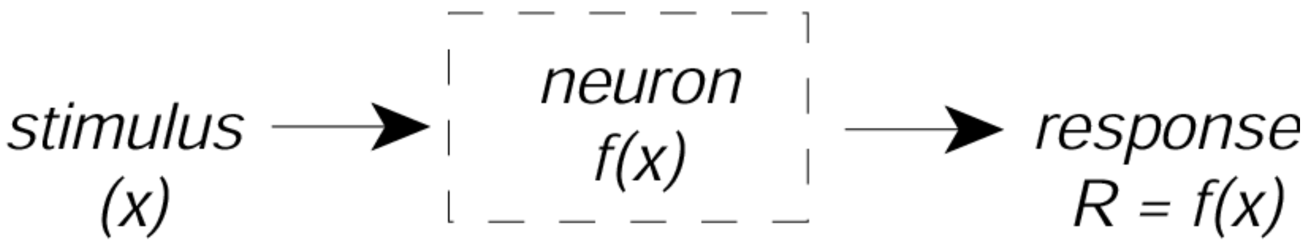
Spike-Triggered Approaches

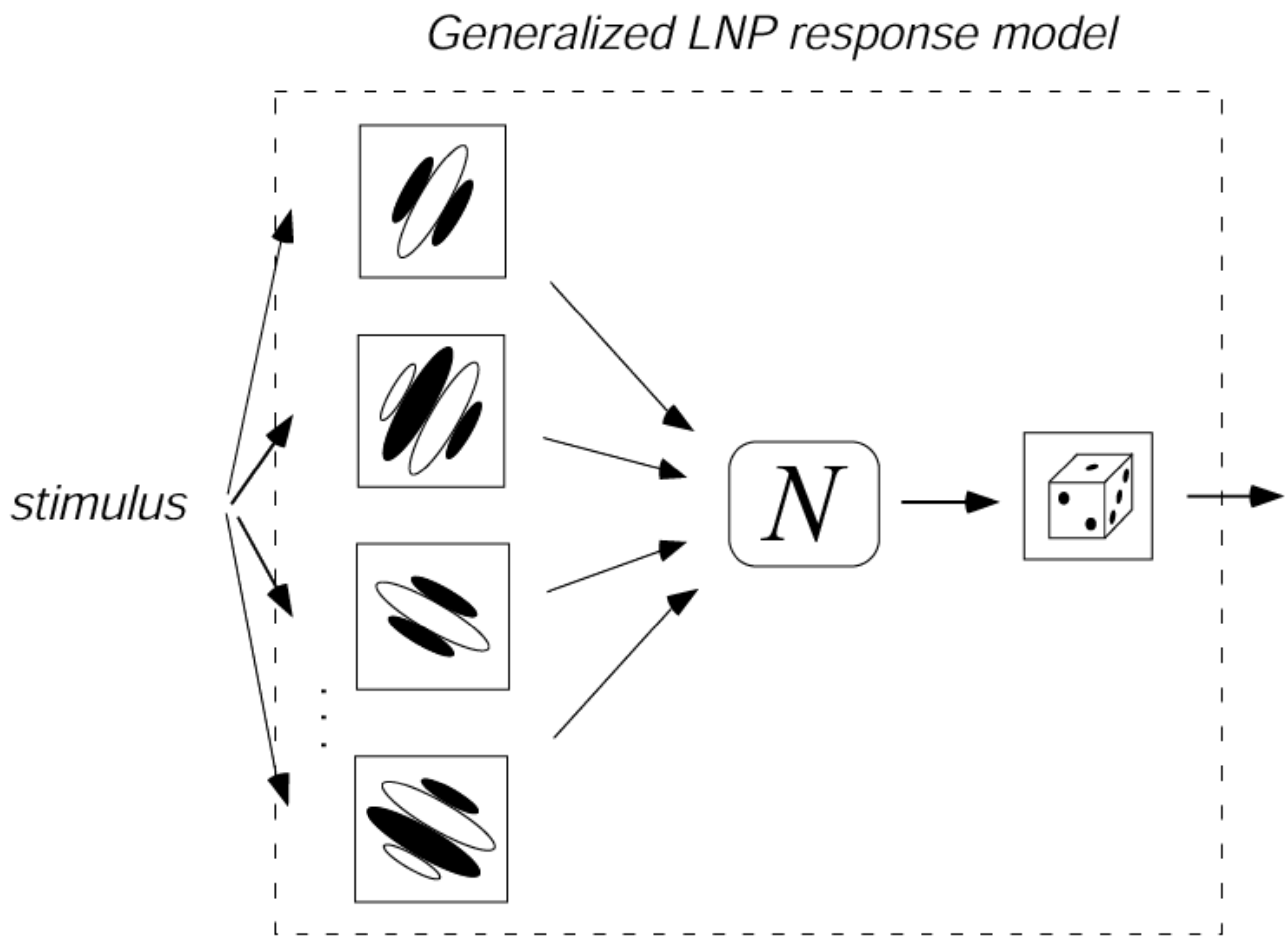
Odelia Schwartz

2016

Characterizing neural responses

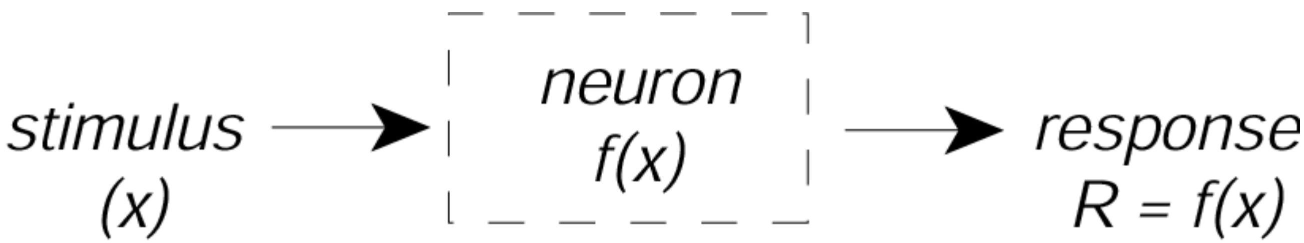


V1 Experiment



Methods paper on solving with Spike-triggered approaches:
Schwartz, Pillow, Rust, Simoncelli 2006

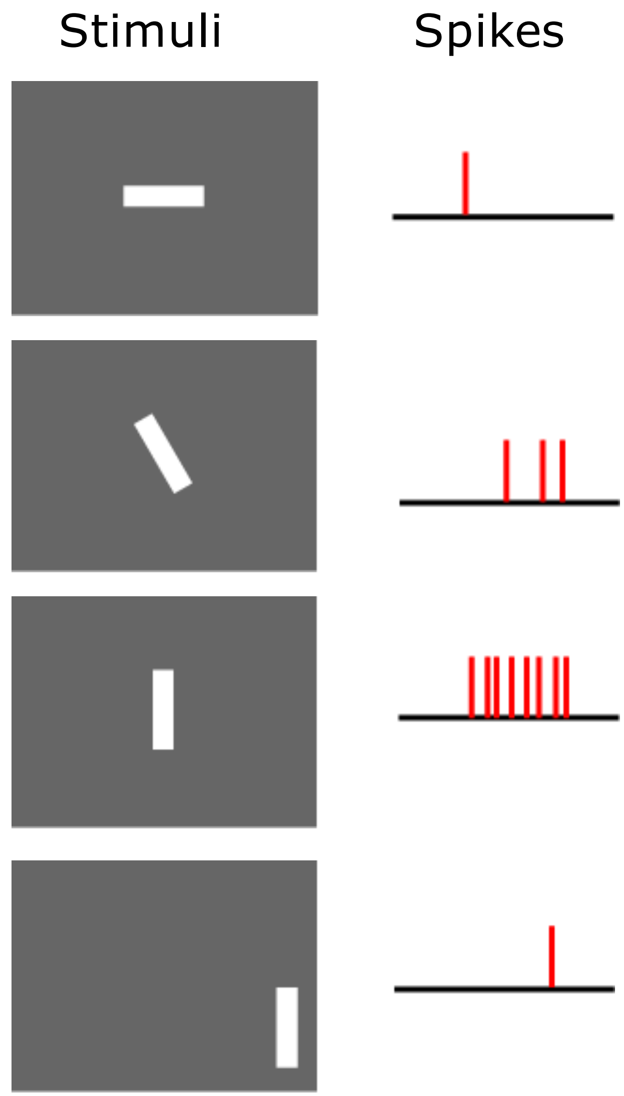
Characterizing neural responses



- Simple cell – traditional approach
- Simple cell (STA)
- When STA fails
- Complex cell (STC)
- Another example (STC)
- More generic model with multiple filters (STA and STC)

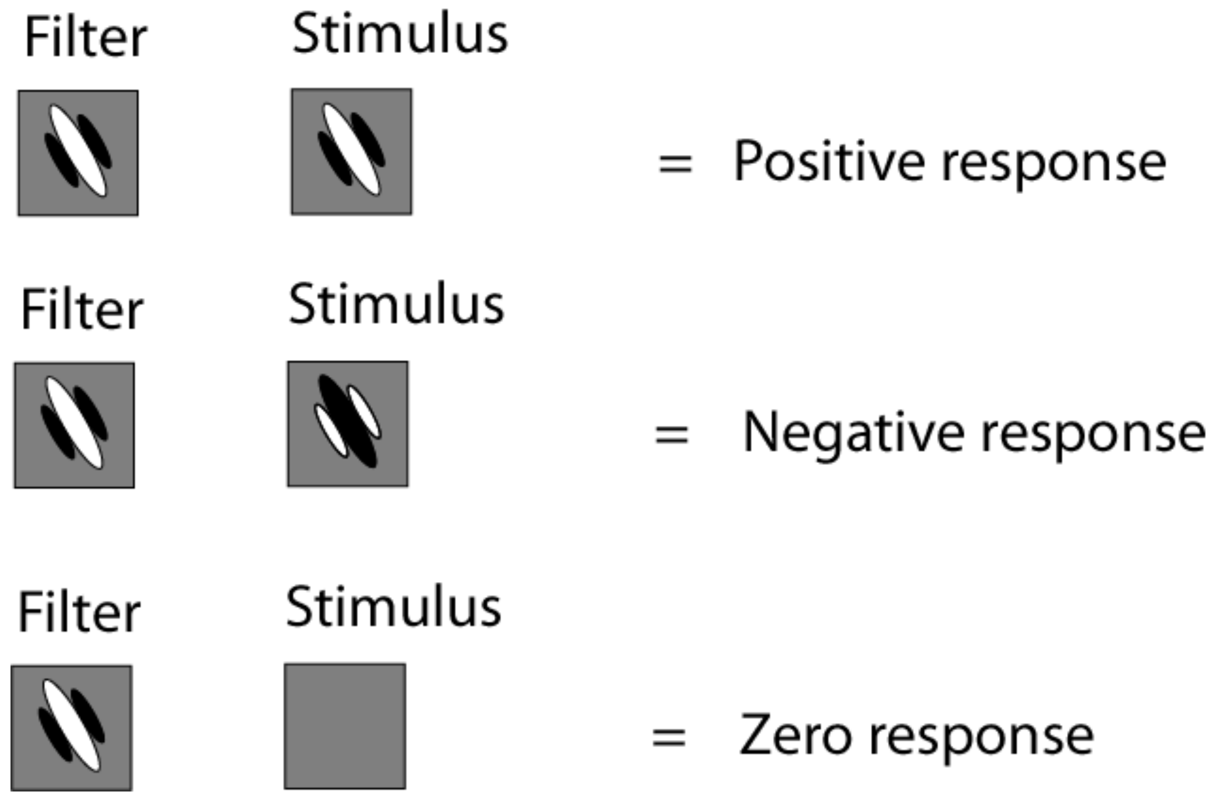
Experimental receptive field (filter)

Hubel and Wiesel, 1959



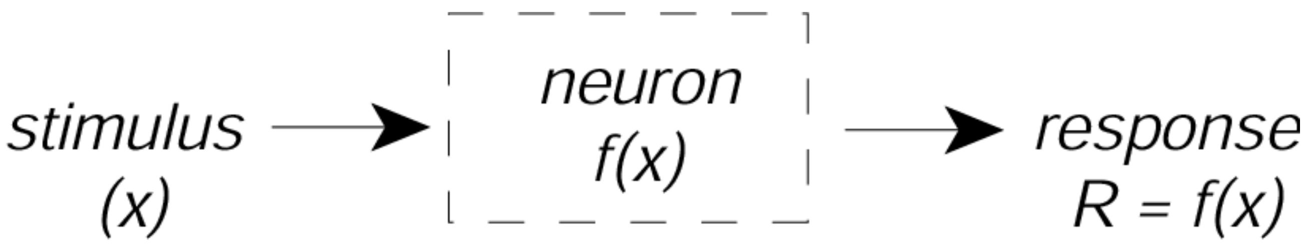
Experimental receptive field (filter)

Experimental receptive field (filter)



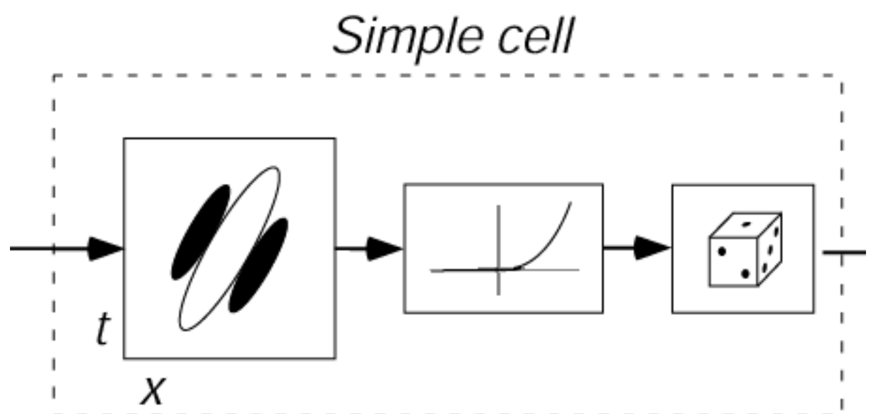
- Response of a filter
  = inner/dot product/projection of filter with stimulus

Characterizing neural responses



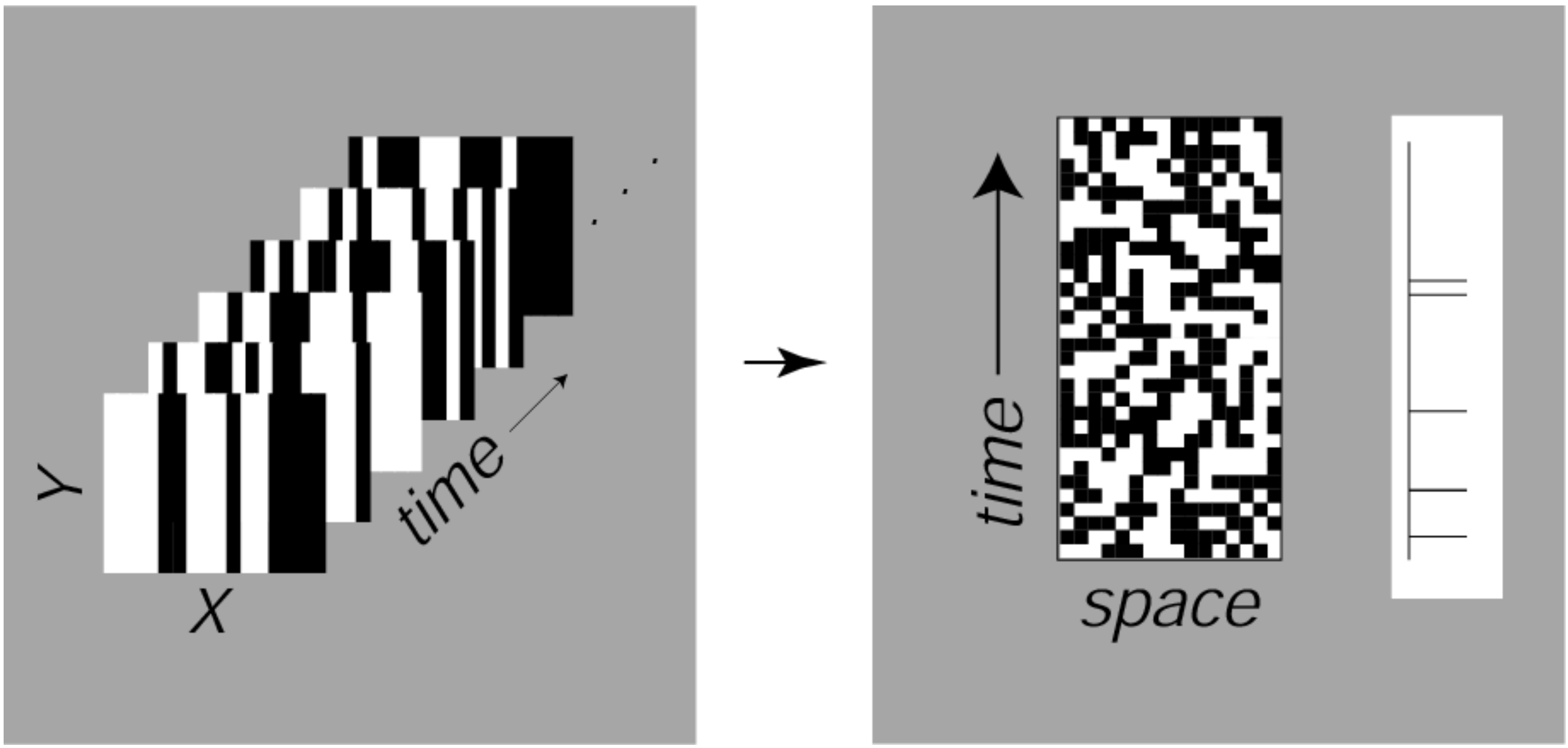
- Simple cell – traditional approach
- Simple cell (STA)
- When STA fails
- Complex cell (STC)
- Another example (STC)
- More generic model with multiple filters (STA and STC)

Spike-triggered average (STA)

