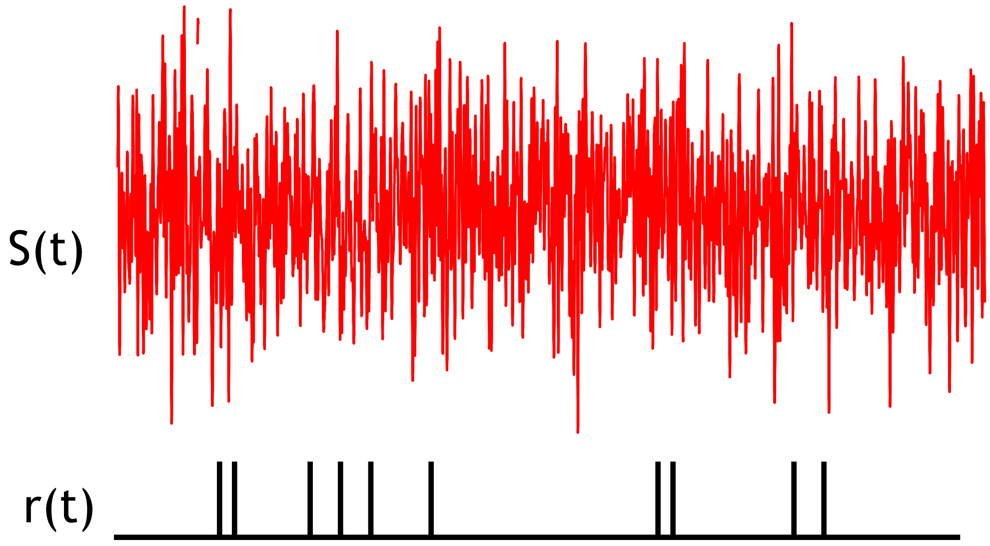
-- predict the time-varying firing rate

-- reconstruct the stimulus from the spikes

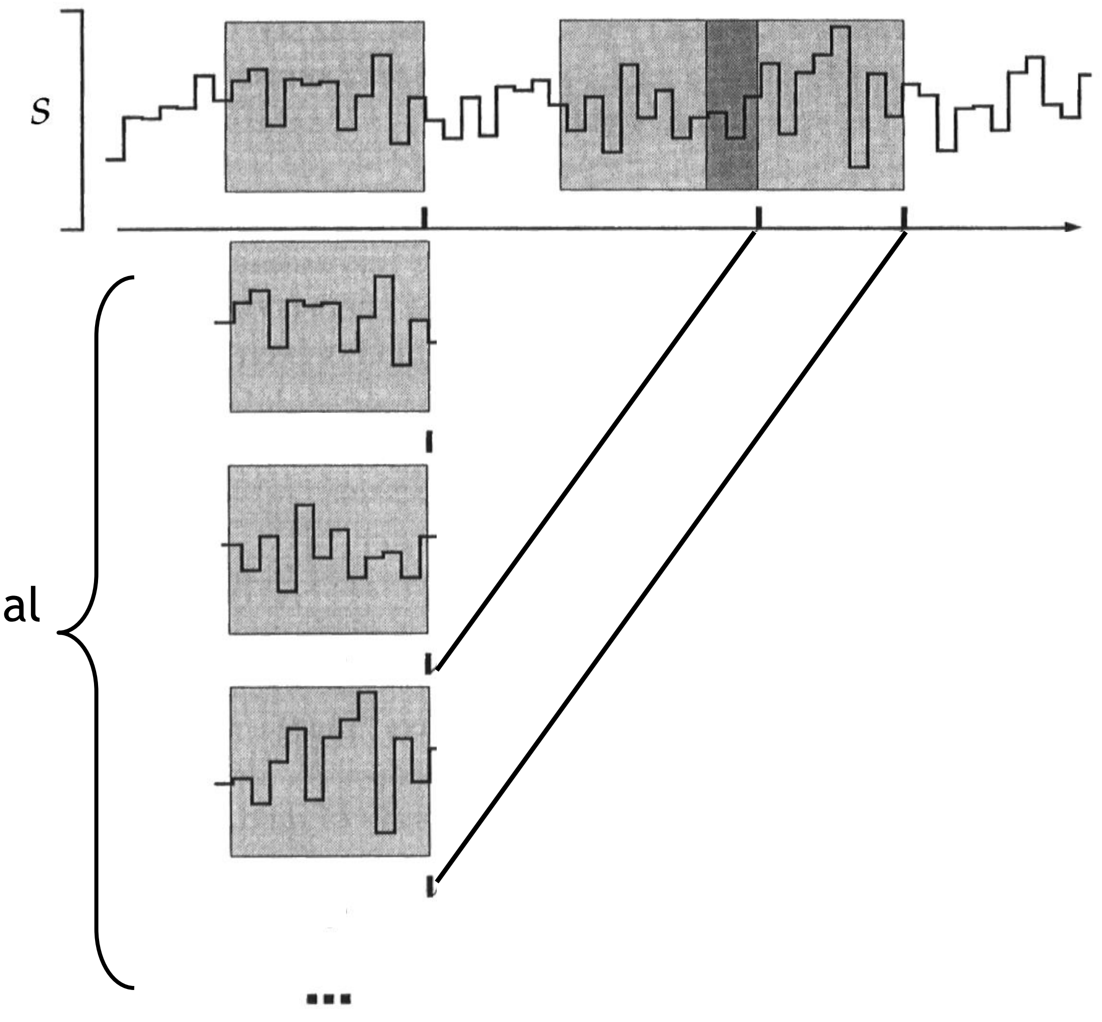
Reverse correlation

Basic idea: throw random stimuli at the system and collect the ones that cause a response

Typically, use Gaussian, white noise stimulus: an unbiased stimulus which samples all directions equally



Reverse correlation

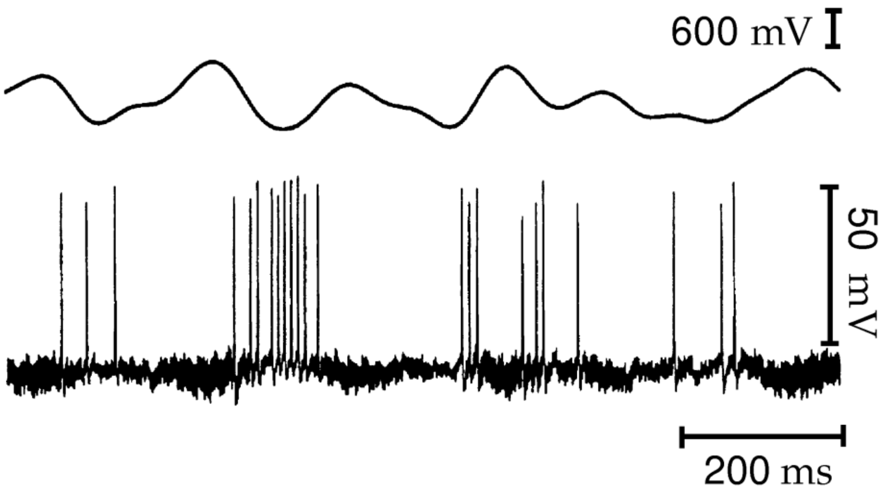


Spike-conditional ensemble

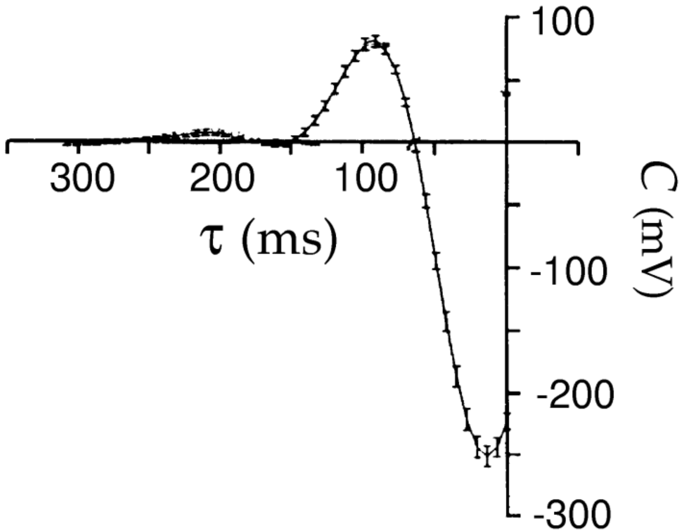
Goal: simplify!