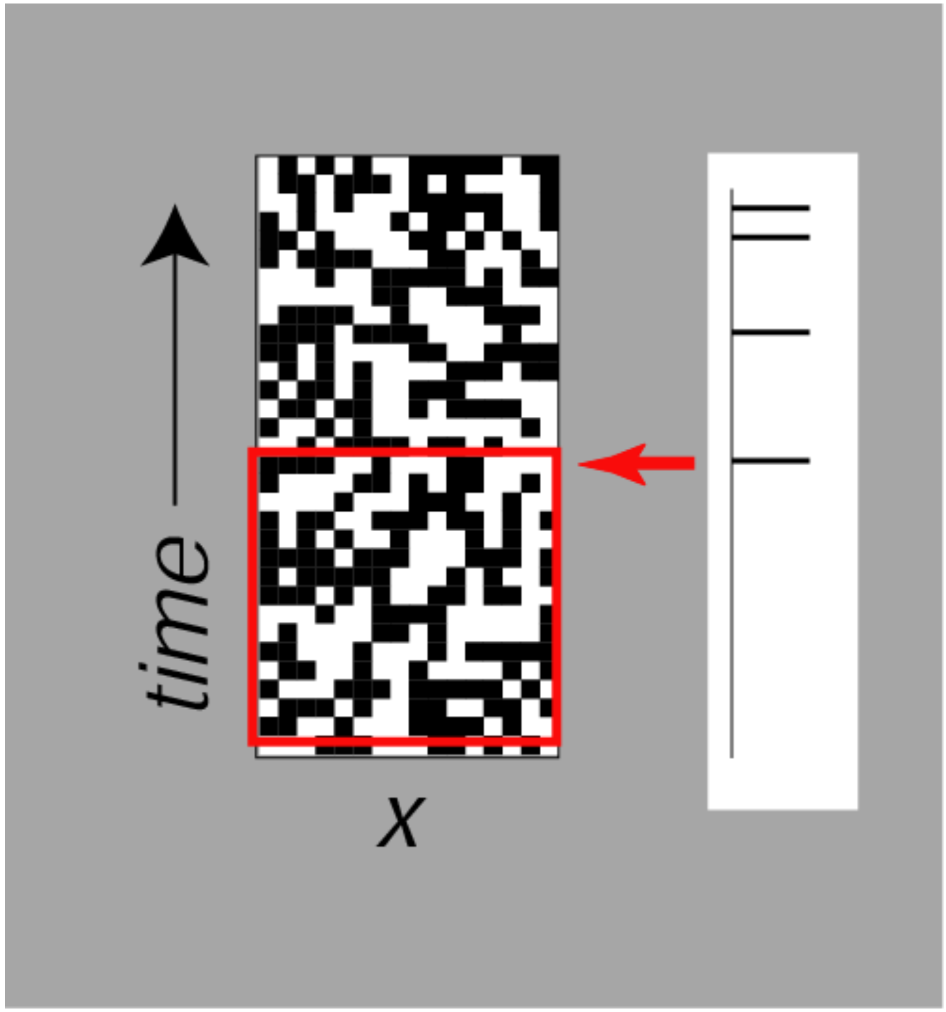


Spike-triggered approach

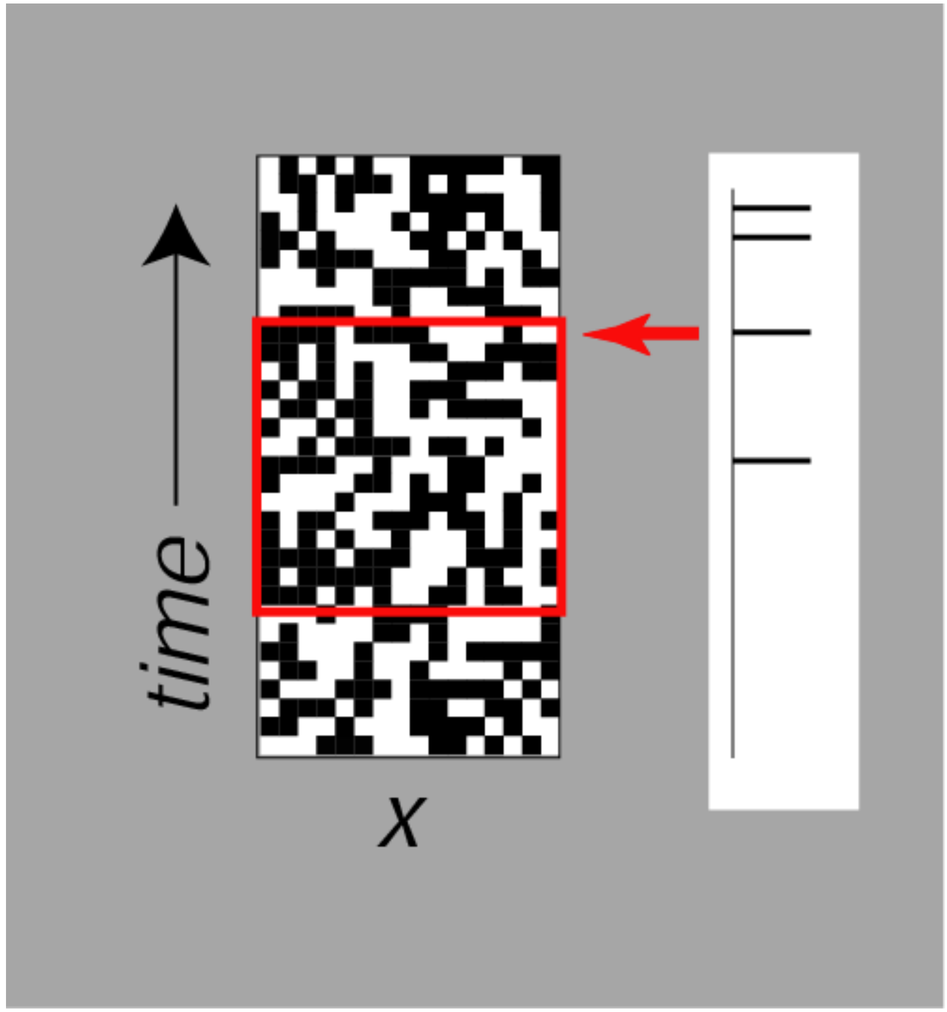
At each time step, we present randomly chosen bars



Spike-triggered approach



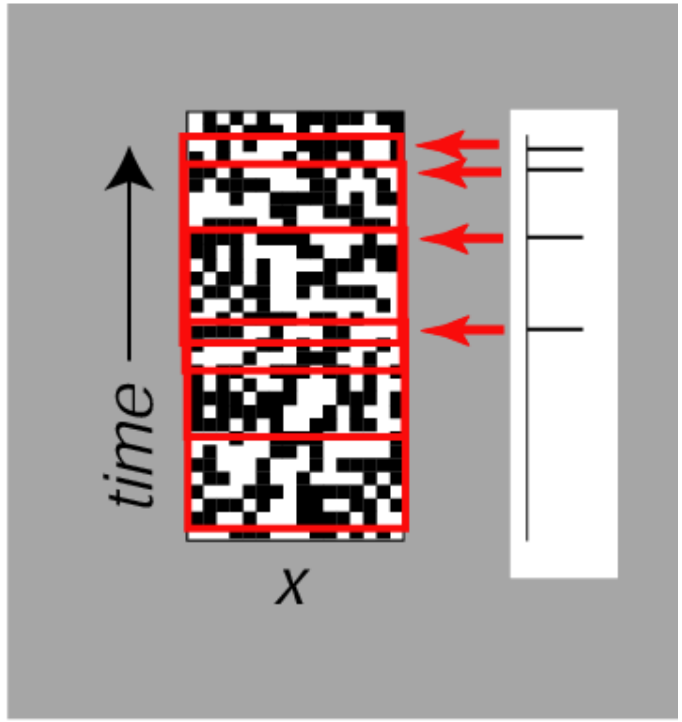
Spike-triggered approach



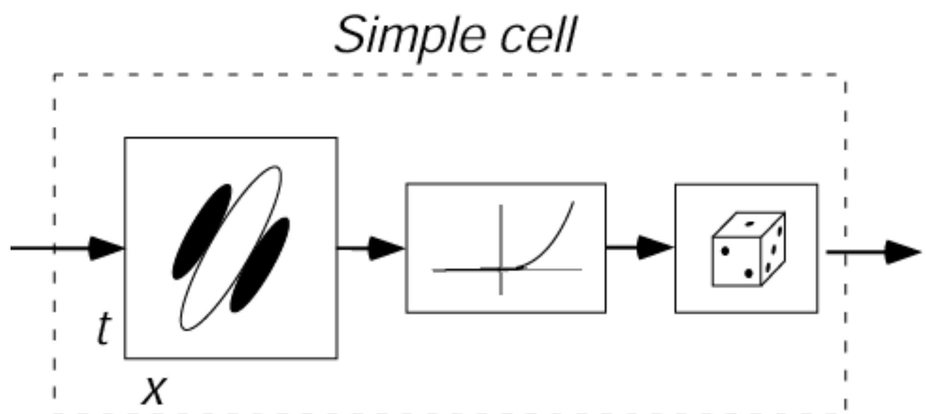
Spike-triggered average (STA)

STA

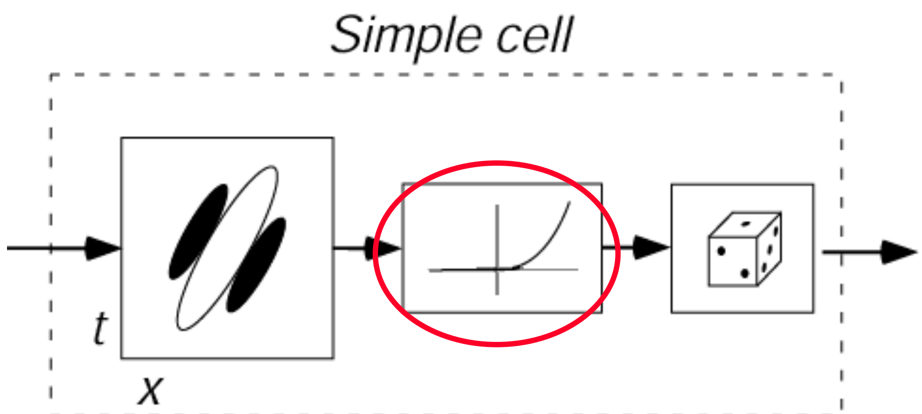
Average of
spike-triggered
stimuli



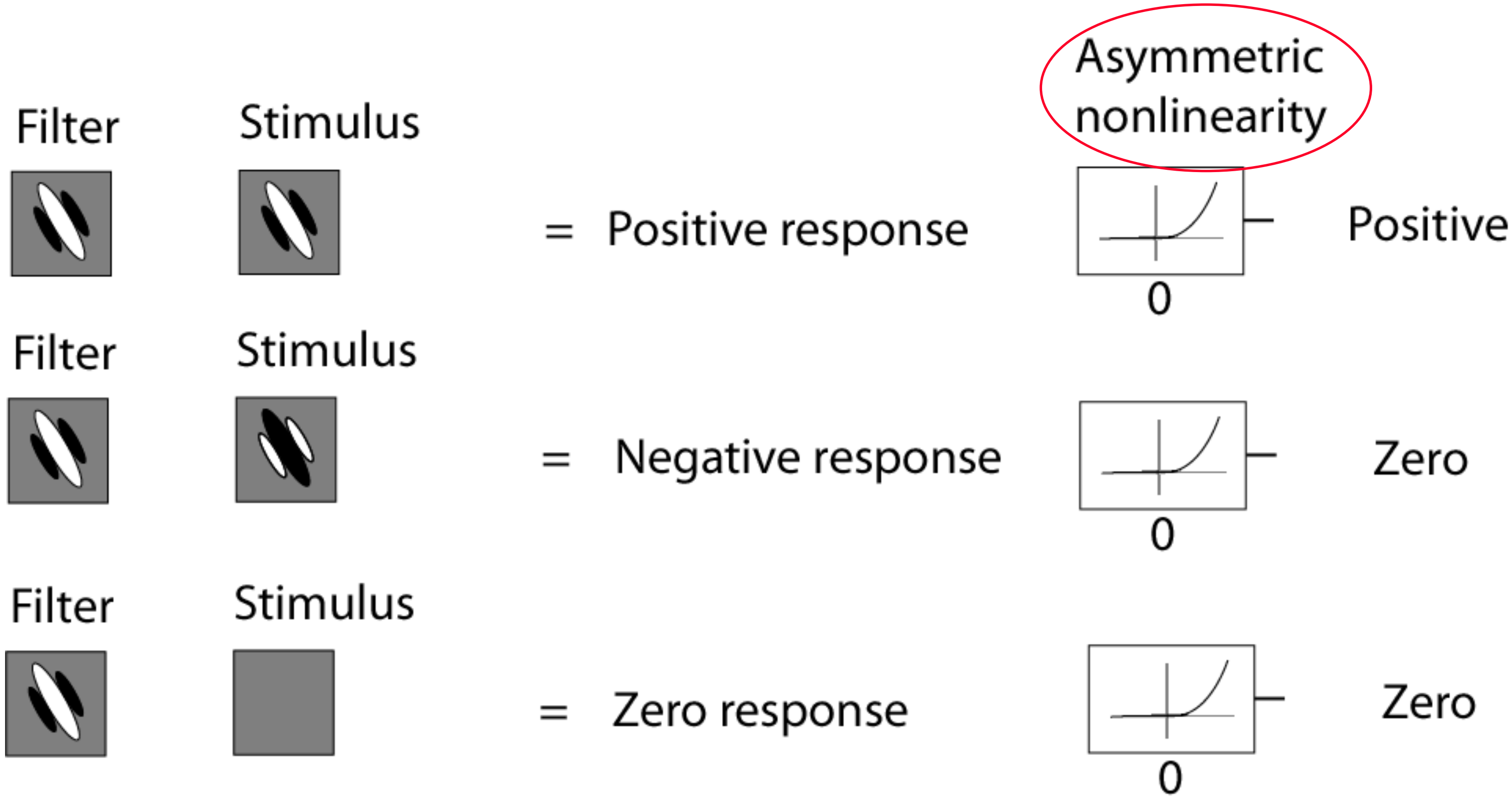
Effect of nonlinearity in model?



Effect of nonlinearity in model?

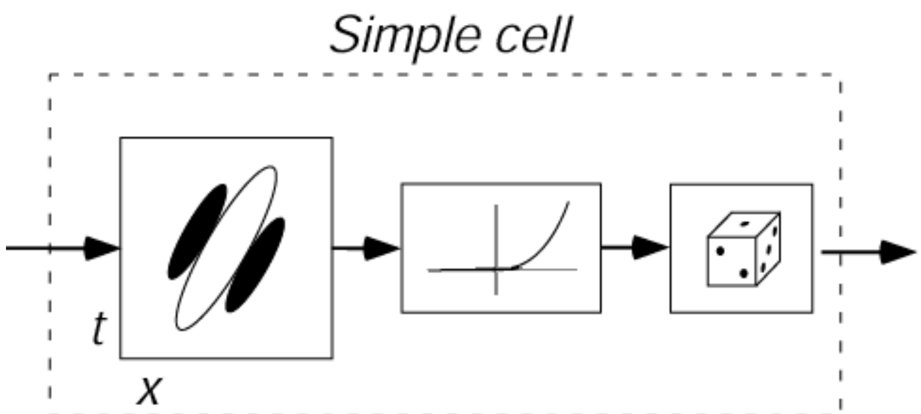


Effect of nonlinearity in model?



- Nonlinearity sets negative filter responses to zero (firing rates are positive)

Spike-triggered average (STA)

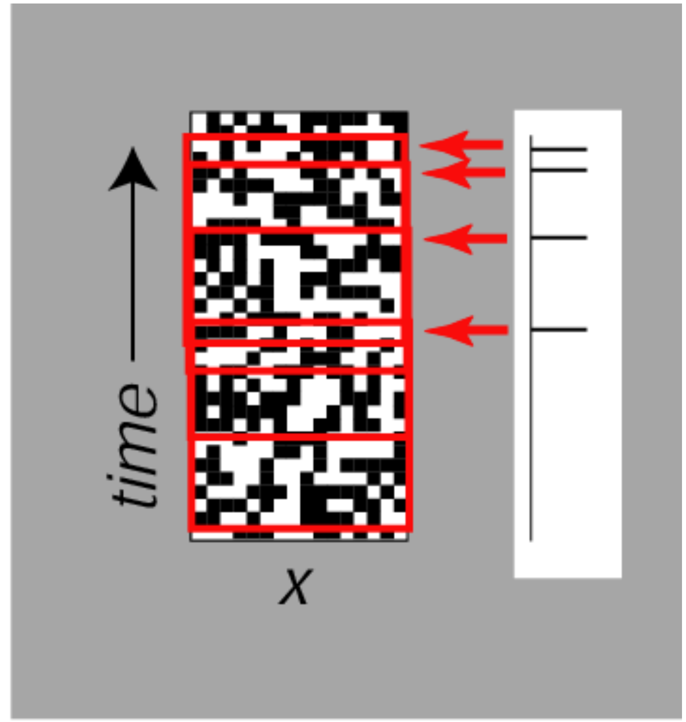


Stimuli that are more similar to filter are more likely to elicit a spike…

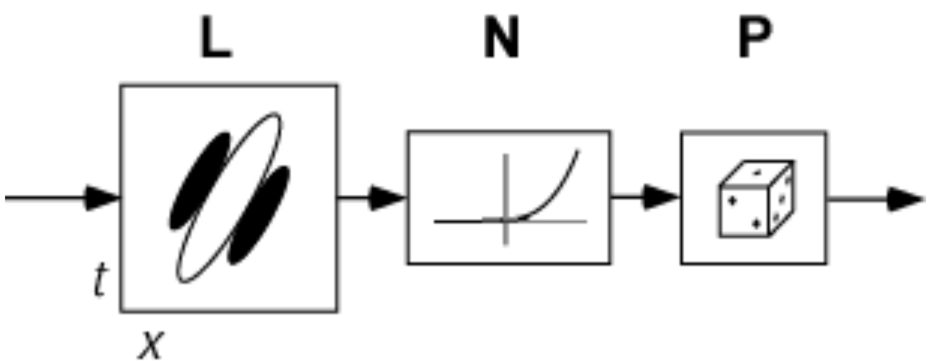
Spike-triggered average (STA)

STA

Average of spike-triggered stimuli



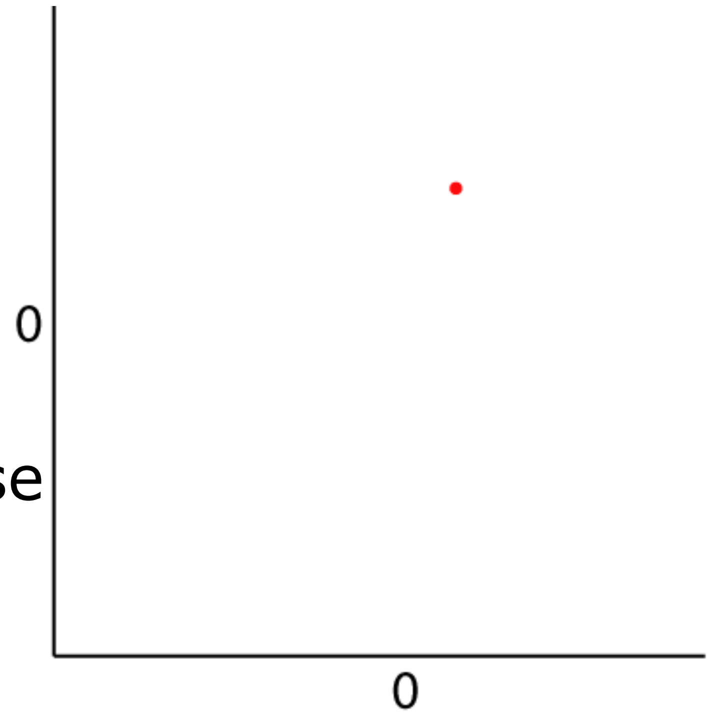
Model:

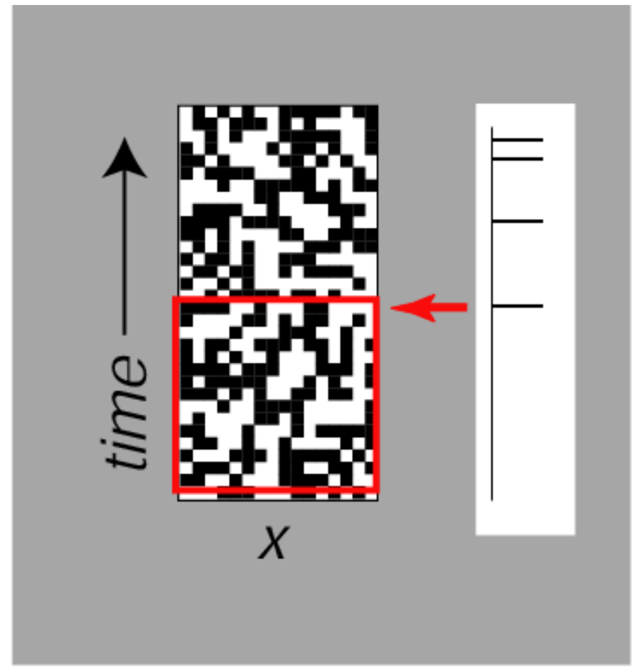


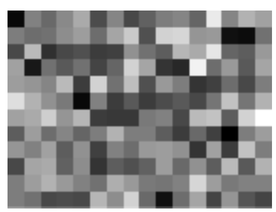
Spike-triggered average (STA)

Geometrical view:

STA response







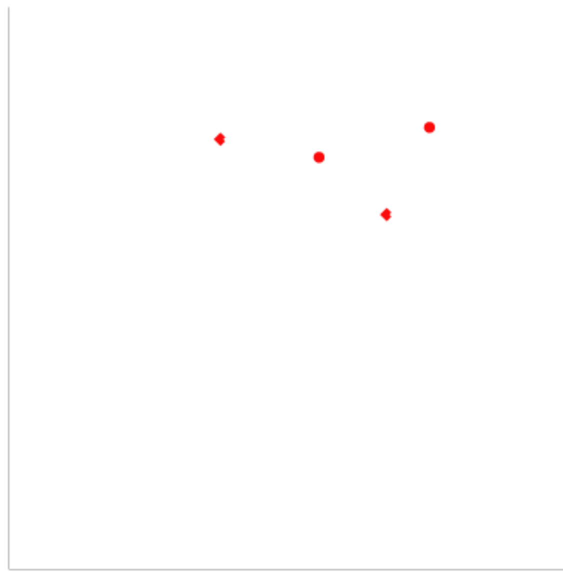
Random filter response

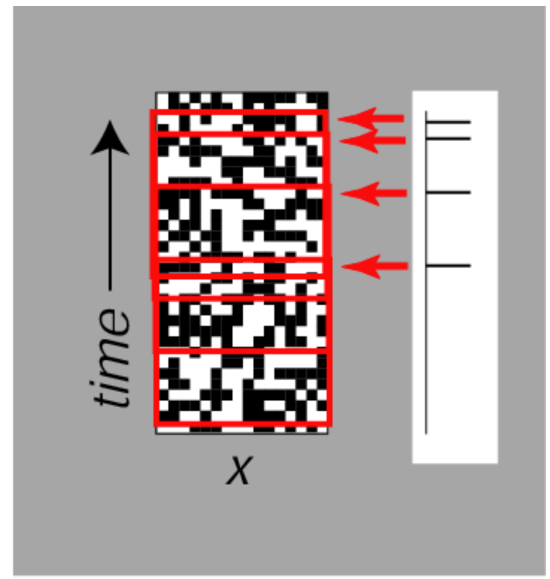
Spike-triggered average (STA)

Geometrical view:

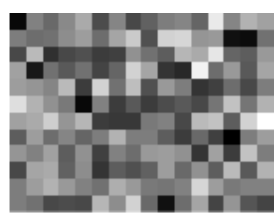
STA response

0





0



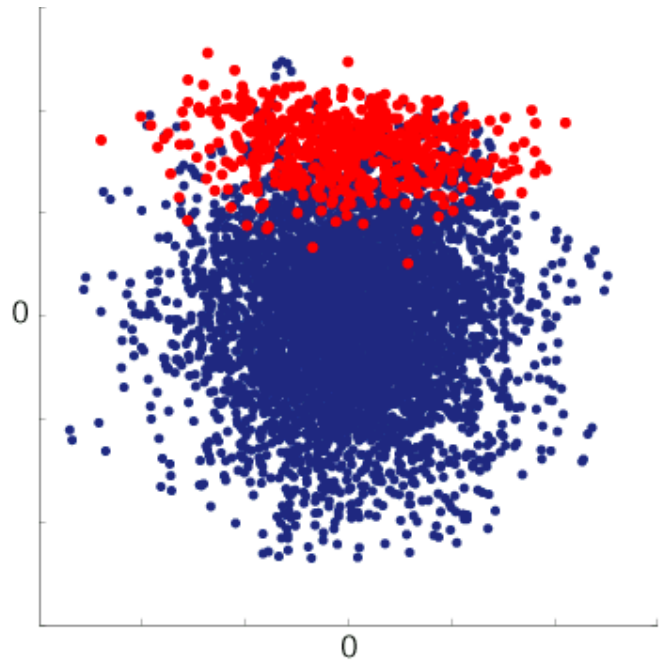
Random filter response

Spike-triggered average (STA)

Geometrical view: change in the mean

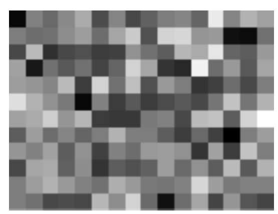
Large filter response likely to elicit spike

STA response



Spike stimuli

Raw stimuli

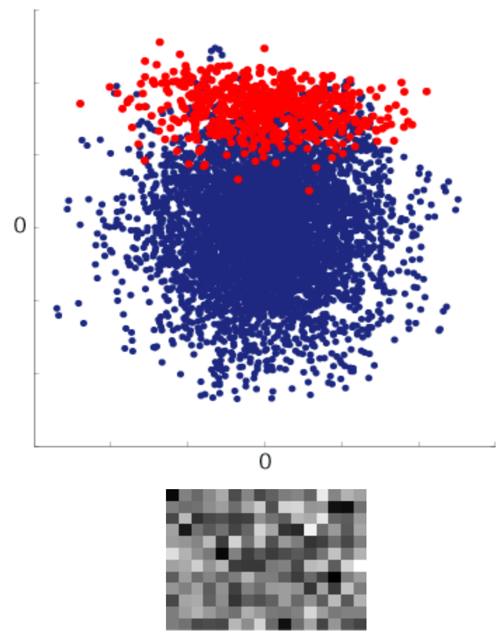


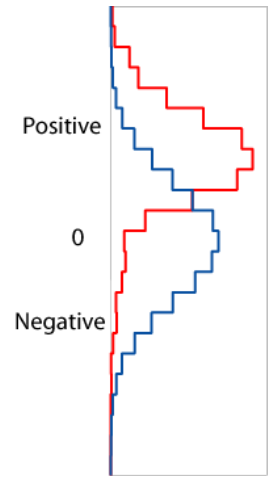
Random filter response

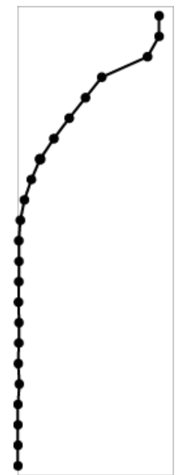
Spike-triggered average (STA)

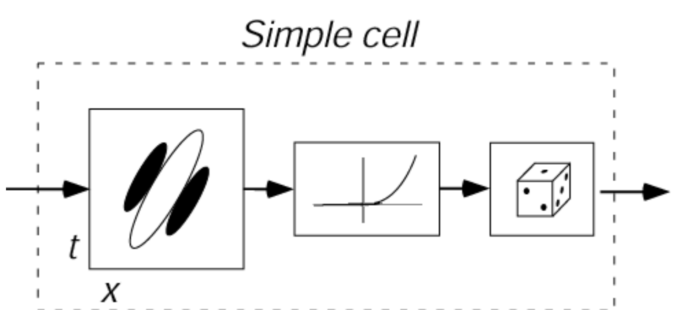
We can also recover the nonlinearity

STA







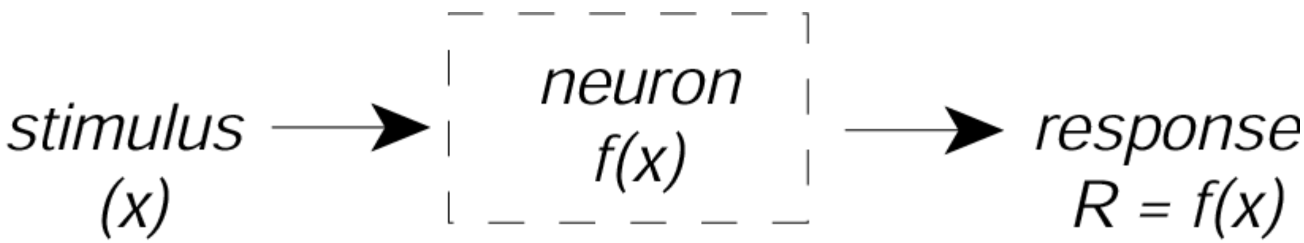


Steps

1. Assume a model (filter/s, nonlinearity)
   (we assumed one filter and asymmetric nonlinearity)

2. Estimate model components (filter/s, nonlinearity)
   (we looked for changes in mean: STA)

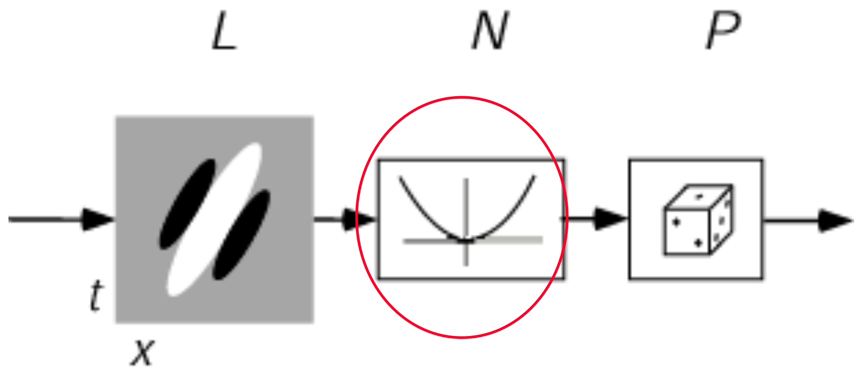
Characterizing neural responses



- Simple cell – traditional approach
- Simple cell (STA)
- When STA fails
- Complex cell (STC)
- Another example (STC)
- More generic model with multiple filters (STA and STC)

But STA does not always work...

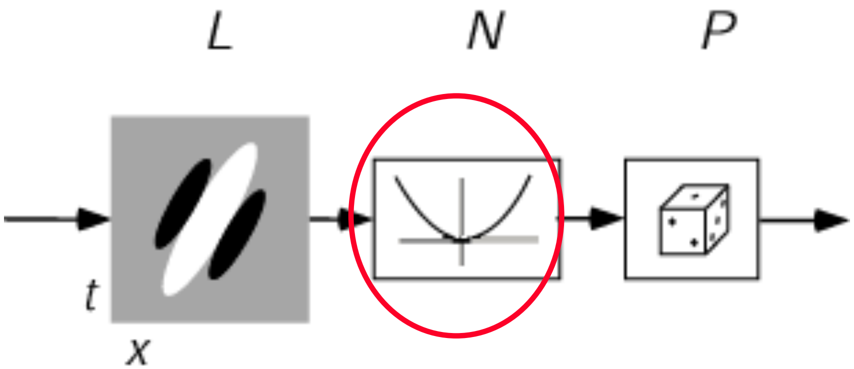
Example: Symmetric nonlinearity



STA filter?

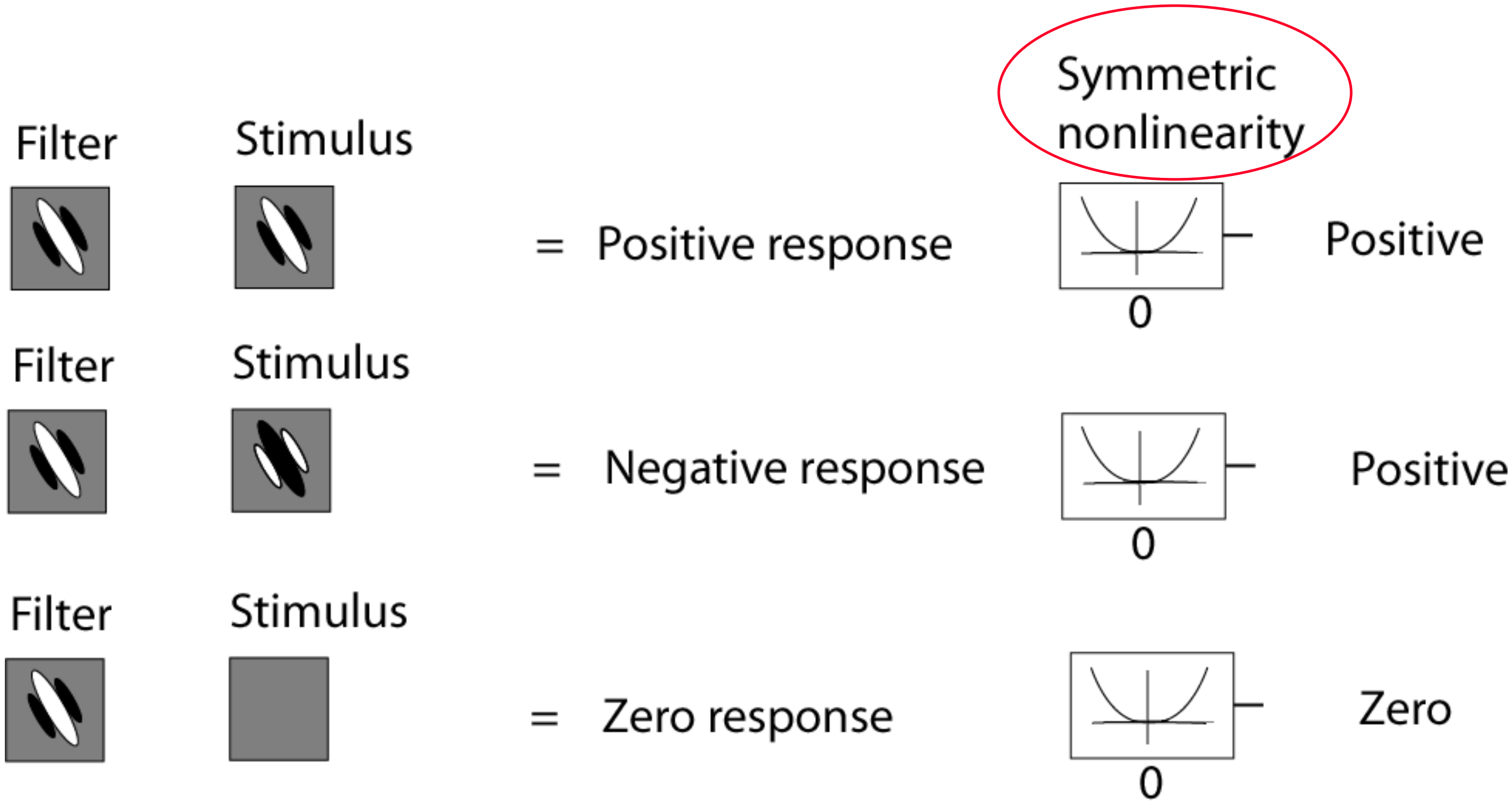
But STA does not always work...

Example: Symmetric nonlinearity



STA filter!

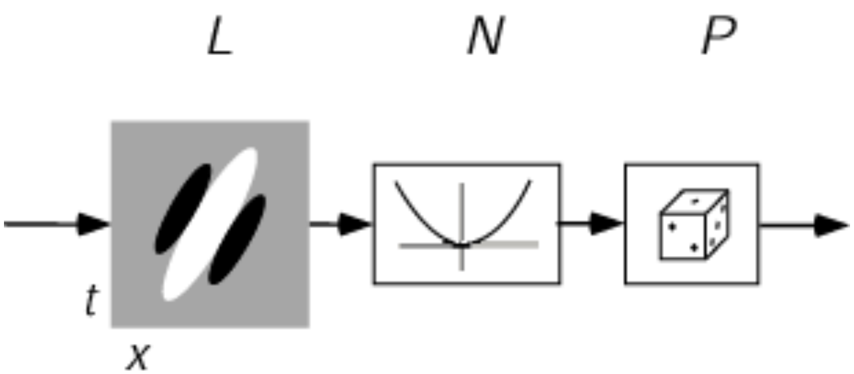
What happened?