Example: a neuron in the ELL of a fish

stimulus = fluctuating potential
(generates electric field)

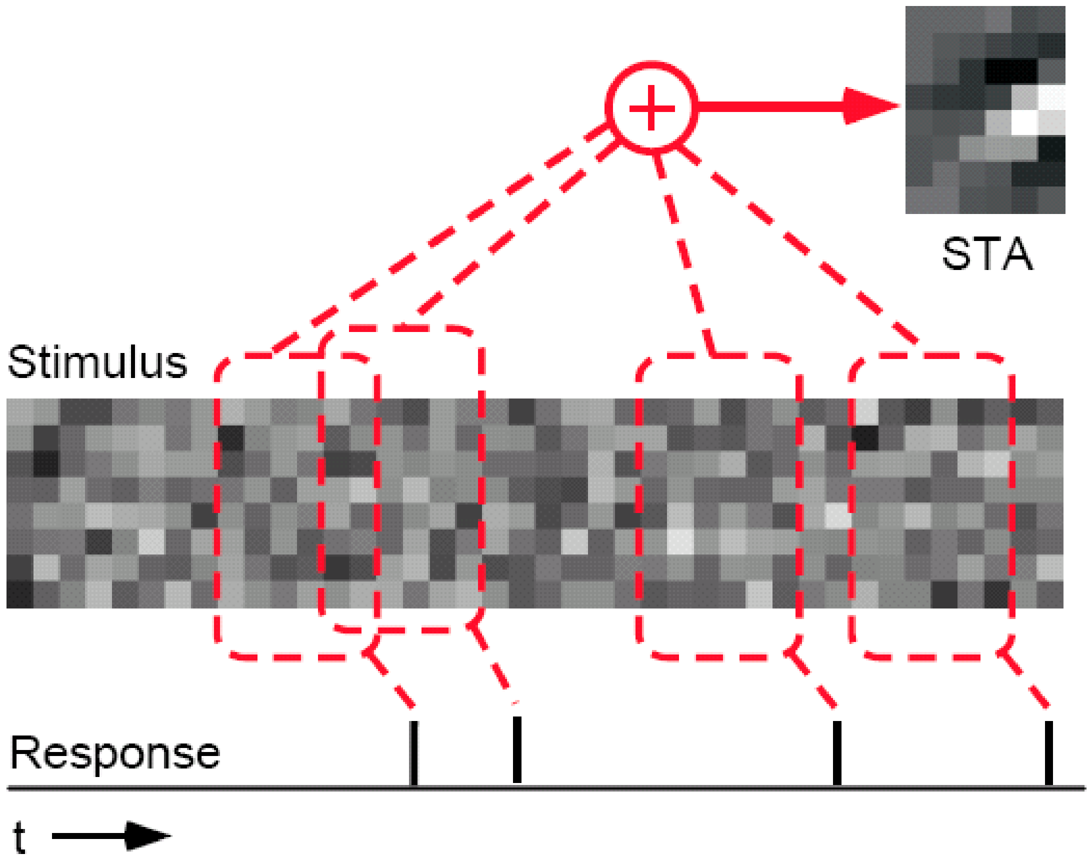


Spike-triggered Average



This can be done with other dimensions of stimulus as well

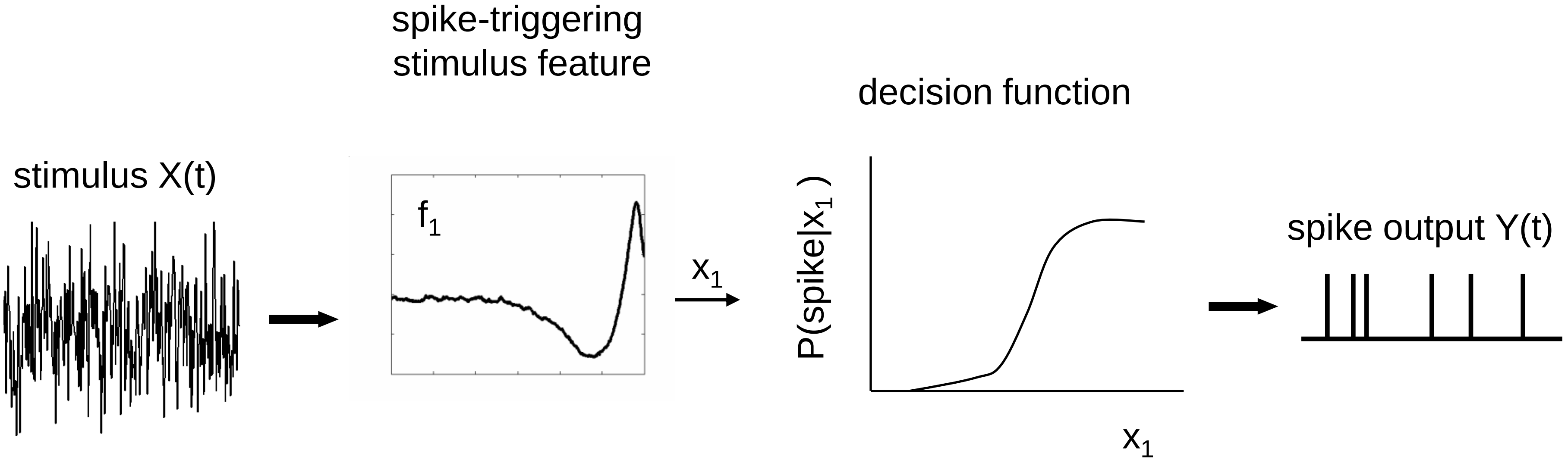
Spatio-temporal receptive field



Modeling spike encoding

Given a stimulus, when will the system spike?

Decompose the neural computation into a linear stage and a nonlinear stage.

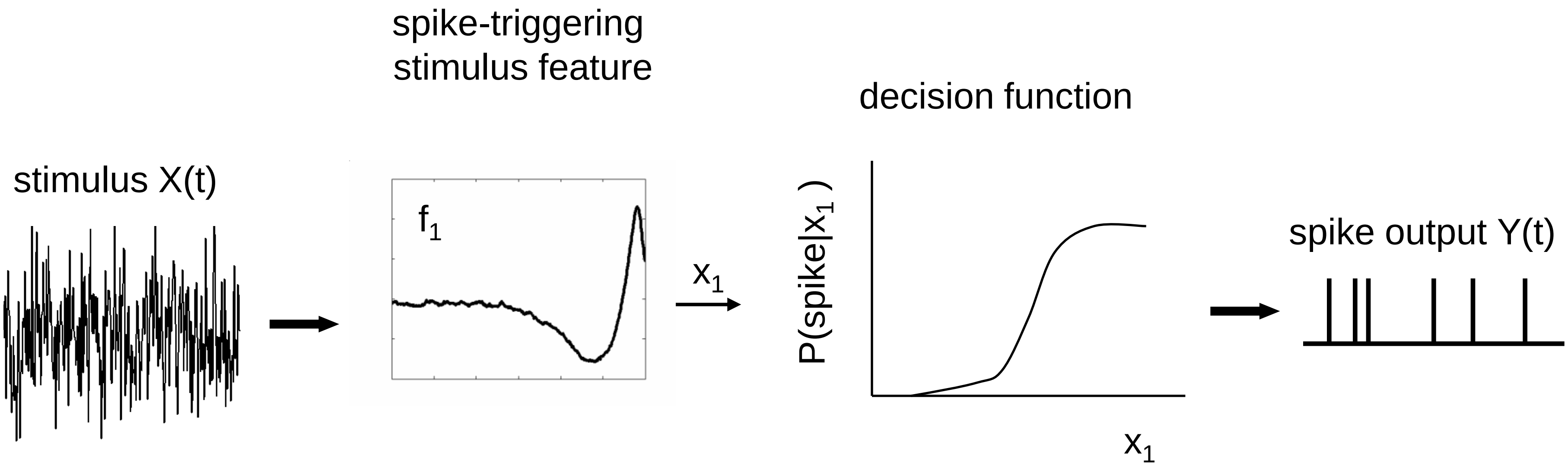


Simple example: the integrate-and-fire neuron

To what feature in the stimulus is the system sensitive?