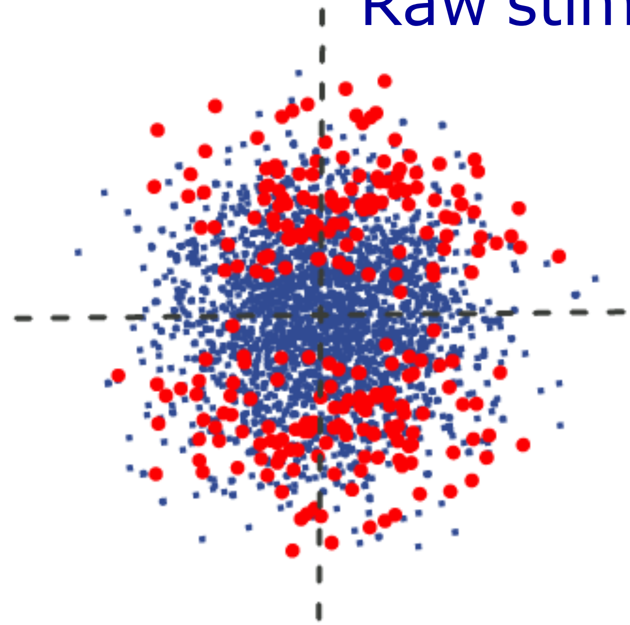
- Nonlinearity sets negative filter responses to positive (firing rates are positive)

What happened?

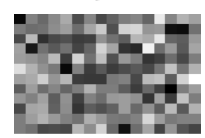
Large or small filter response likely to elicit spike
Mean stimuli eliciting spikes = 0



Spike stimuli
Raw stimuli



Model filter



Random filter response

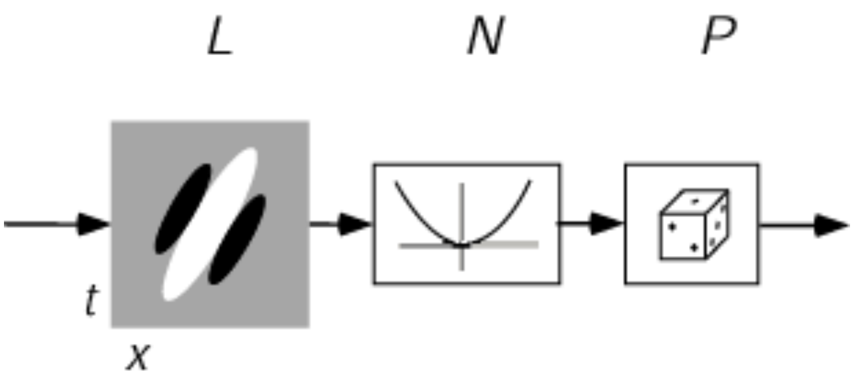
STA filter!

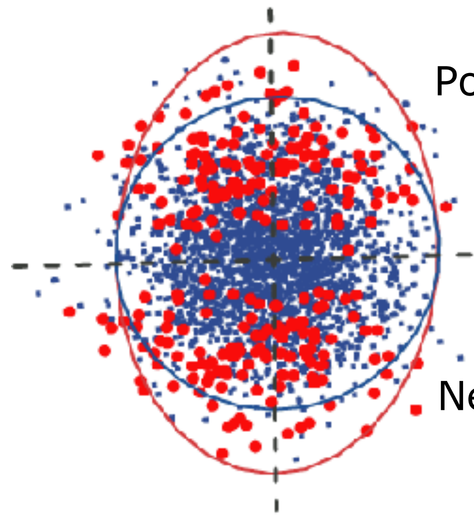
Change in the variance

Large or small filter response likely to elicit spike

Spike stimuli

Raw stimuli





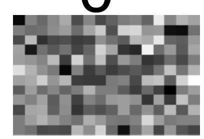
Positive

Model filter

0

Negative

0

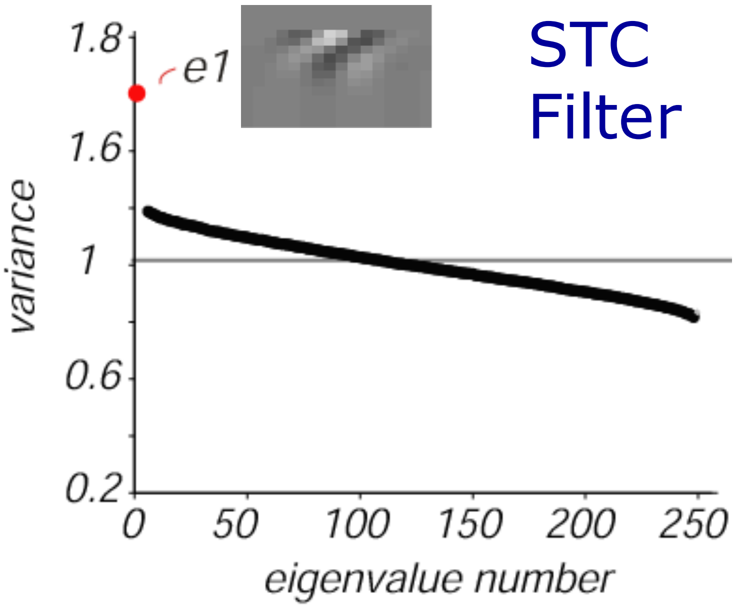


STA filter!

Random filter response

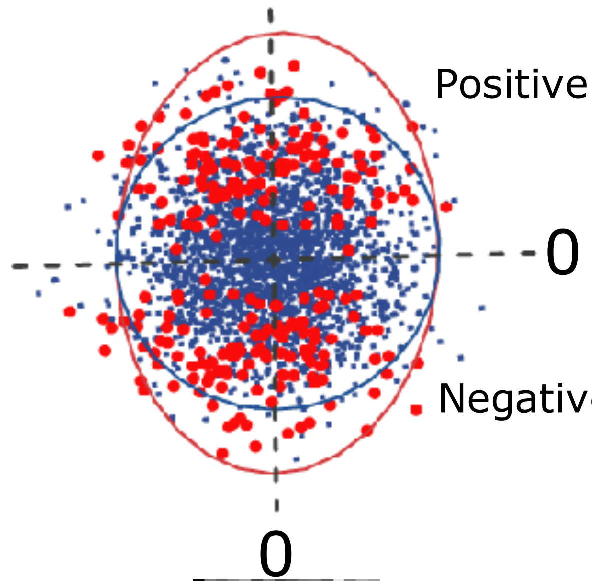
Change in the variance (STC)

Standard algebra techniques (eigenvector analysis) recovers changes in variance

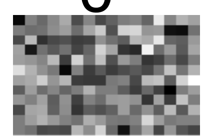


STC
Filter

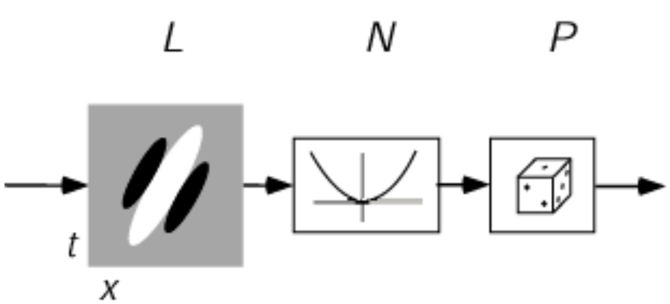
Spike stimuli
Raw stimuli



Model
filter



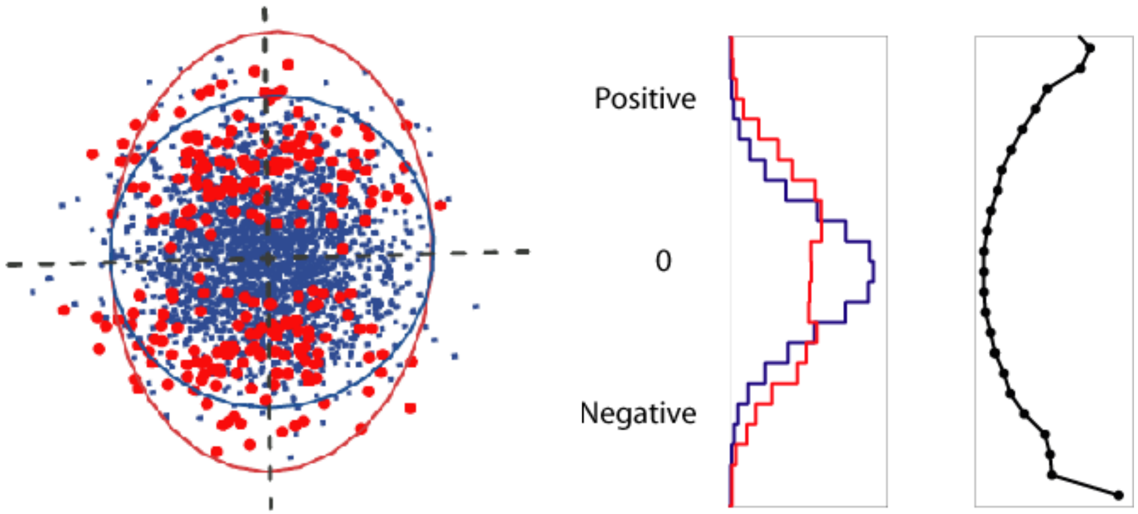
Random filter response

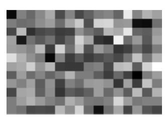


Change in the variance (STC)

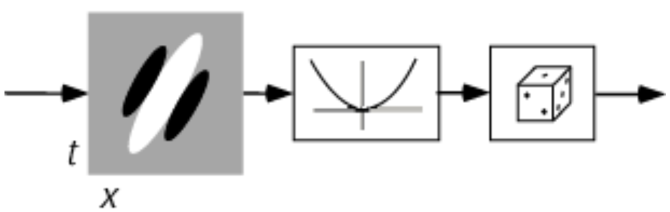
We can also recover the nonlinearity

Model filter





Random filter response

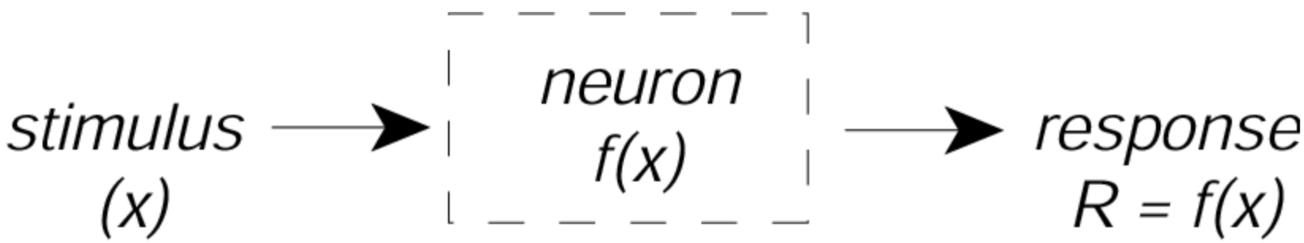


Steps

1. Assume a model (filter/s, nonlinearity)
   (we assumed one filter and symmetric nonlinearity)

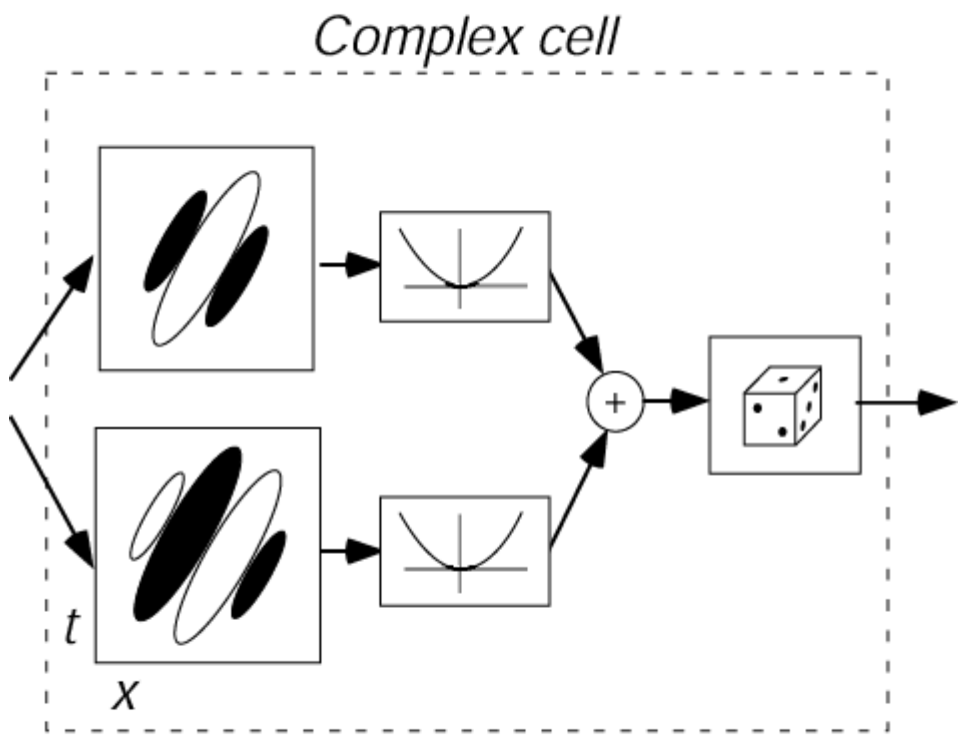
2. Estimate model components (filter/s, nonlinearity)
   (STA failed)
   (we looked for changes in variance: STC)

Characterizing neural responses



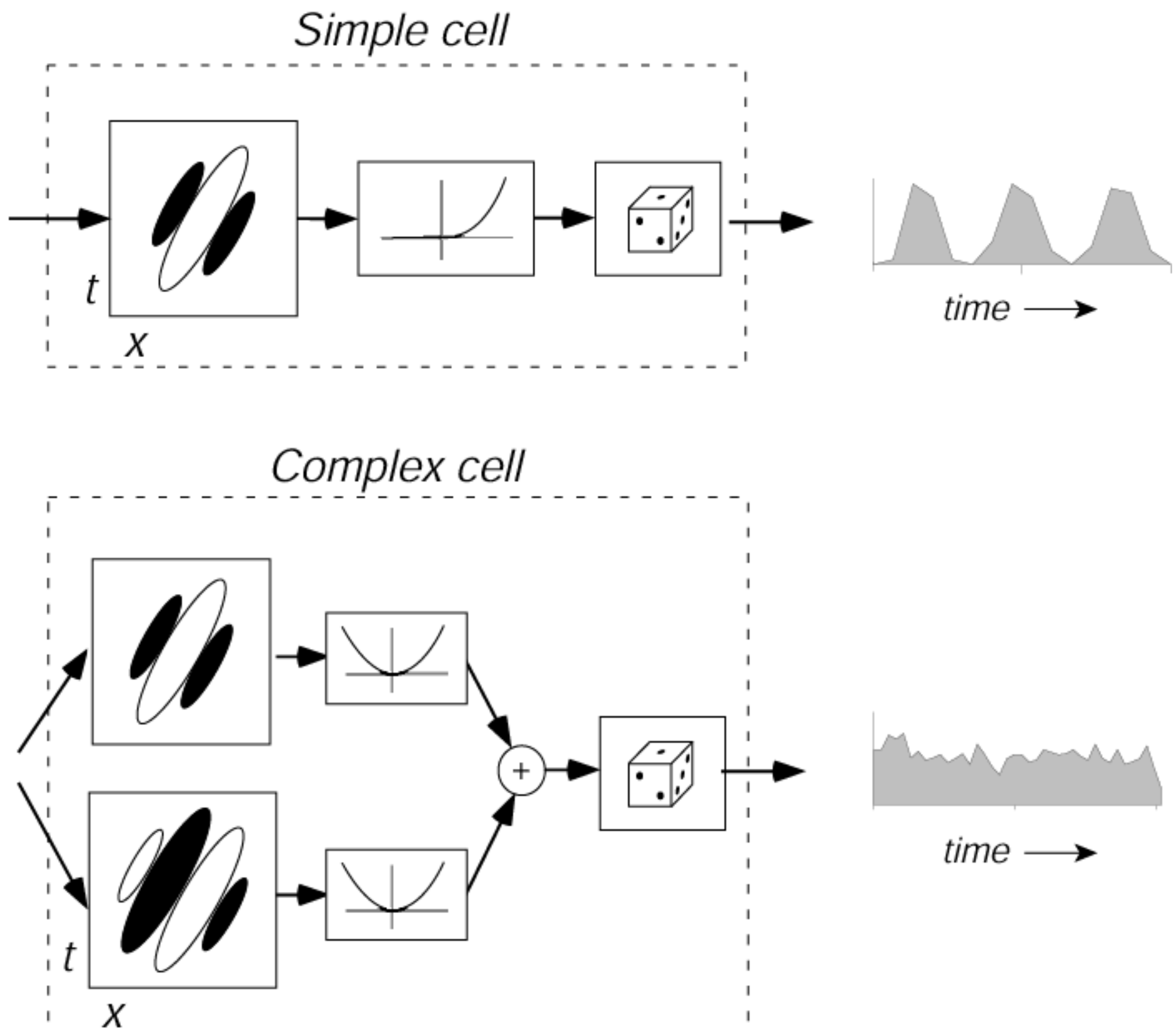
- Simple cell – traditional approach
- Simple cell (STA)
- When STA fails
- Complex cell (STC)
- Another example (STC)
- More generic model with multiple filters (STA and STC)

What about multiple filters??



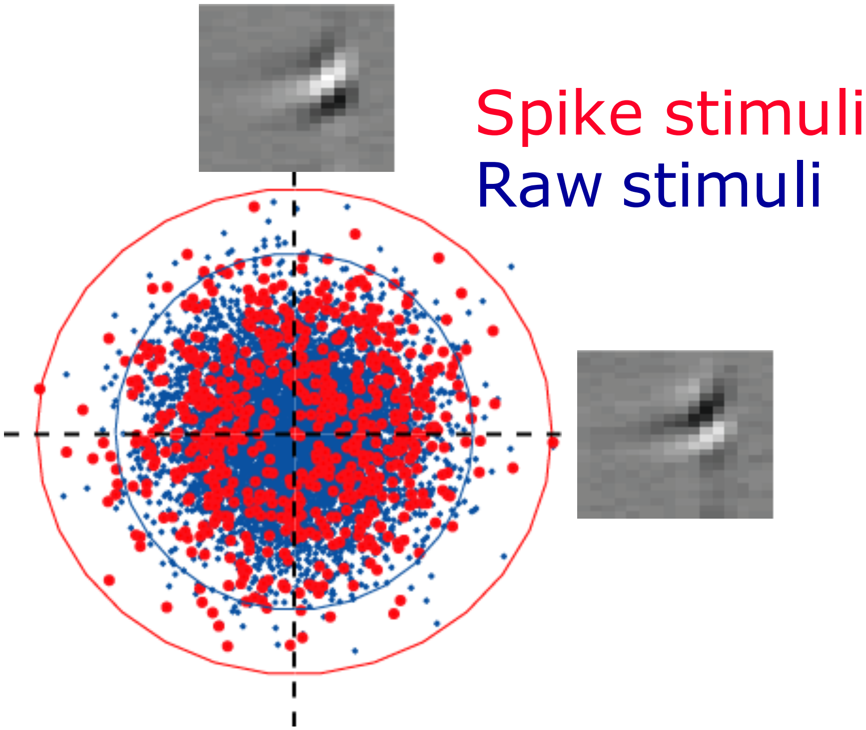
Adelson & Bergen (1985)

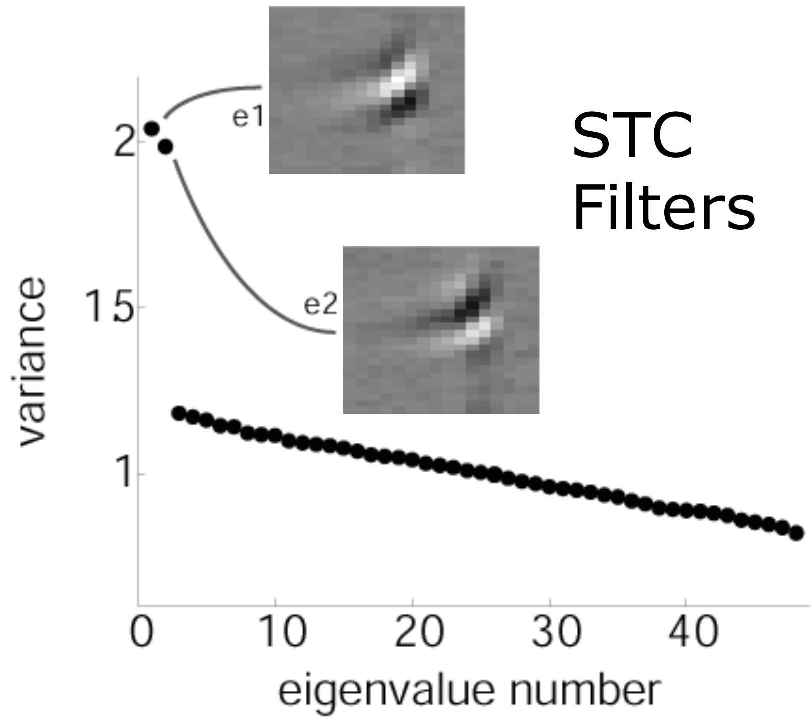
What about multiple filters??



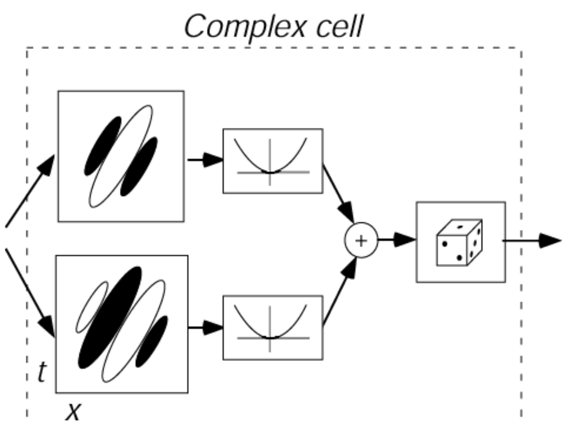
Adelson & Bergen (1985)

Changes in the variance (STC)



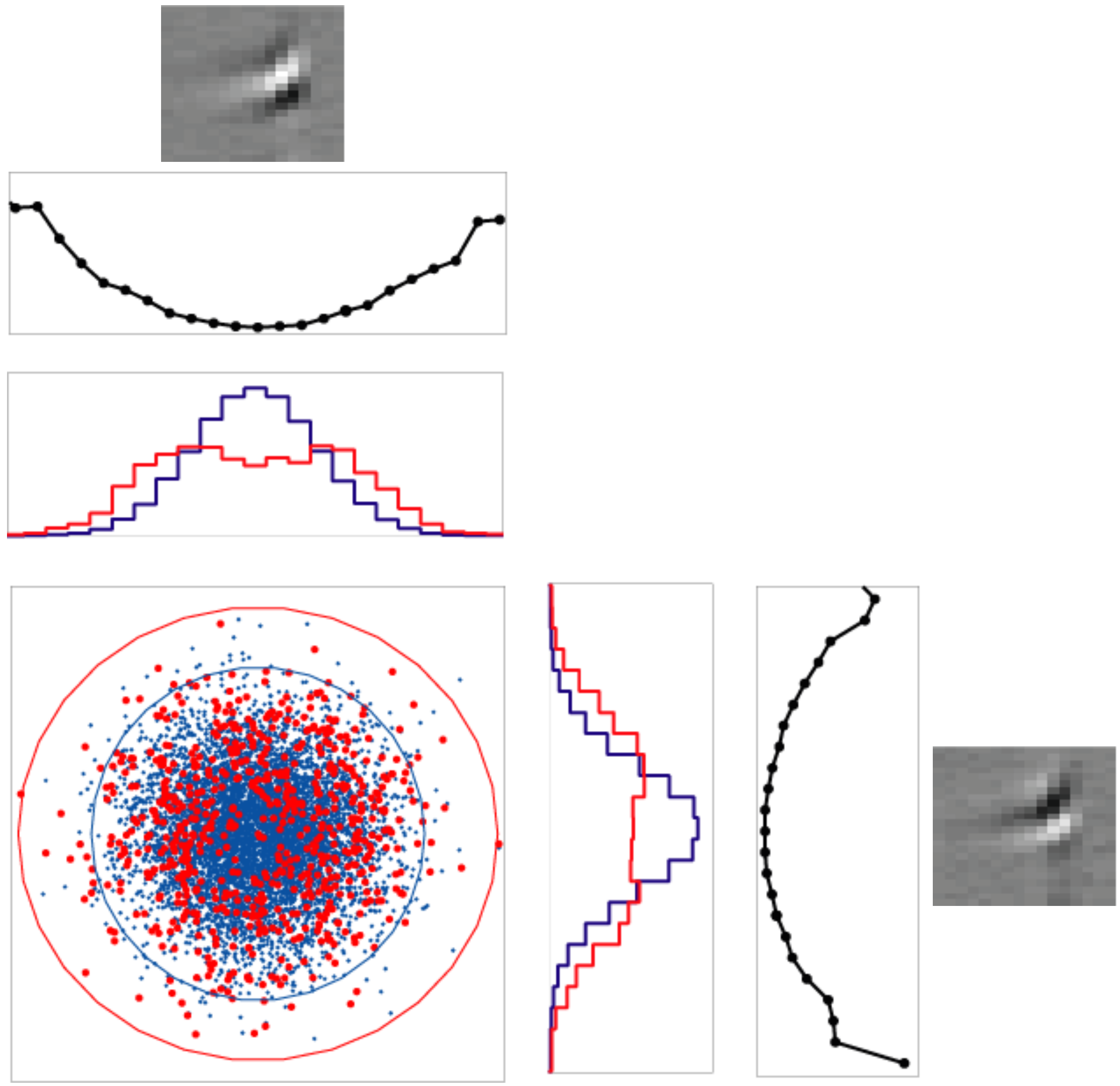


STC
Filters



STA filter!

Changes in the variance (STC)



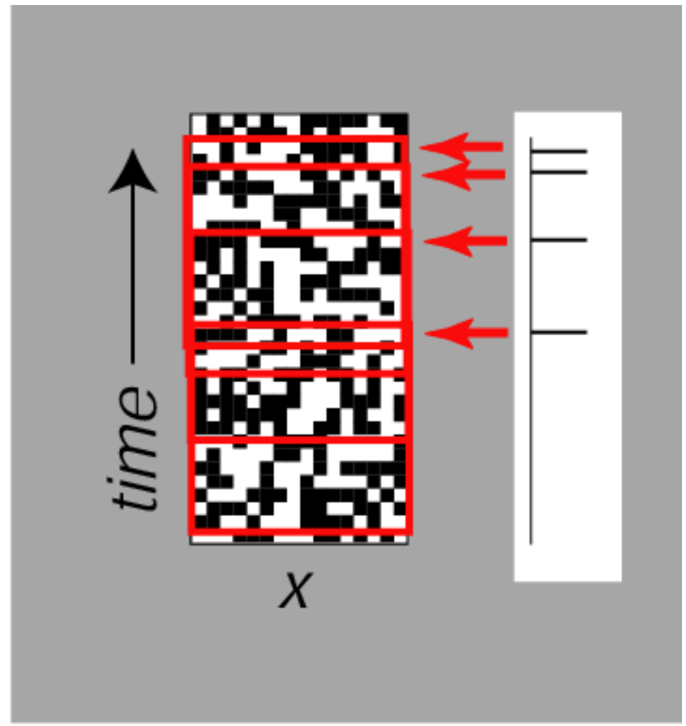
Steps

1. Assume a model (filter/s, nonlinearity)
   (we assumed more than one filter and symmetric nonlinearity)

2. Estimate model components (filter/s, nonlinearity)
   (we looked for changes in variance: STC)

Spike-triggered covariance (STC)

Covariance of
Spike-triggered
stimuli

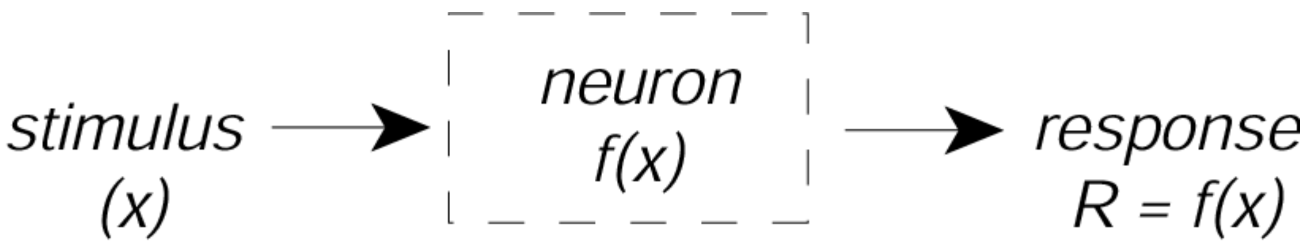


▪

▪

▪ Look for changes in variance of spike-triggered stimuli

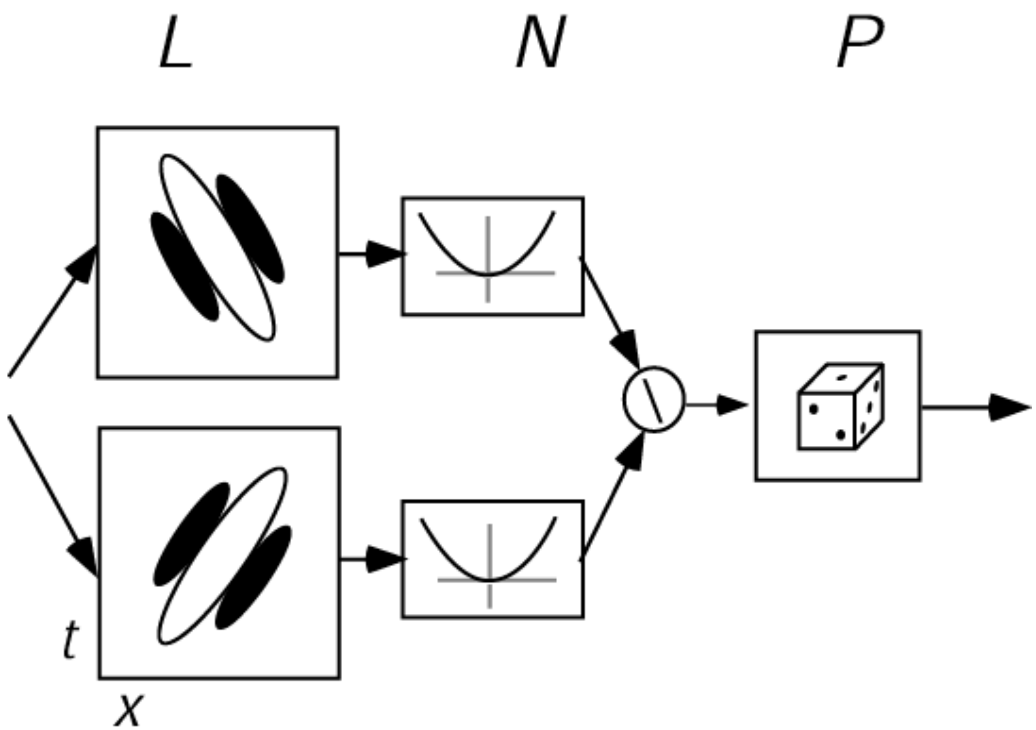
Characterizing neural responses



- Simple cell – traditional approach
- Simple cell (STA)
- When STA fails
- Complex cell (STC)
- Another example (STC)
- More generic model with multiple filters (STA and STC)

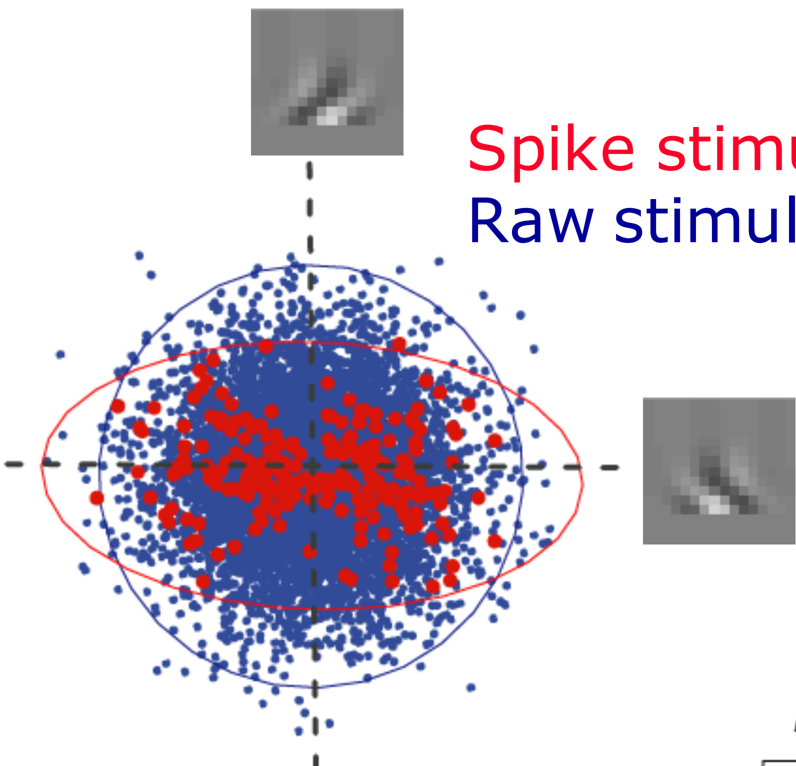
What about multiple filters??

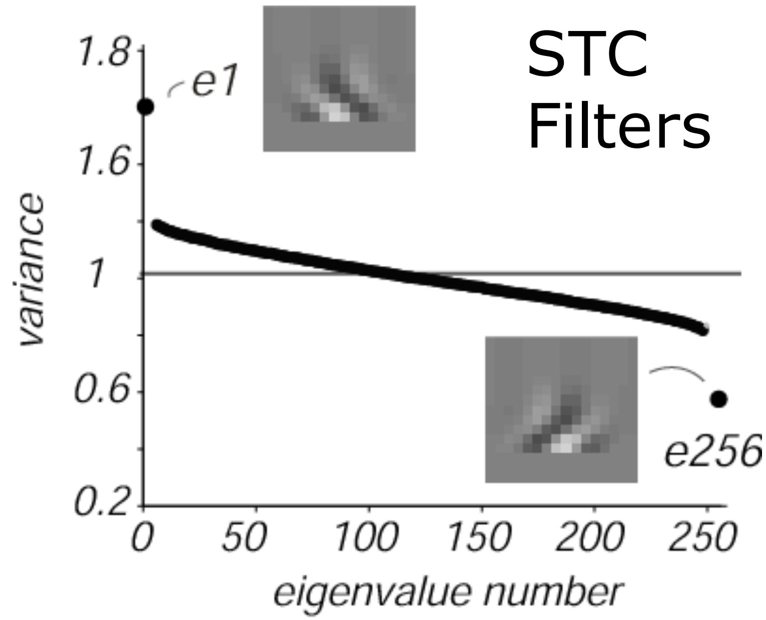
Second filter suppressive (here division)

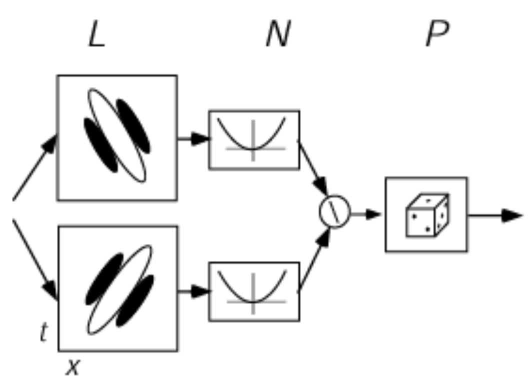


What about multiple filters??

Second filter brings about reduction in variance!