Gerstner, spike response model; Aguera y Arcas et al. 2001, 2003; Keat et al., 2001

Modeling spike encoding

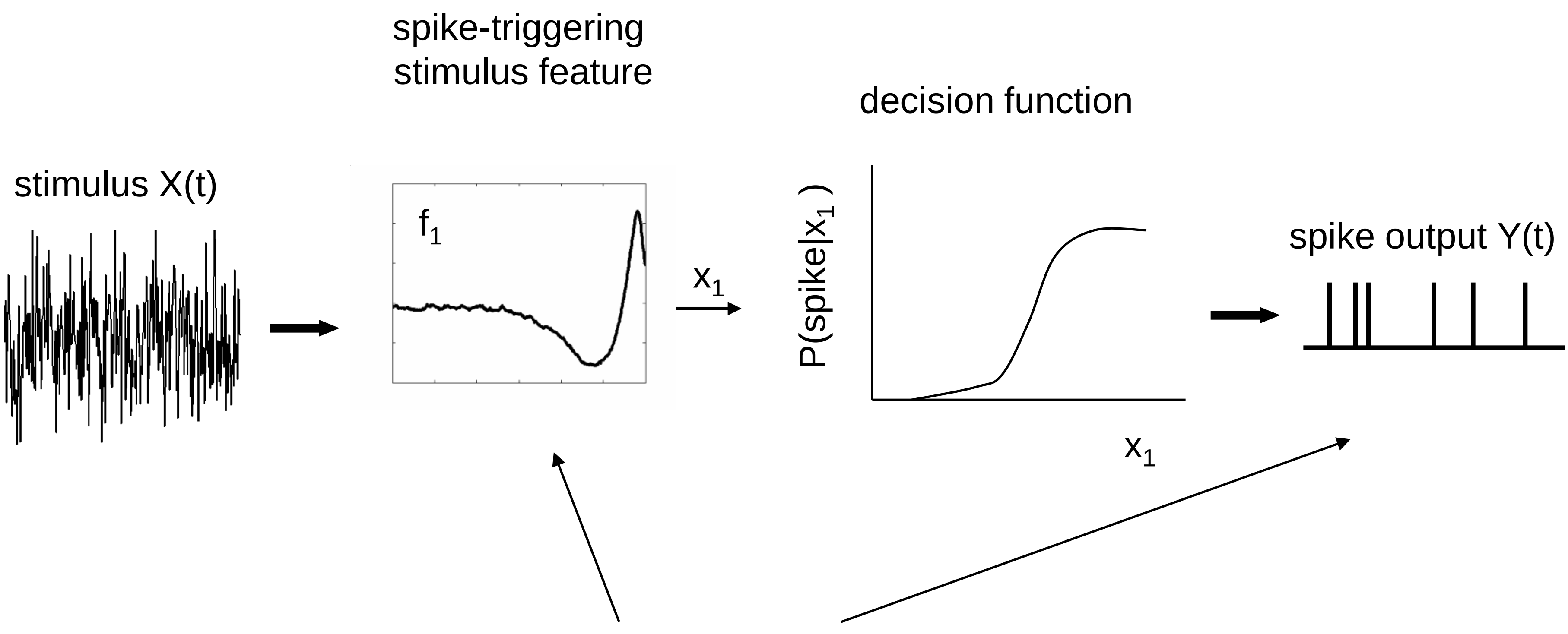


The decision function is $P(spike|x_1)$.
Derive from data using Bayes' theorem:

$$P(spike|x_1) = P(spike)\, P(x_1 \mid spike) \,/\, P(x_1)$$

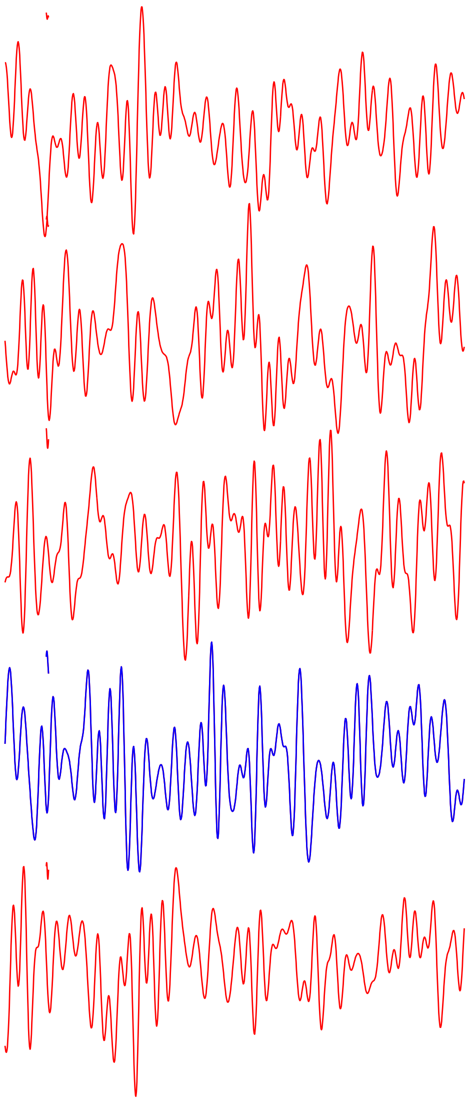
$P(x_1)$ is the *prior :* the distribution of all projections onto f_1
$P(x_1 \mid spike)$ is the *spike-conditional ensemble :*
the distribution of all projections onto f_1 given there has been a spike
P(spike) is proportional to the mean firing rate

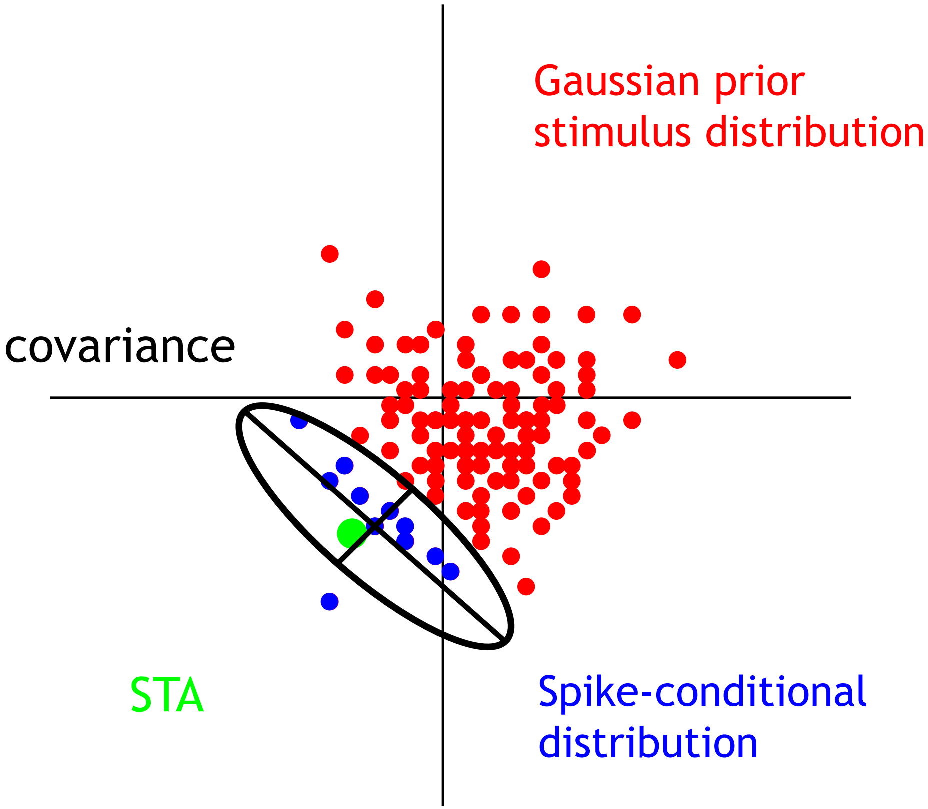
Models of neural function



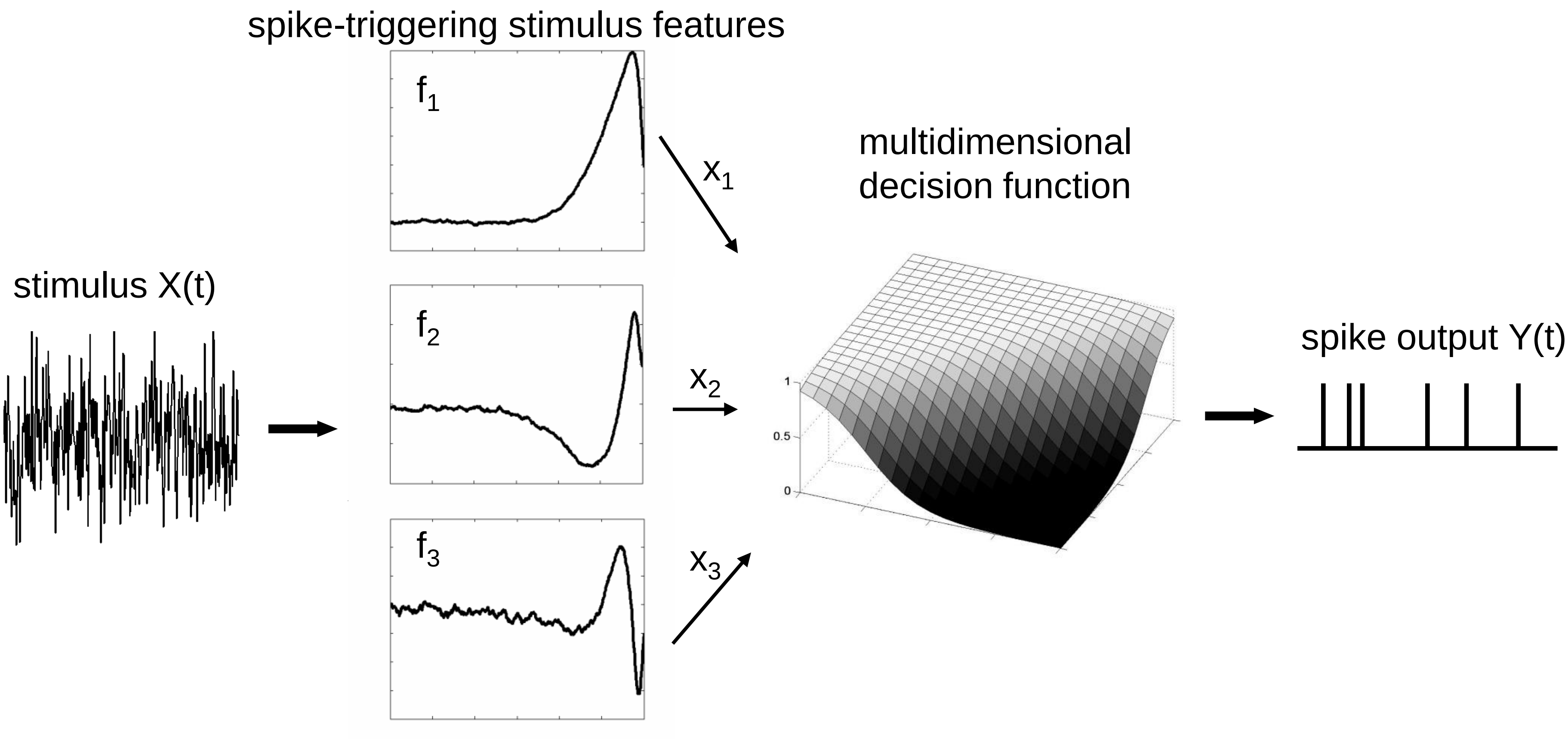
Weaknesses

Reverse correlation: a geometric view

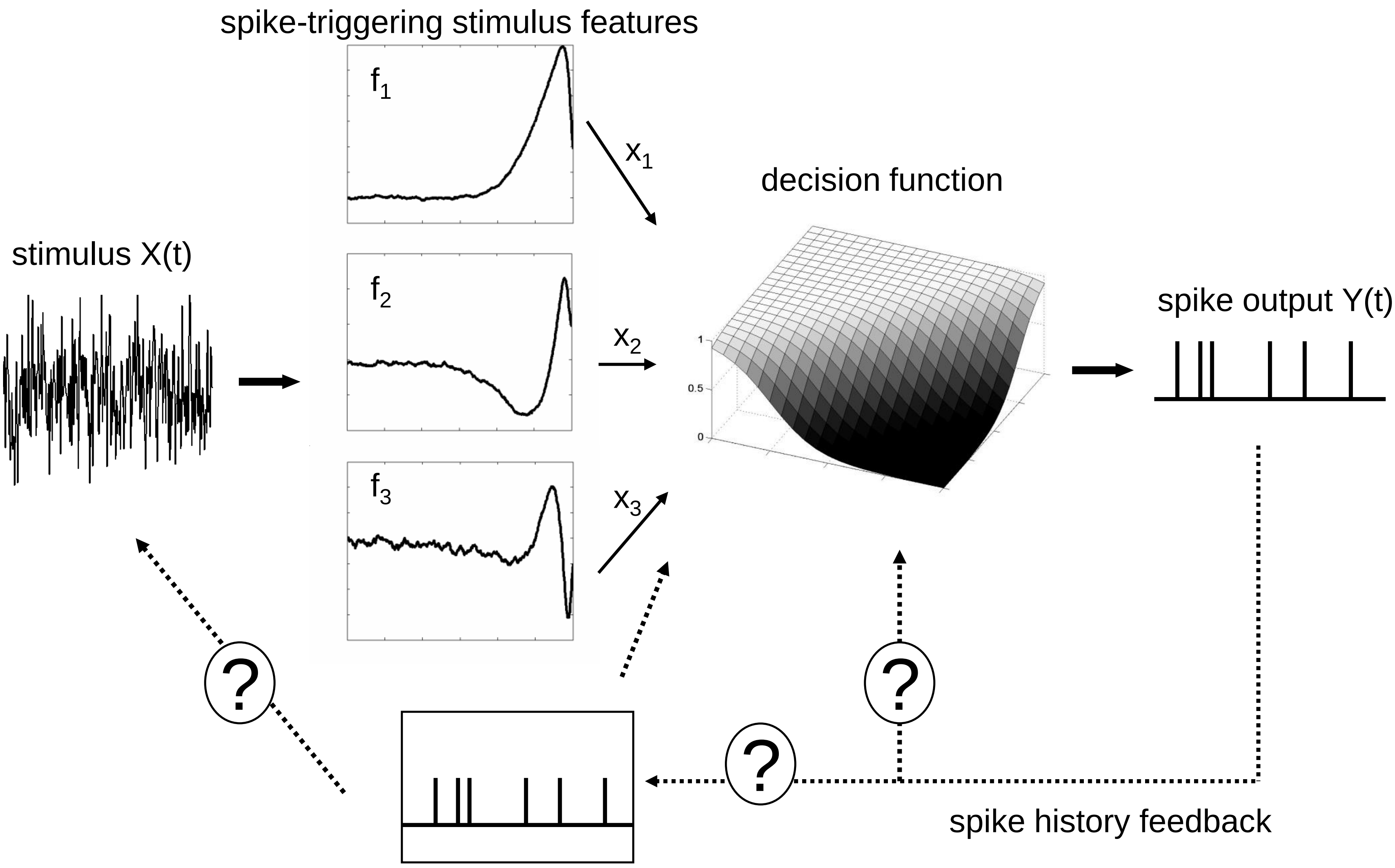




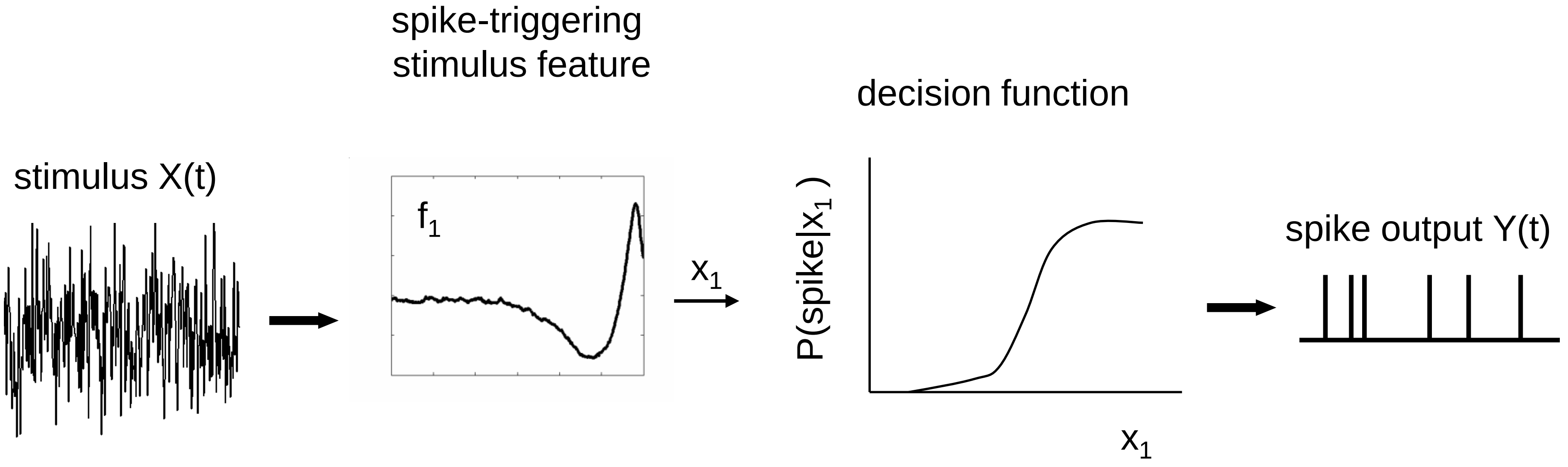
Functional models of neural response



Functional models of neural response



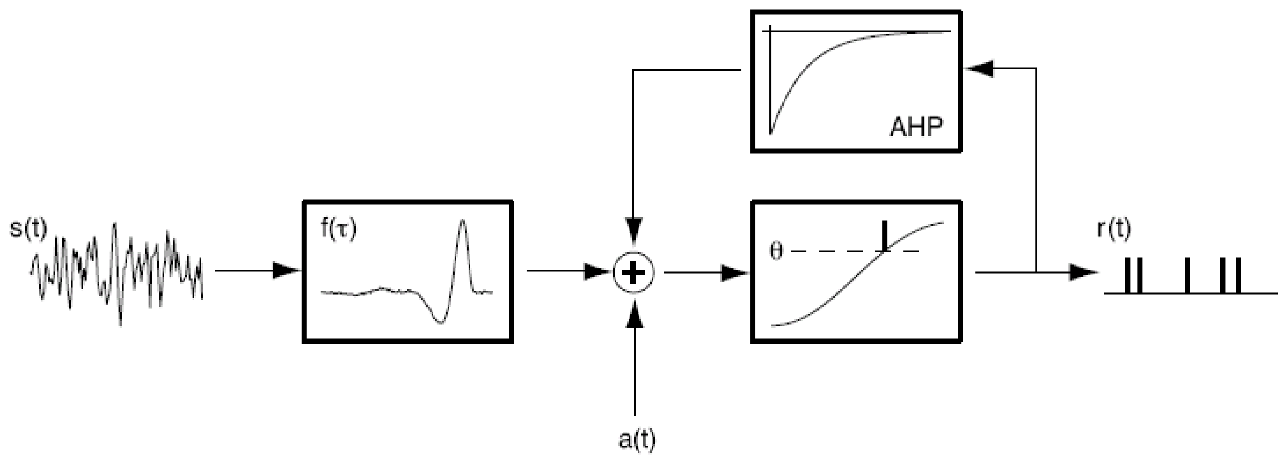
Functional models of neural response



Covariance analysis