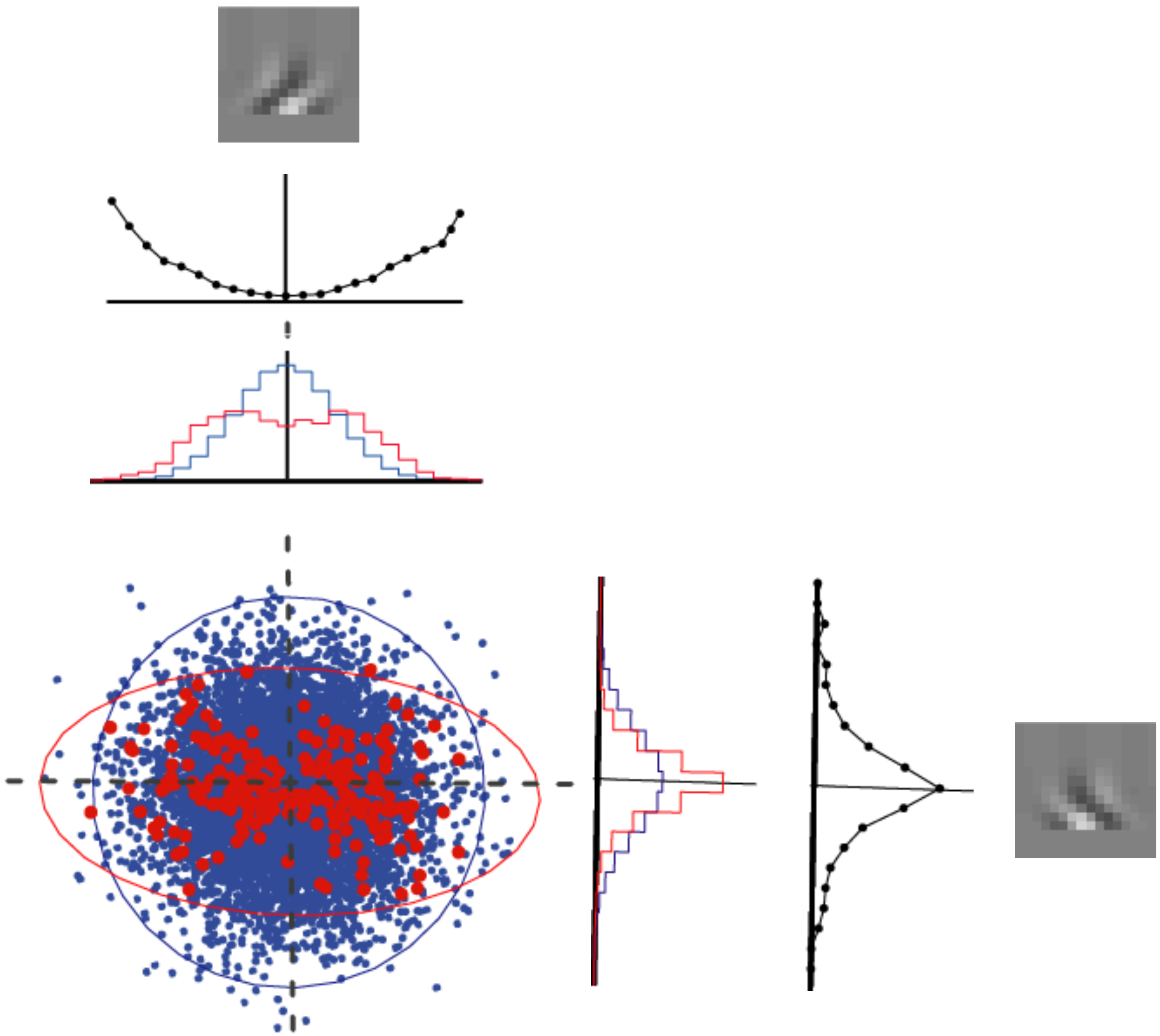






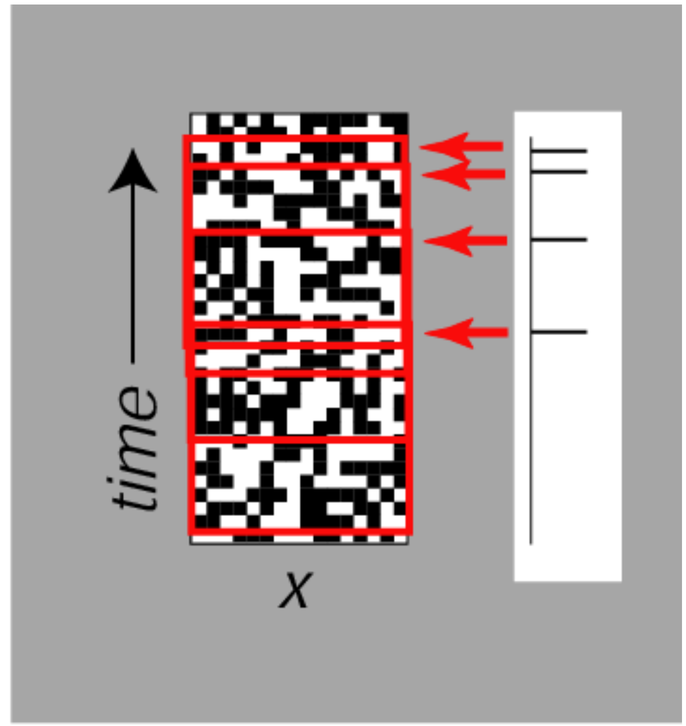
What about multiple filters??

Second filter brings about reduction in variance!



Spike-triggered covariance (STC)

Covariance of
Spike-triggered
stimuli



Look for increase or decrease of
variance of spike-triggered stimuli

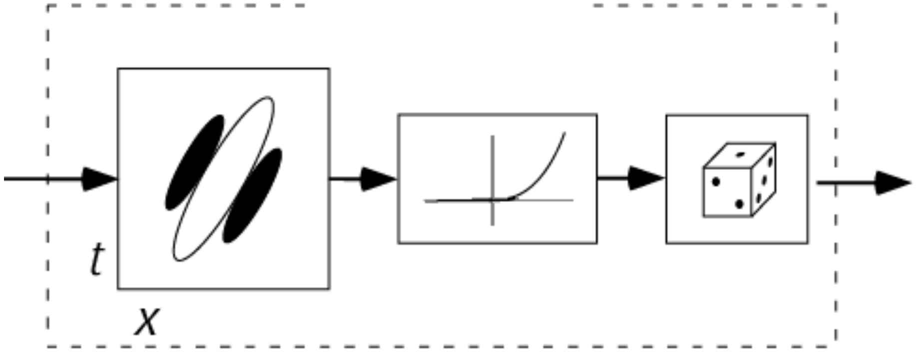
Steps

1. Assume a model (filter/s, nonlinearity)
   (we assumed more than one filter and symmetric nonlinearity)

2. Estimate model components (filter/s, nonlinearity)
   (we looked for changes in variance: STC)

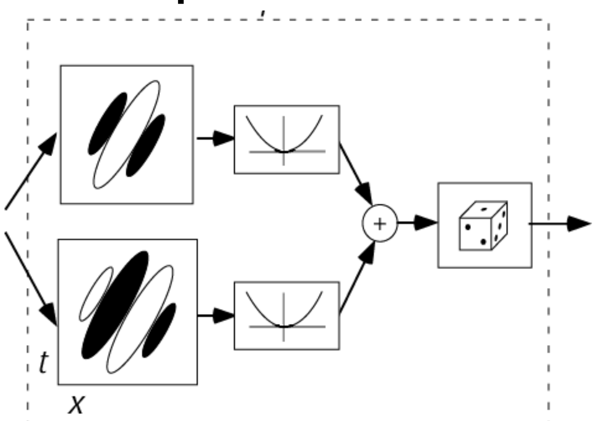
Spike-triggered approaches

Simple cell

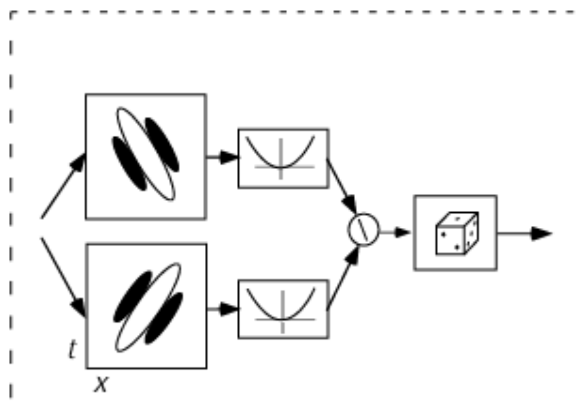


Change in the mean (STA)

Complex cell

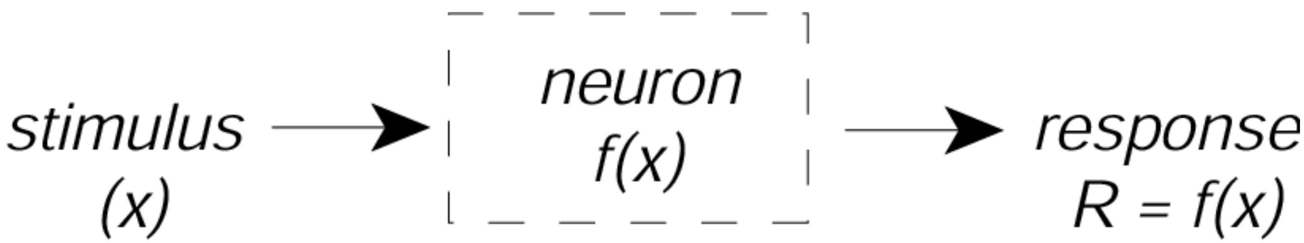


Divisive normalization



Changes in the variance (STC)

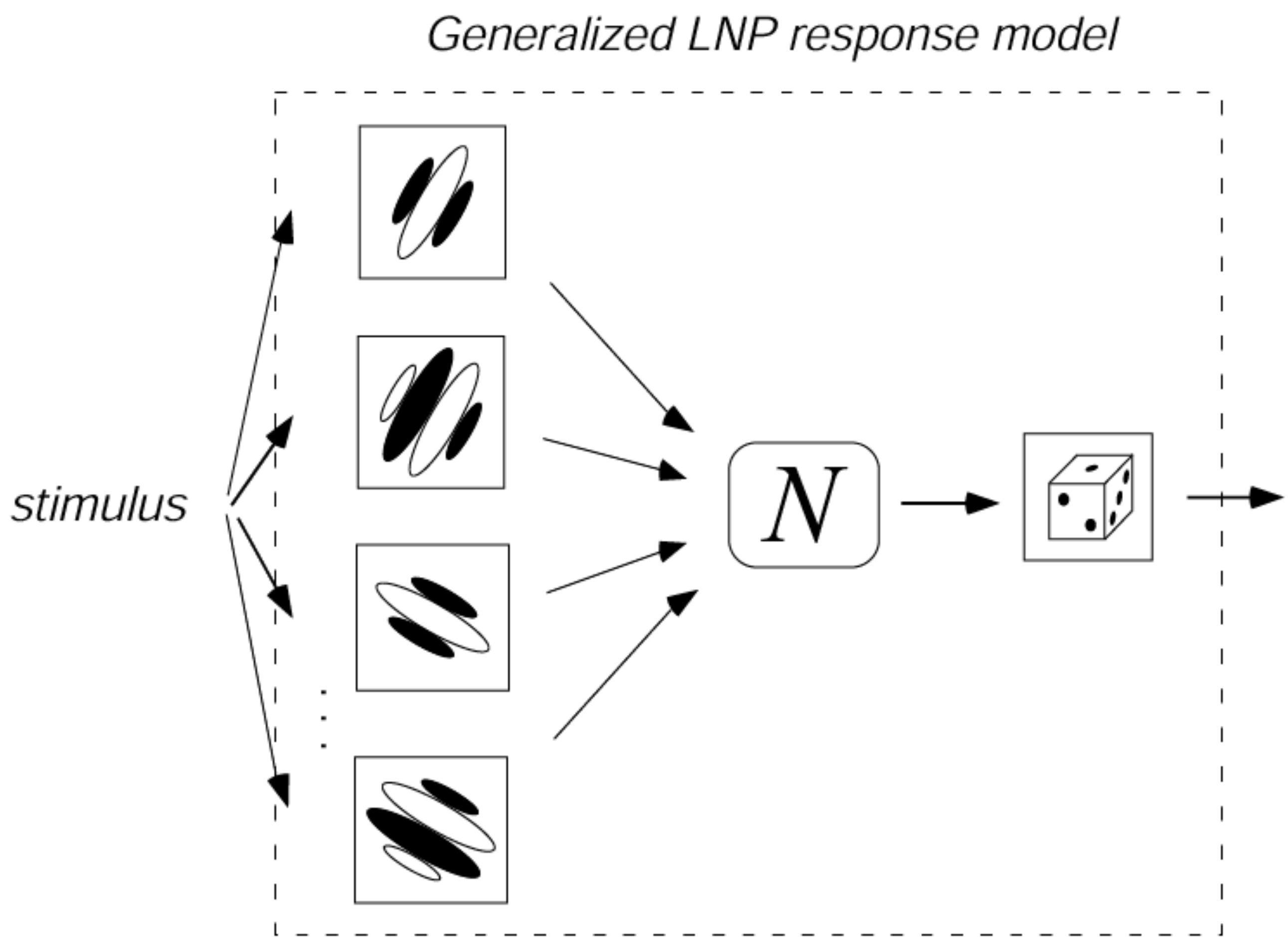
Characterizing neural responses



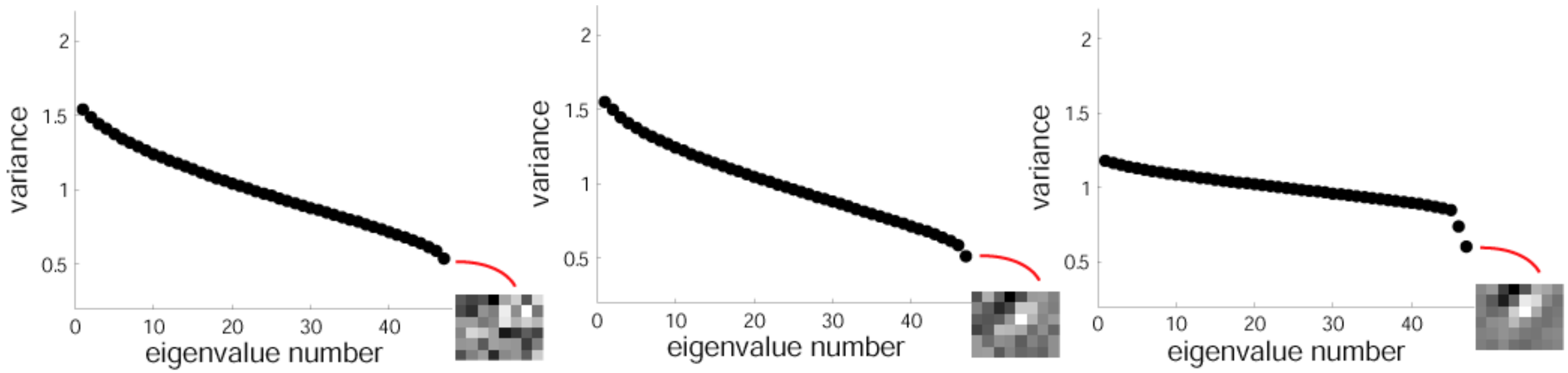
- Simple cell – traditional approach
- Simple cell (STA)
- When STA fails
- Complex cell (STC)
- Another example (STC)
- More generic model with multiple filters (STA and STC)

More general class of model

Look for changes in both the mean and in the variance…



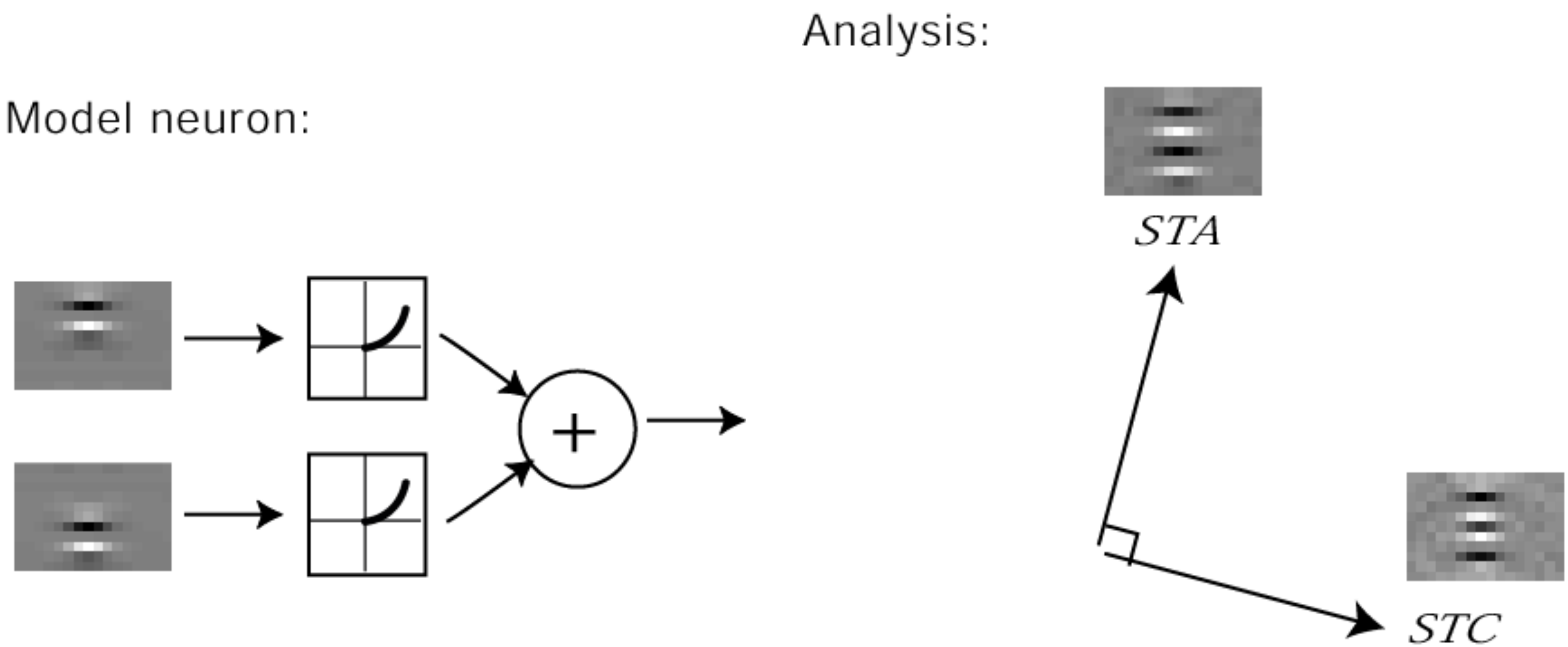
Issues: How many spikes?



Filter estimate depends on:

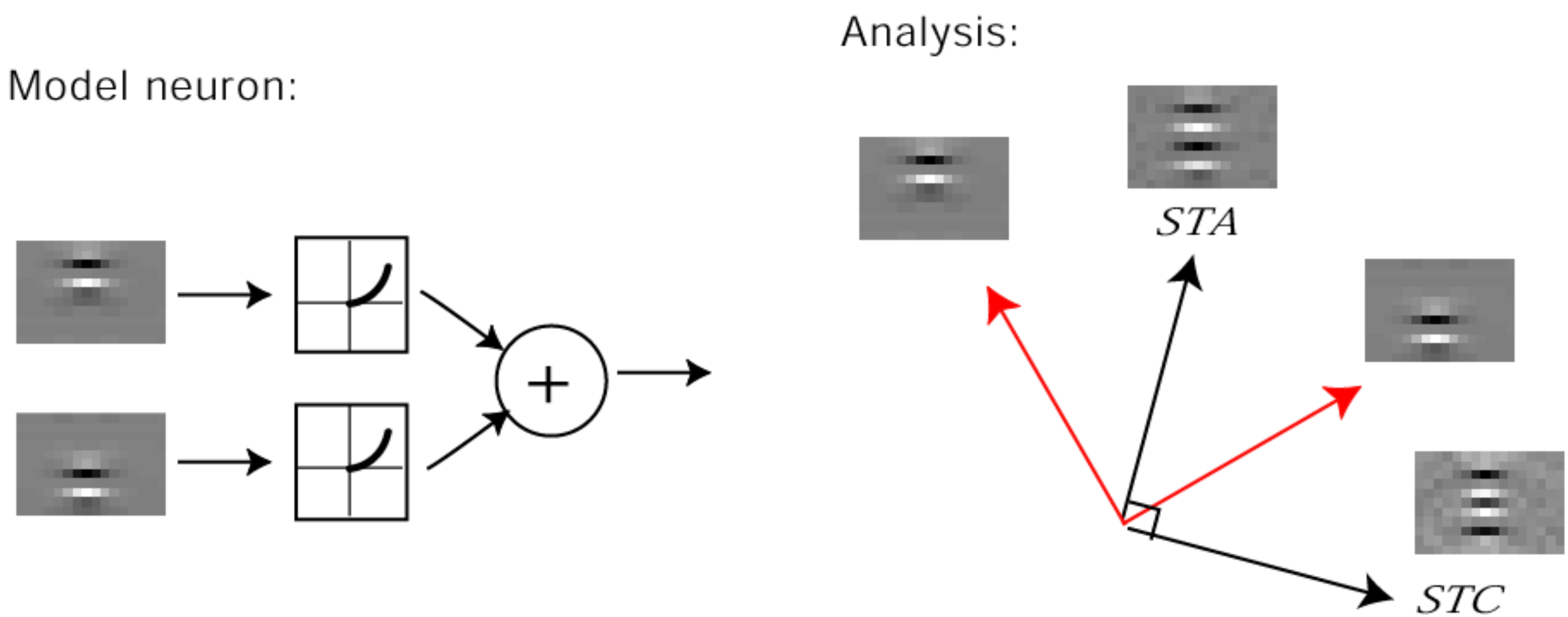
- Spatial and time dimensionality of input stimulus
  (smaller = better estimate)
- Number of spikes
  (more = better estimate)

Caveats



- Analysis forces filters that are 90 degrees apart! Filters should not be taken literally as physiological mechanisms

Caveats



- But true filters are linear combinations of original ("span the same subspace")

Caveats

- Analysis forces filters that are 90 degrees apart!
  Filters should not be taken literally as physiological mechanisms

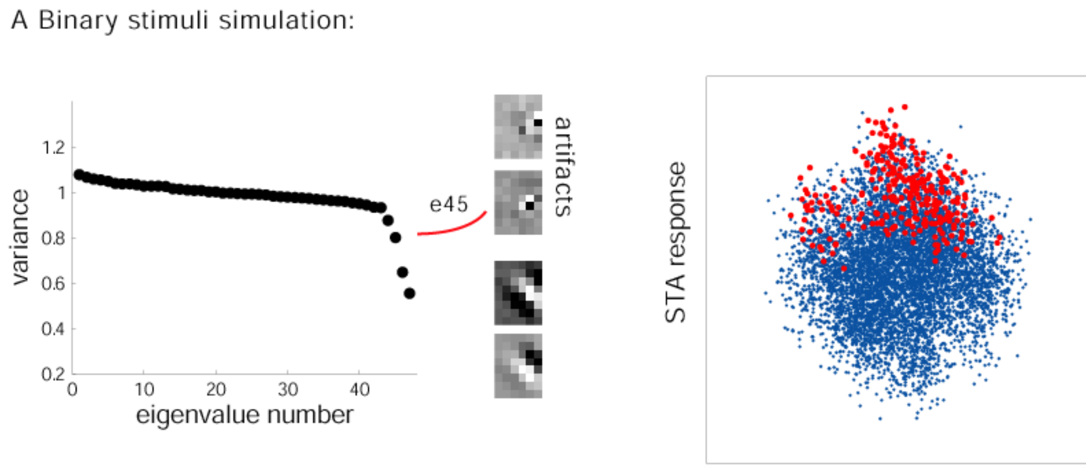
- Spiking in neuron may be non Poisson (bursts; refractory period; etc.)
  Filters should not be taken literally as physiological mechanisms

- There might be more filters affecting neural response than what analysis finds

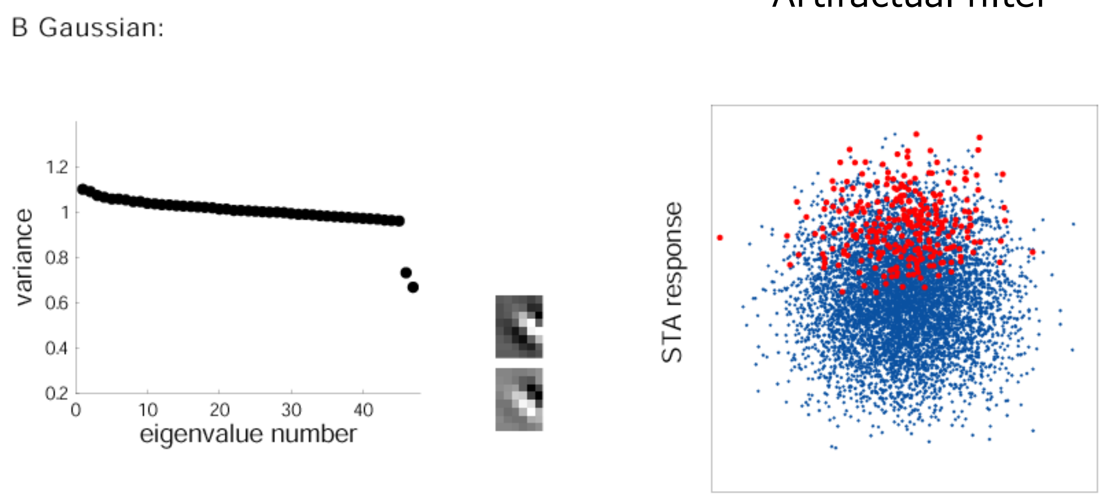
- Labeling of excitatory and suppressive based on net change in mean and variance