Let's develop some intuition for how this works: the Keat model

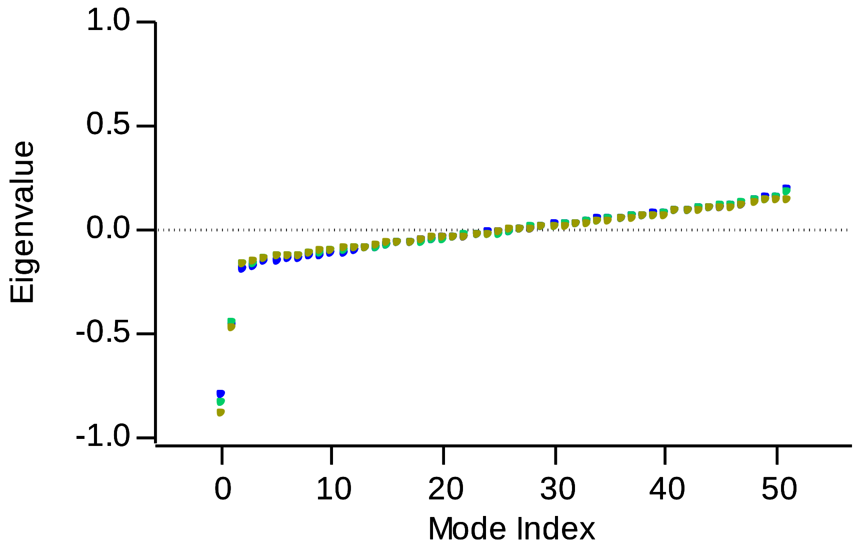
Keat, Reinagel, Reid and Meister, Predicting every spike. Neuron (2001)

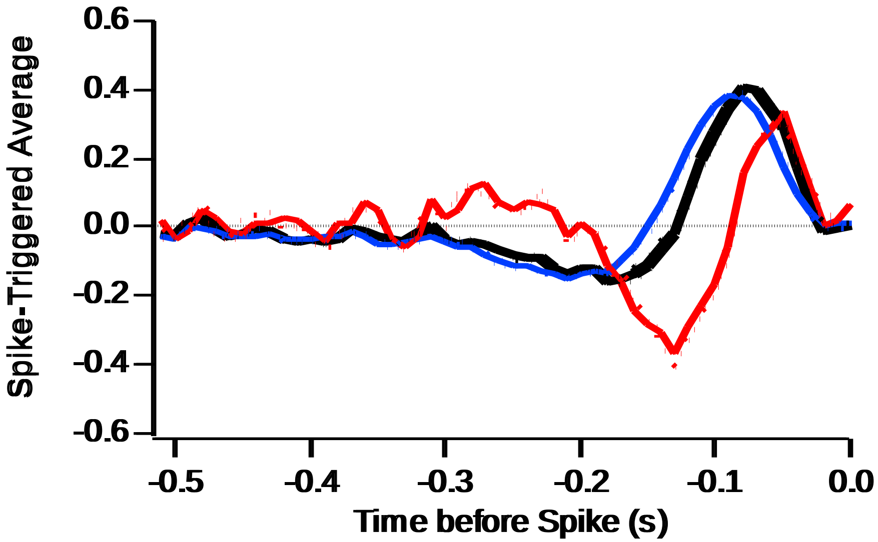


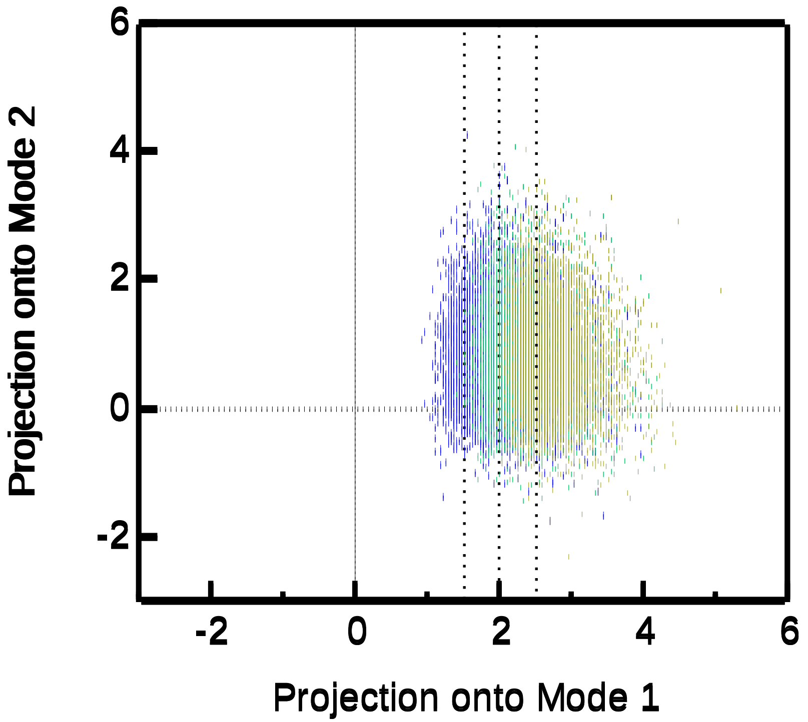
- Spiking is controlled by a single filter
- Spikes happen generally on an upward threshold crossing of the filtered stimulus

➔ expect 2 modes, the filter F(t) and its time derivative F'(t)

Covariance analysis



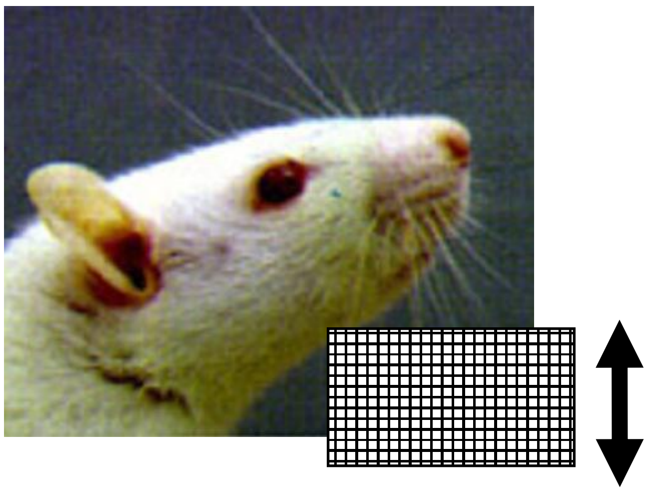




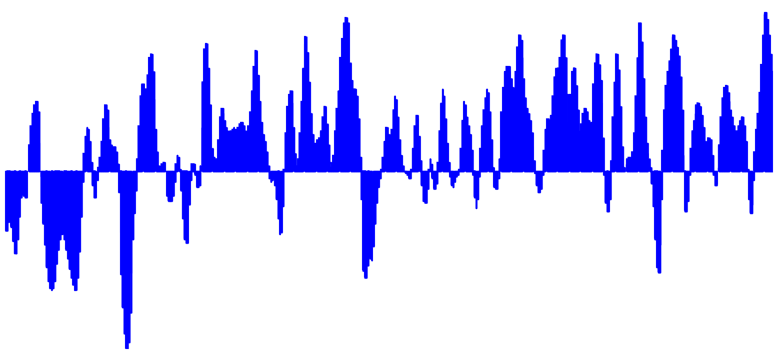
Covariance analysis

Let's try a real neuron: rat somatosensory cortex

(Ras Petersen, Mathew Diamond, SISSA)

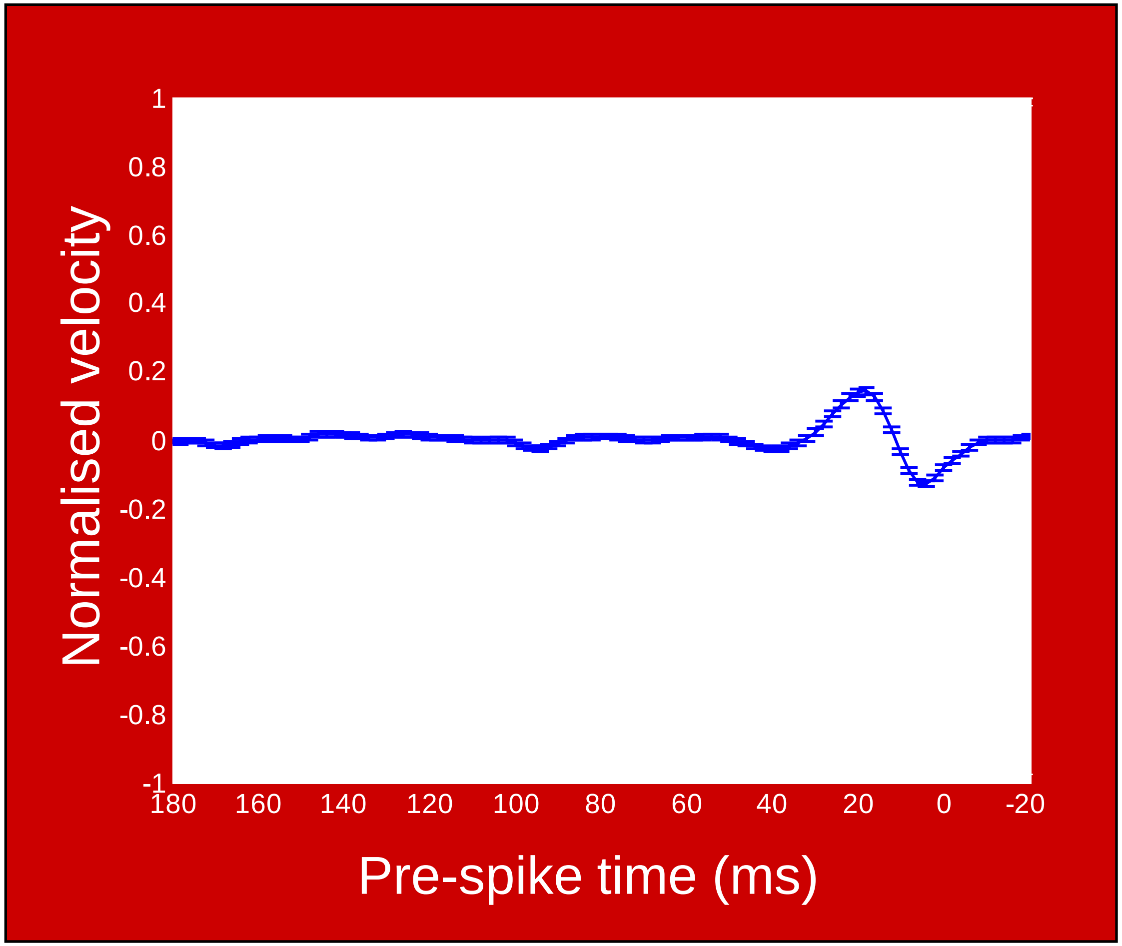


Record from single units in barrel cortex



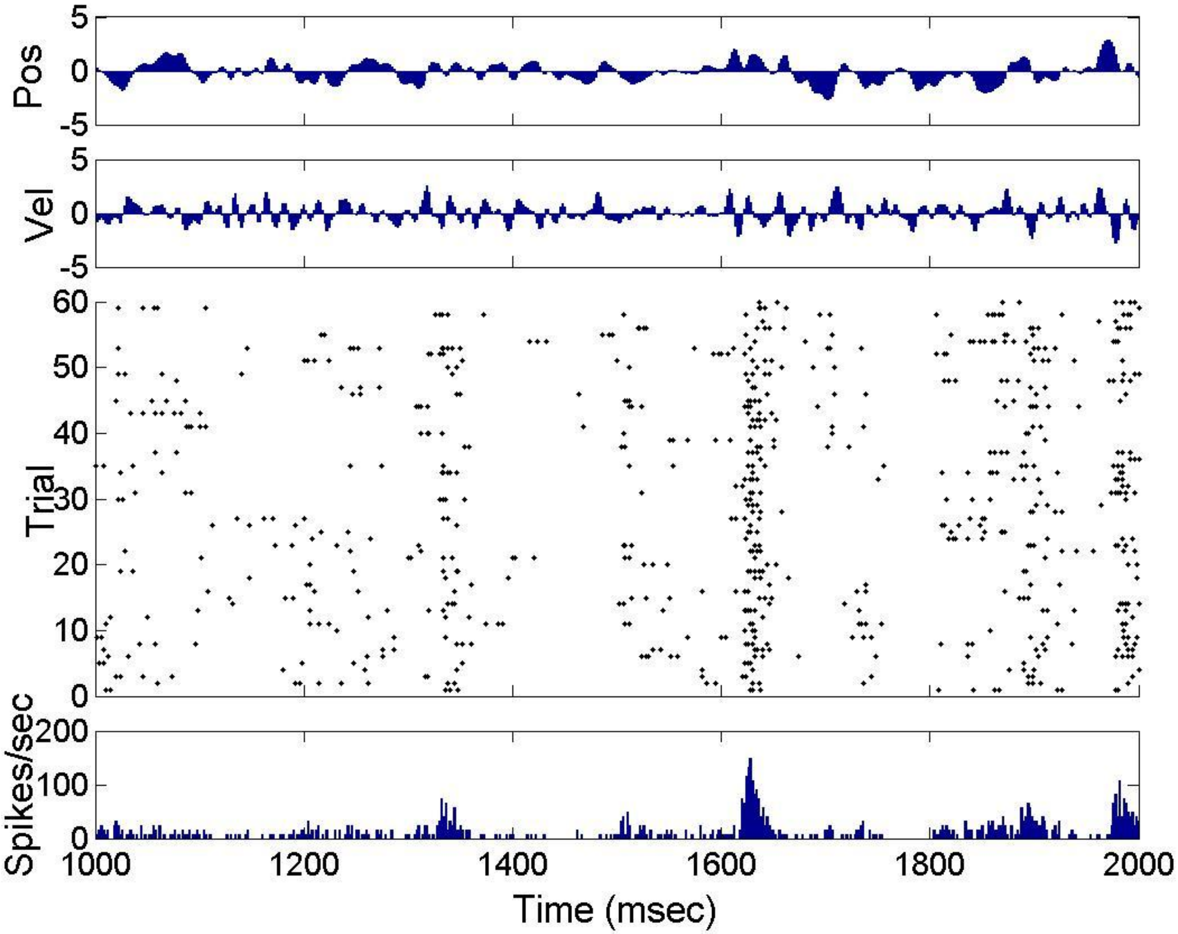
Covariance analysis

Spike-triggered average:



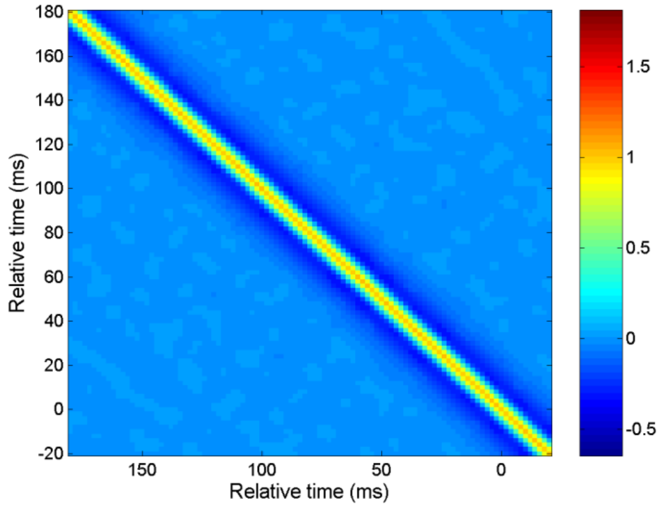
Covariance analysis

Is the neuron simply not very responsive to a white noise stimulus?