Failure modes

- STC Guaranteed to work only for Gaussian stimuli

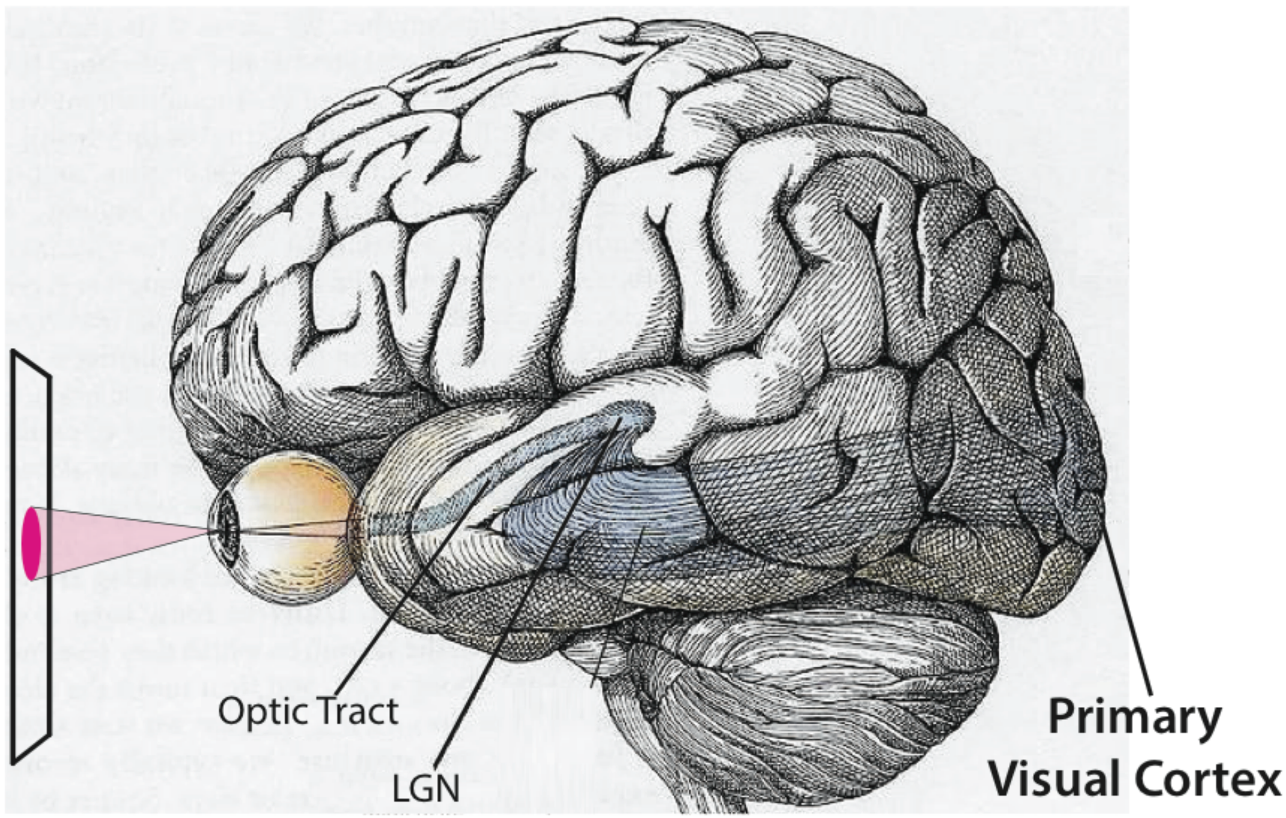


Artifactual filter

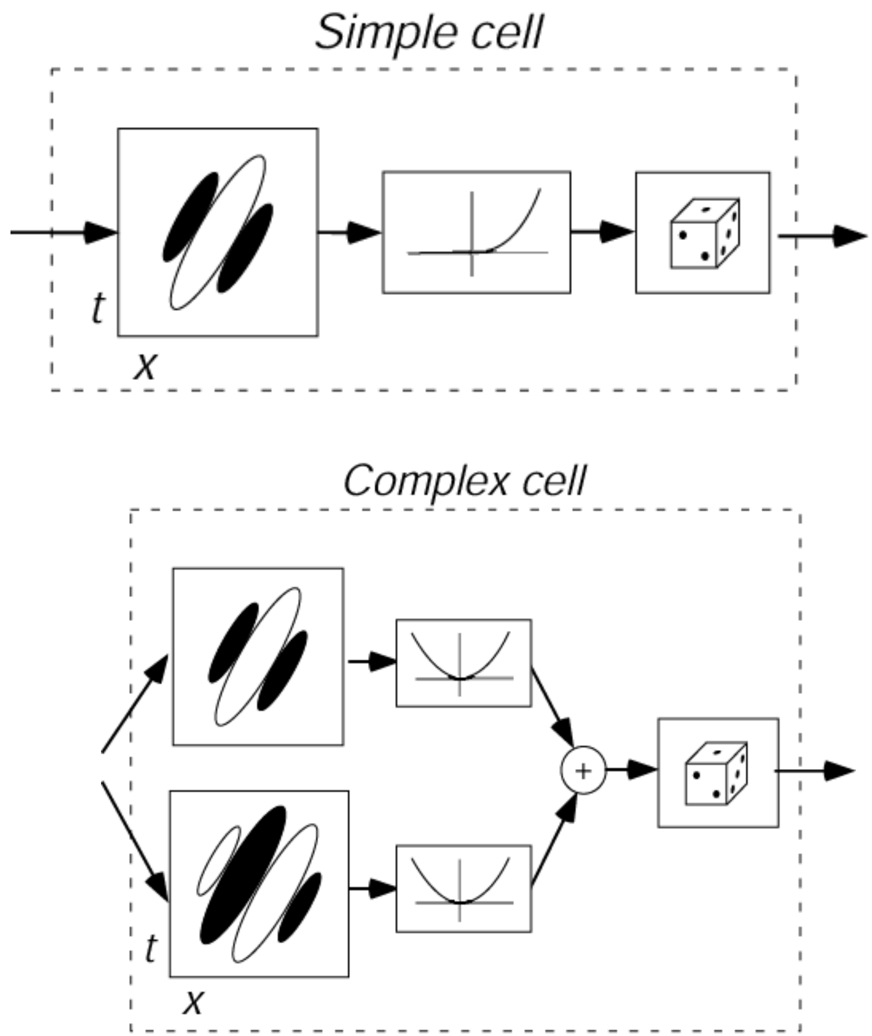


Filter corrected

Application: V1 experiment

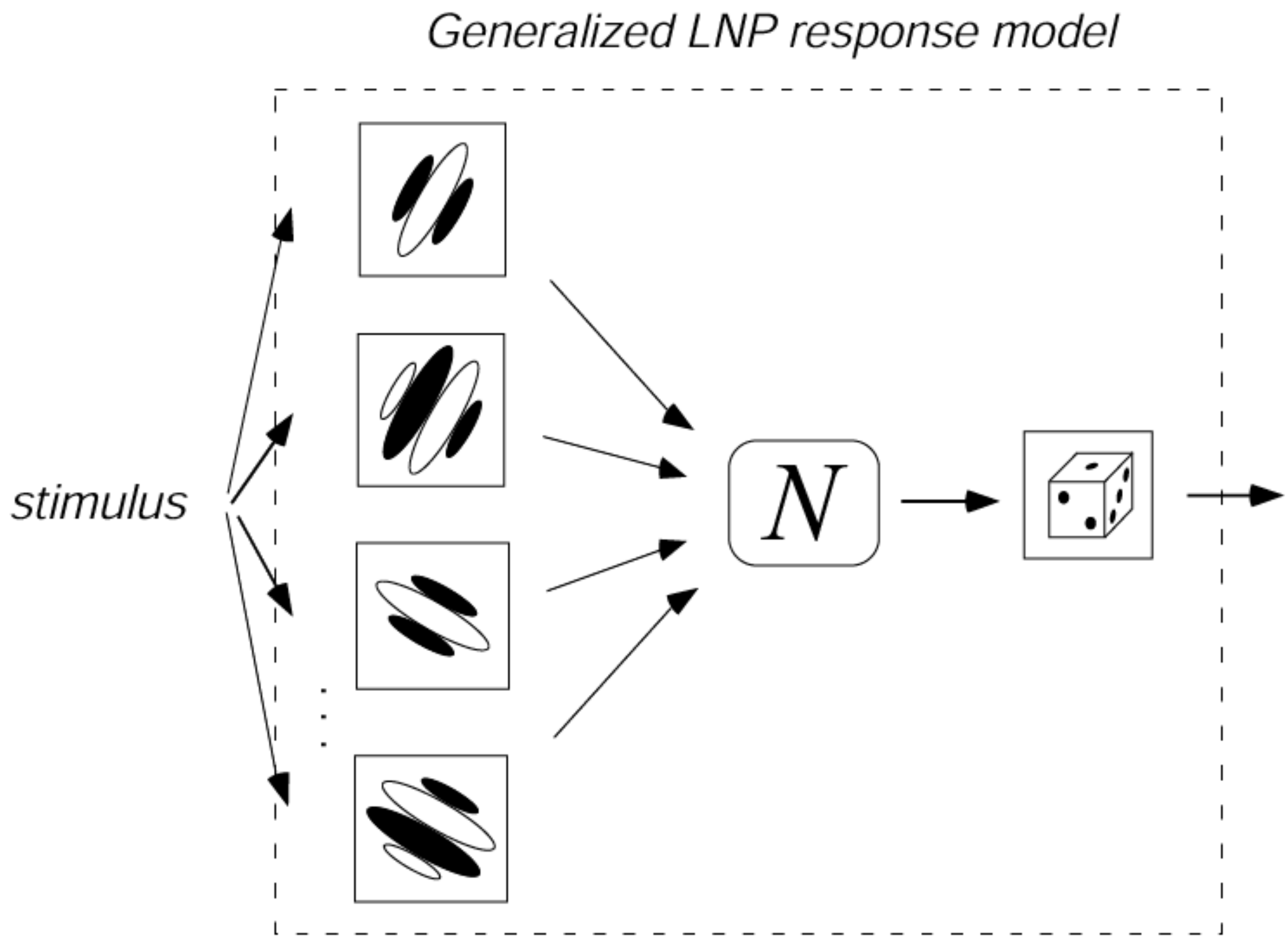


Standard models



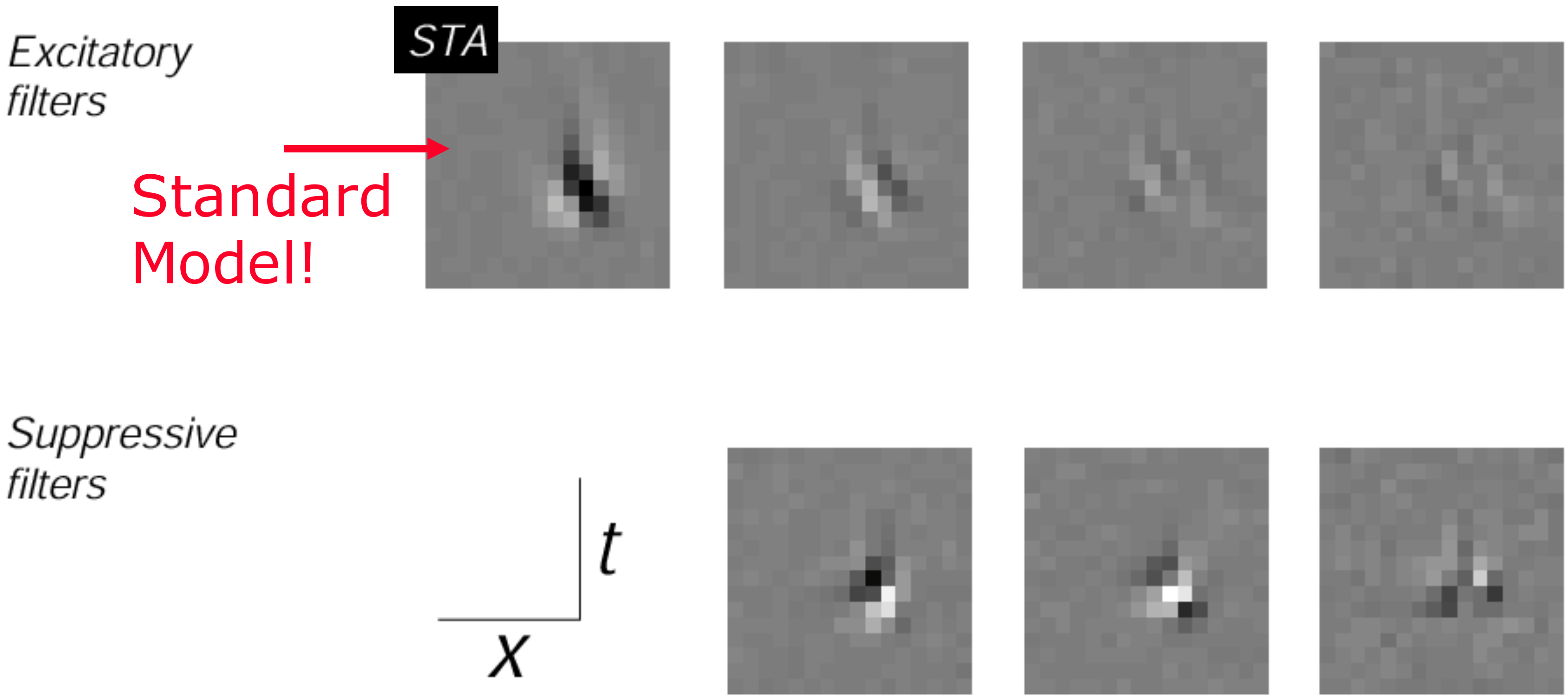
Adelson & Bergen (1985)

V1 Experiment



Simple Cell is Not so Simple

Estimating multiple filters in an experiment

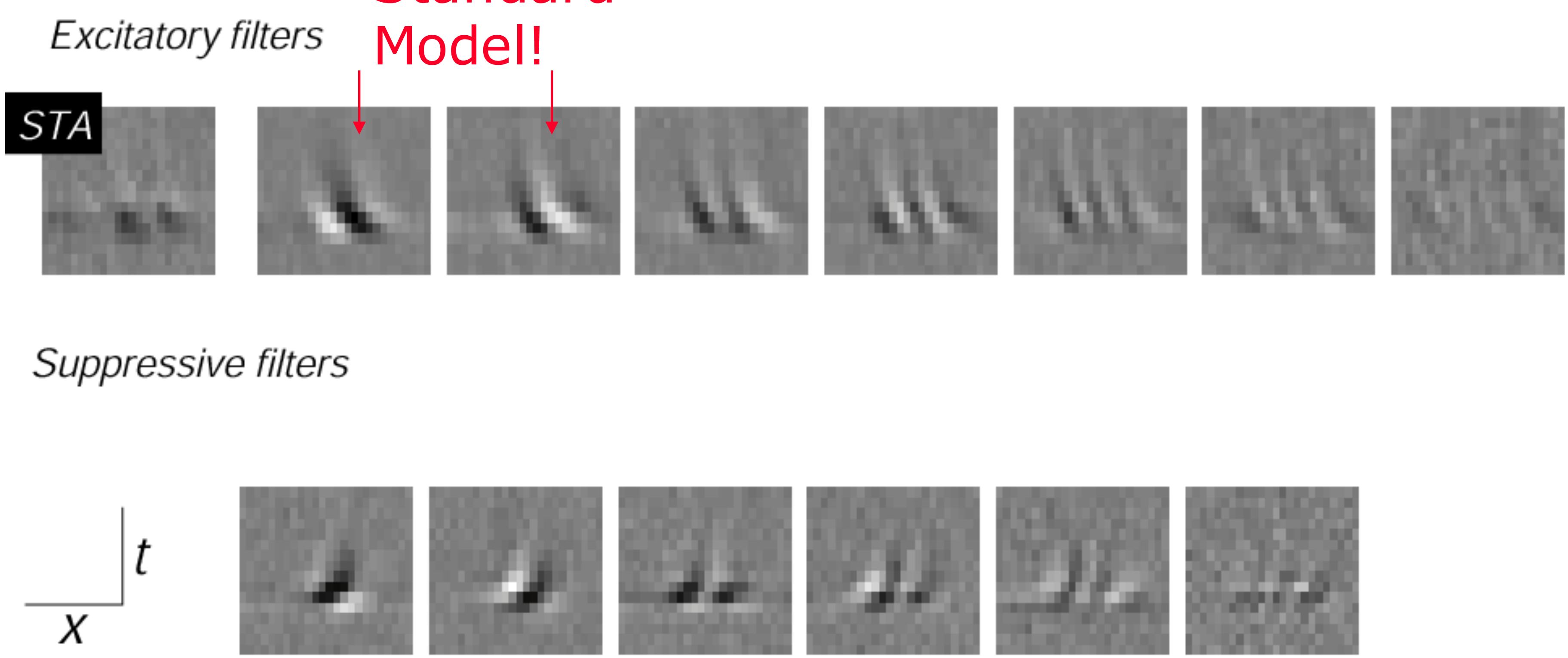


Data from Rust, Schwartz, Movshon, Simoncelli, 2005

Complex Cell

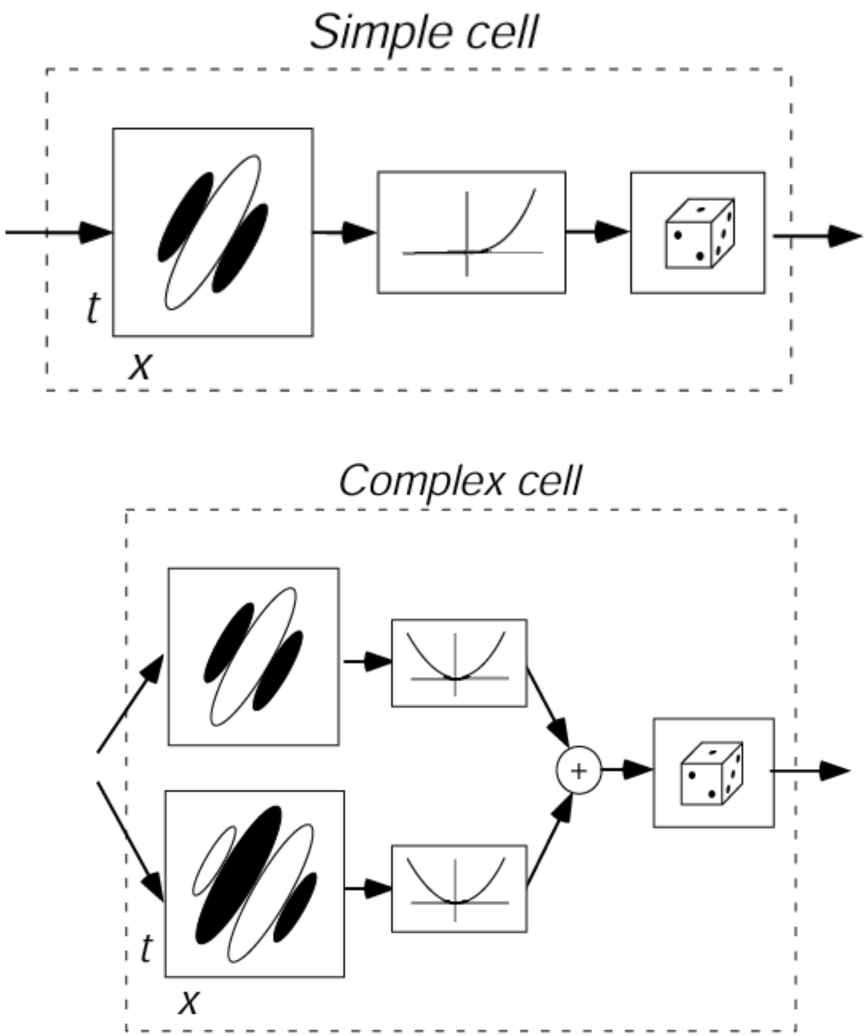
Estimating multiple filters in an experiment

Standard
Model!



Data from Rust, Schwartz, Movshon, Simoncelli, 2005

Recall the standard models



Adelson & Bergen (1985)

But…

Data show multiple filters (excitatory and suppressive) for both.

Are these really two different classes of neurons, or is there a continuum??

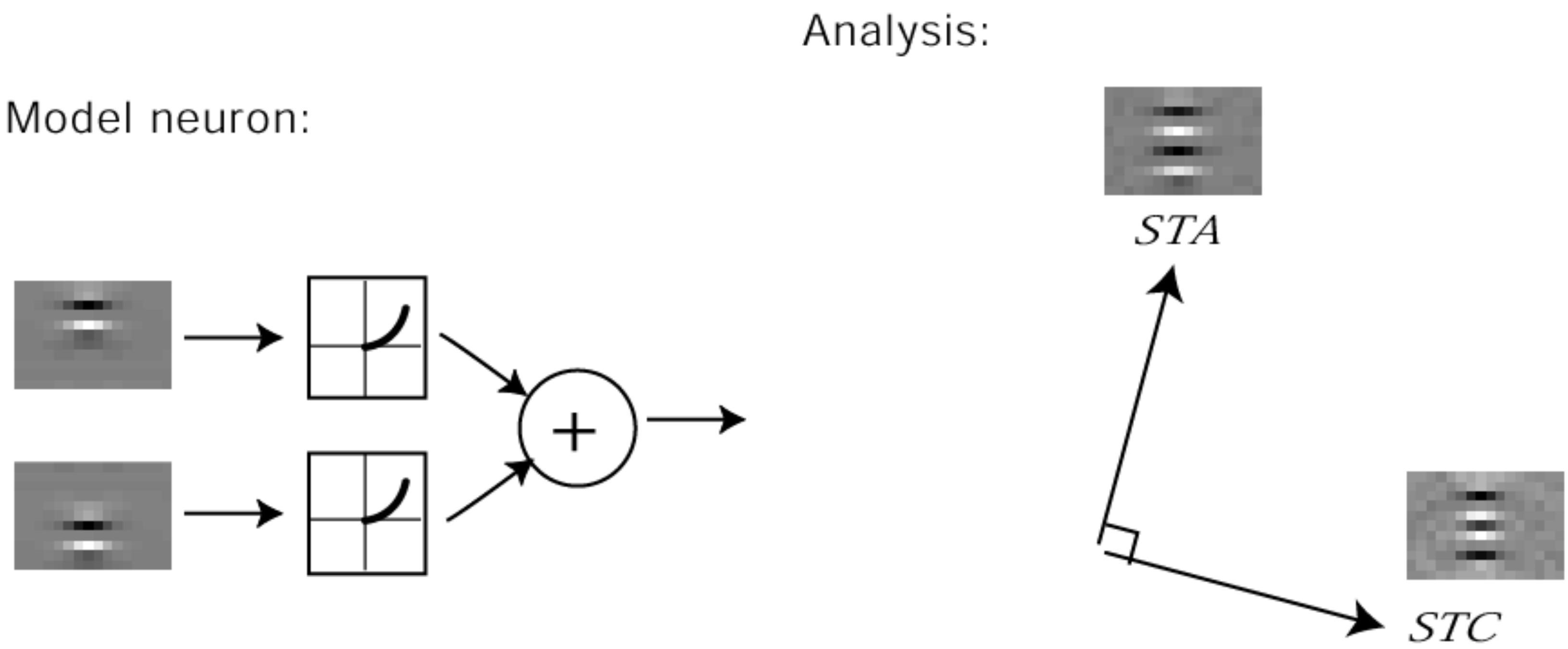
Steps

1. Assume a model (filter/s, nonlinearity)
   (we assumed multiple filters)

2. Estimate model components (filter/s, nonlinearity)
   (we looked for changes in mean and variance)

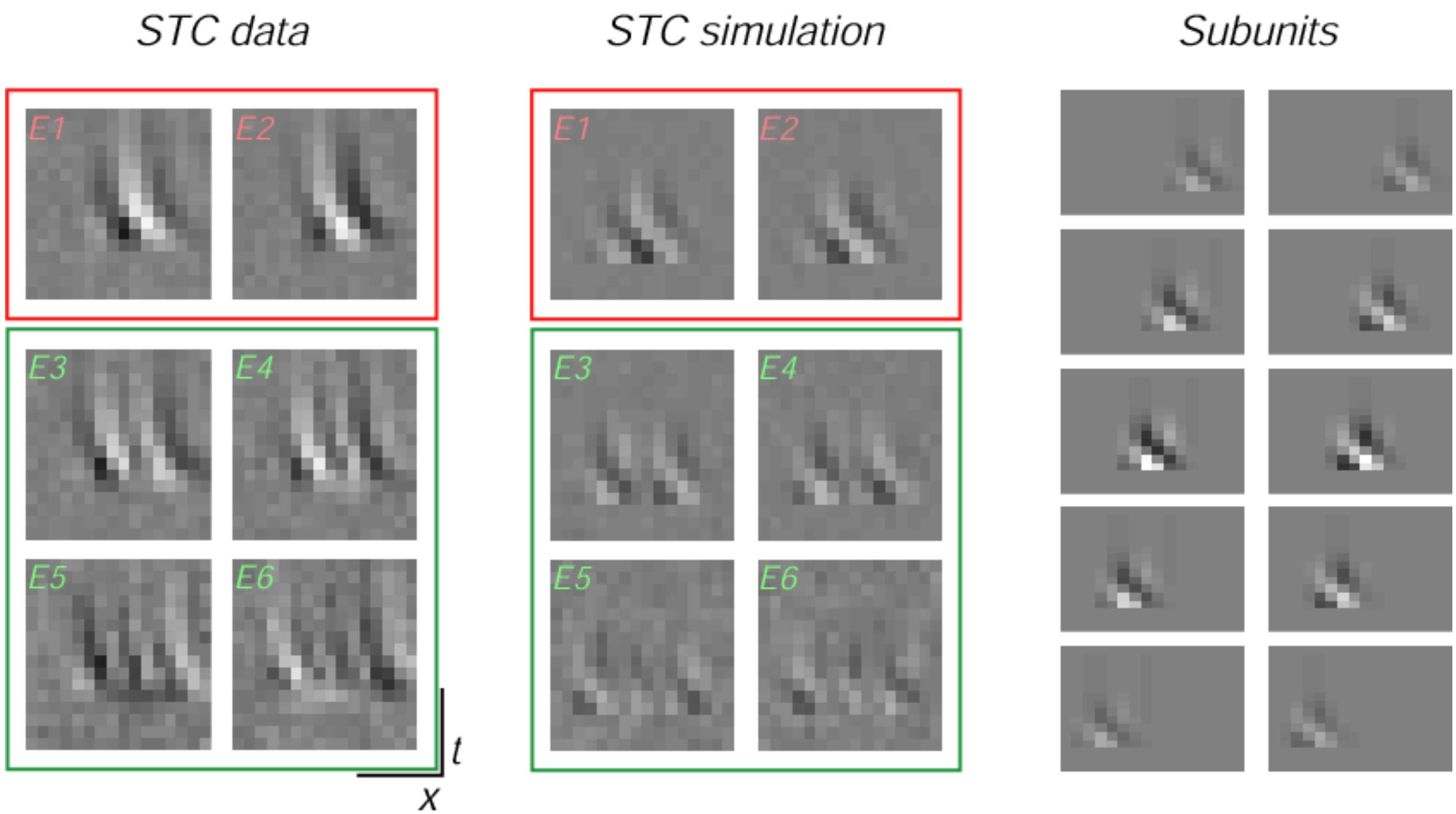
(3. Experimental validation)

Recall: Caveats



- Analysis forces filters that are 90 degrees apart! Filters should not be taken literally as physiological mechanisms

Estimated filters should not be taken literally...

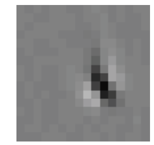


Data from Rust, Schwartz, Movshon, Simoncelli, 2005

Conclusions

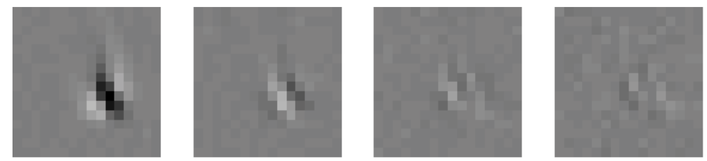
Spike-triggered approaches

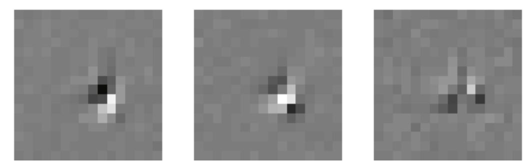
- Changes in the mean (STA)



- Changes in the variance (STC)

  multiple filters!





- Nonlinearity rule

- Ultimate goal: characterize input-output relation such that we can predict response of neuron to any arbitrary stimulus