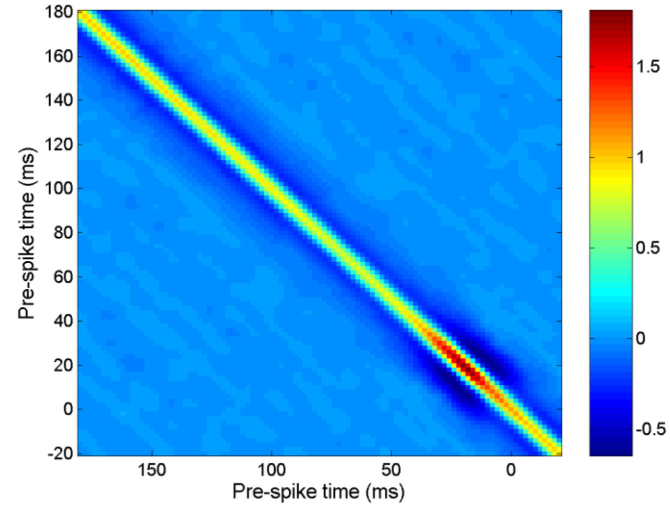


Covariance analysis

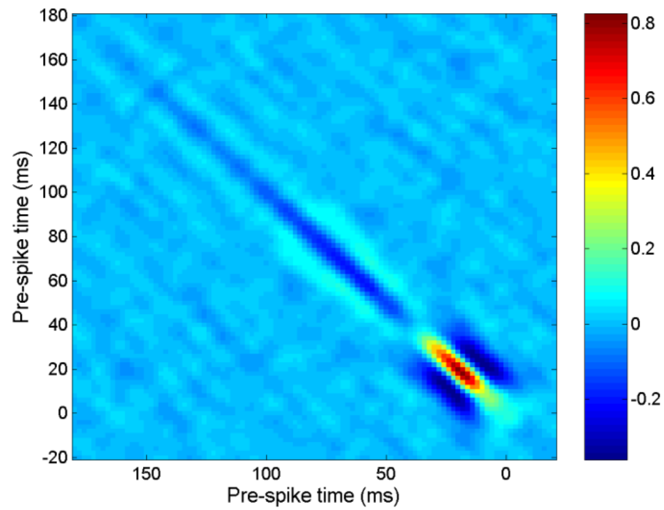
Prior



Spike-triggered



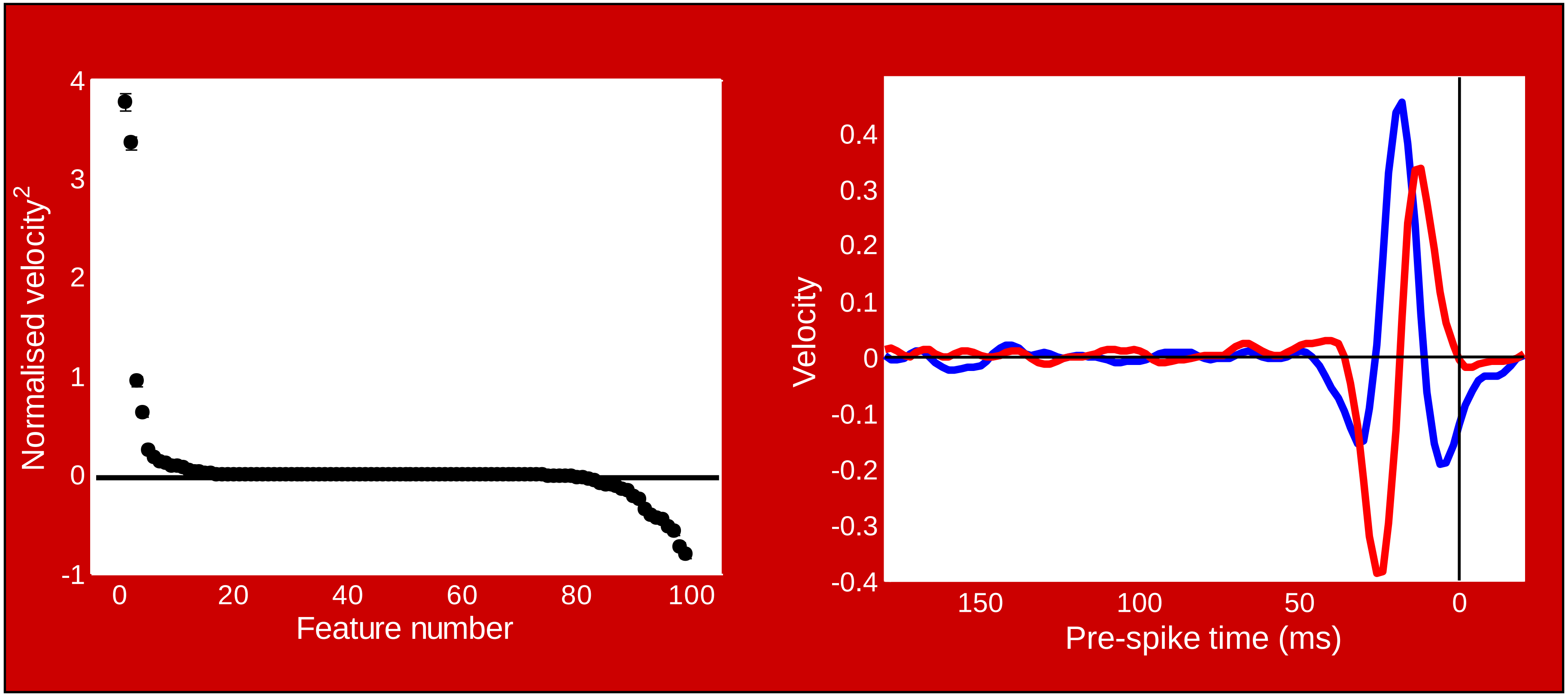
Difference



Covariance analysis

Eigenspectrum

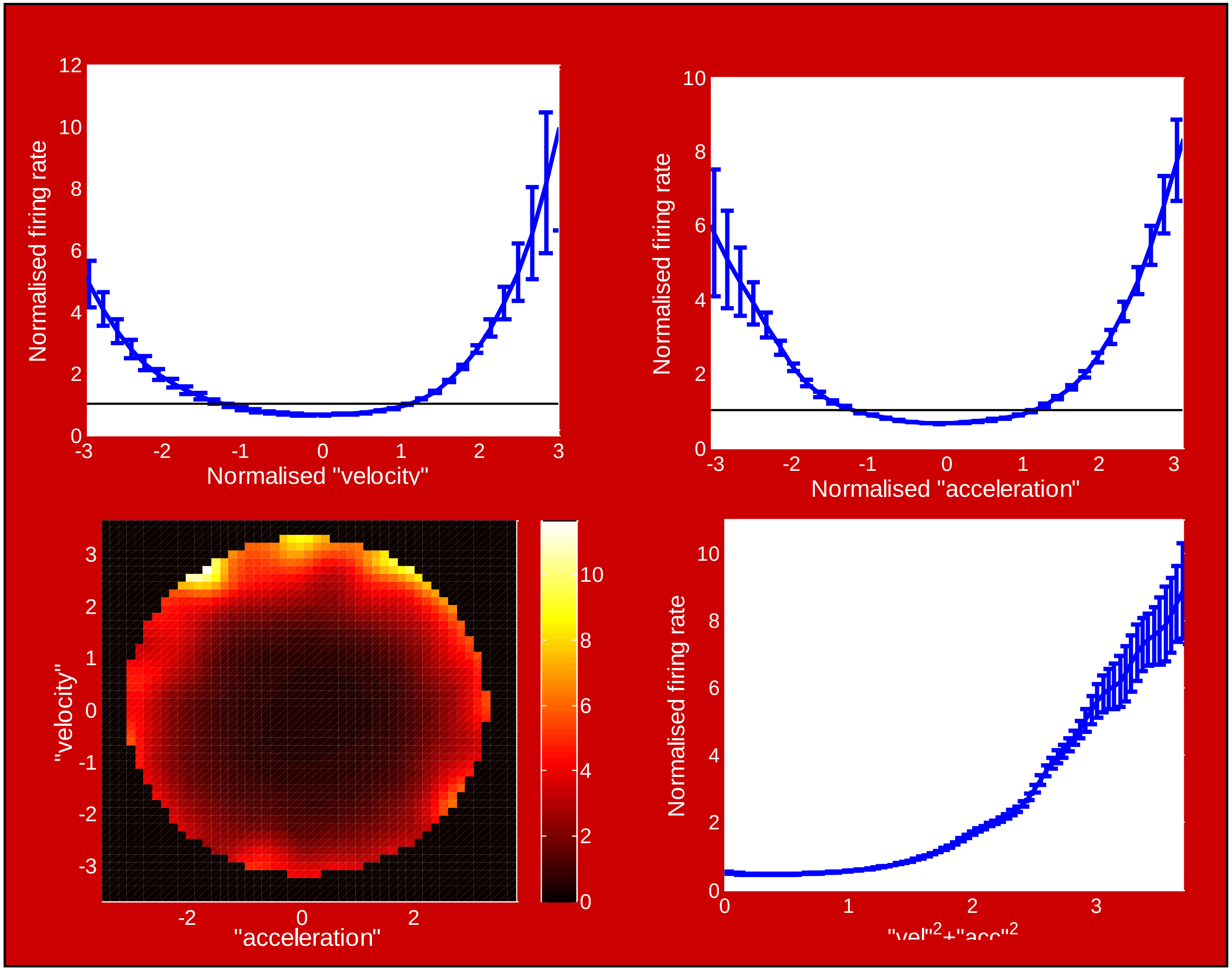
Leading modes



Covariance analysis

Input/output relations wrt first two filters, alone:

and in quadrature:

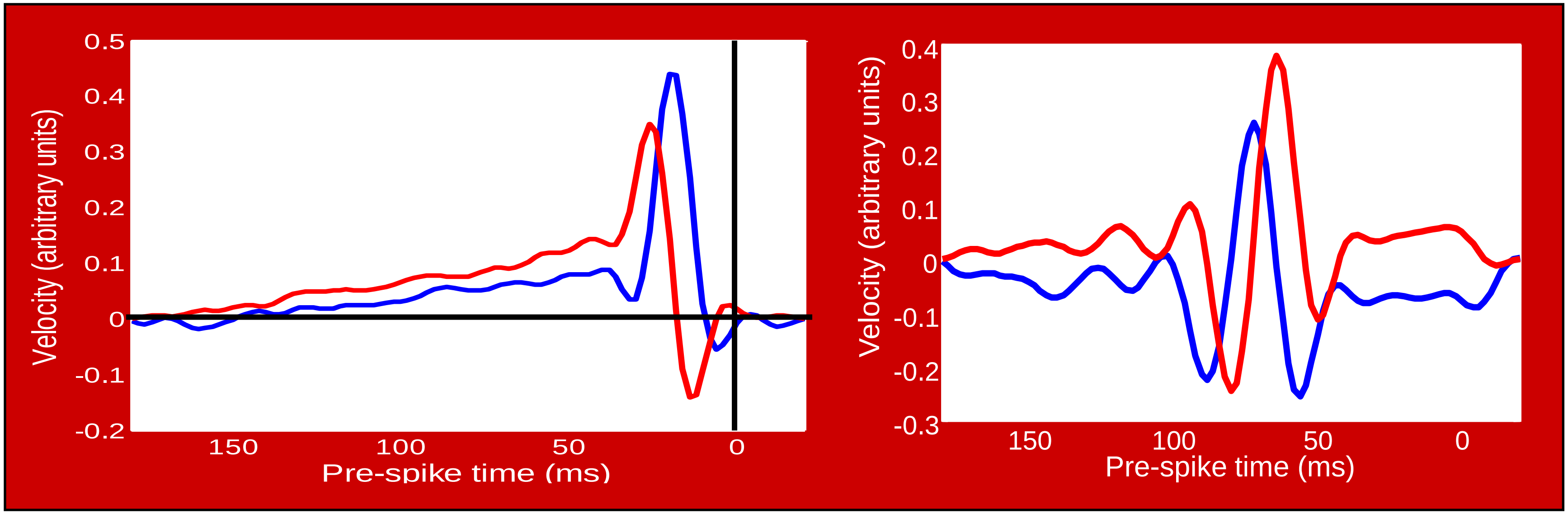


Covariance analysis

How about the other modes?

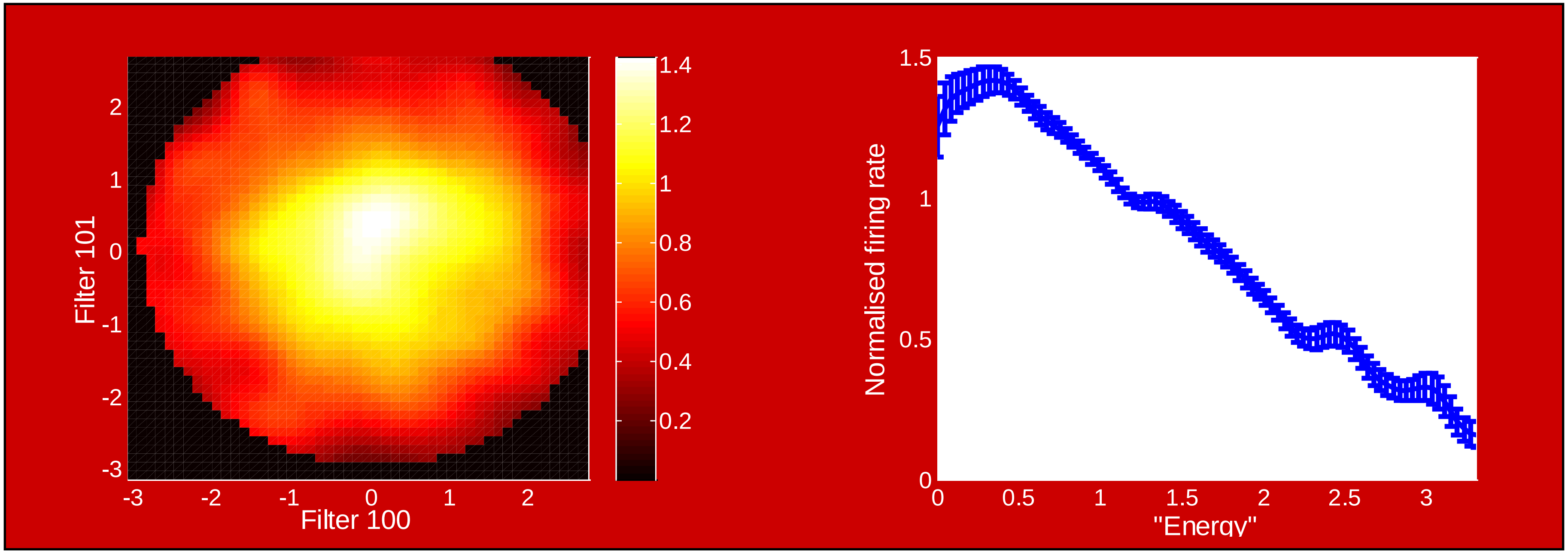
Next pair with +ve eigenvalues

Pair with -ve eigenvalues



Covariance analysis

Input/output relations for negative pair



Firing rate *decreases* with increasing projection:
suppressive modes

Beyond covariance analysis

1. Single, best filter determined by the first moment
2. A family of filters derived using the second moment
3. Use the entire distribution: information theoretic methods

→ Find the dimensions that maximize the ***mutual information*** between stimulus and spike

Removes requirement for Gaussian stimuli

Limitations

Not a completely “blind” procedure:
have to have some idea of the appropriate stimulus space

Very complex stimuli:
does a geometrical picture work or make sense?

Rates vs spikes:
what is our model trying to do? What do we want to recover?

Adaptation:
stimulus representations change with experience!