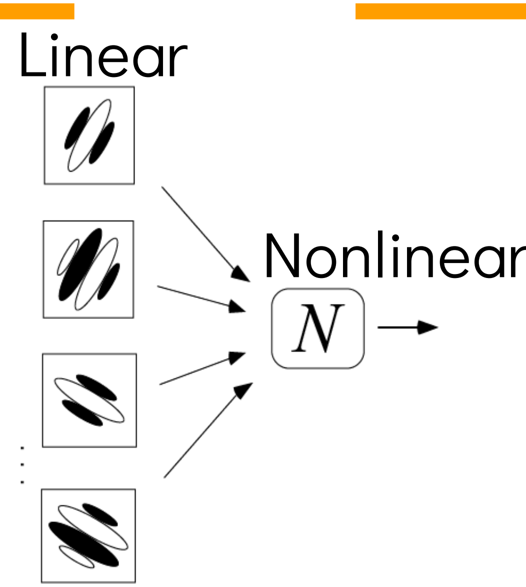
SPIKE TRIGGERED APPROACHES

Odelia Schwartz

Computational Neuroscience Course 2017

LINEAR NONLINEAR MODELS

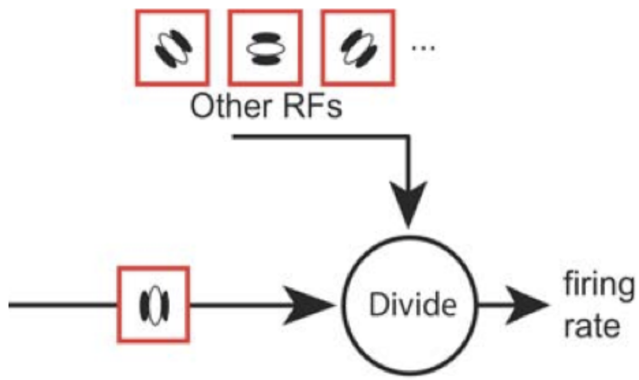


- Often constrain to some form of Linear, Nonlinear computations, e.g. visual receptive fields or filters, followed by nonlinear interactions

LINEAR NONLINEAR MODELS

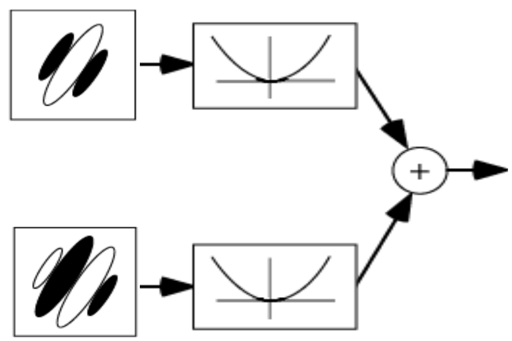
What type of nonlinearities?

DESCRIPTIVE MODELS: DIVISIVE NORMALIZATION



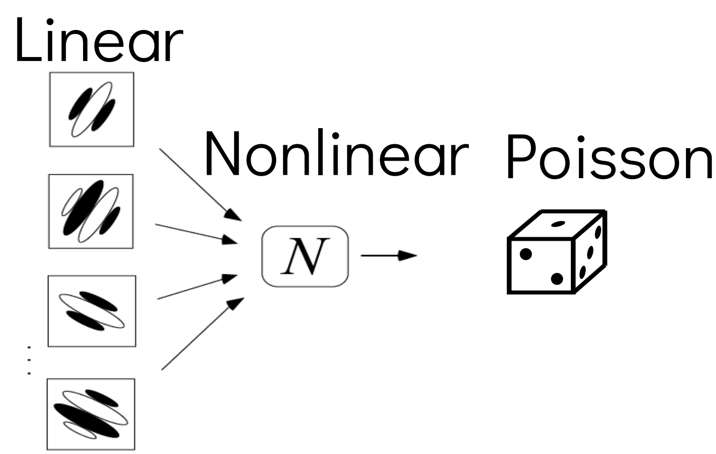
- Canonical computation (Carandini, Heeger, 2013)
- Has been applied to primary visual cortex (V1)
- More broadly, to other systems and modalities, multimodal processing, value encoding, etc

DESCRIPTIVE MODELS: COMPLEX CELLS AND INVARIANCE



- after Adelson & Bergen, 1985

FITTING DESCRIPTIVE MODELS TO DATA

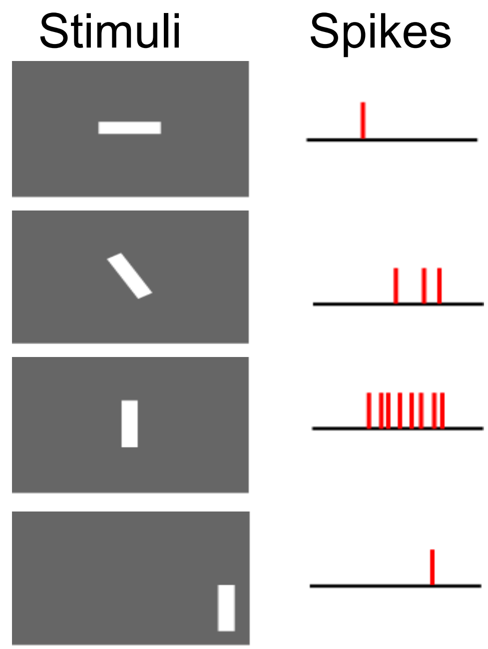


ROADMAP

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

REMINDER: RECEPTIVE FIELD

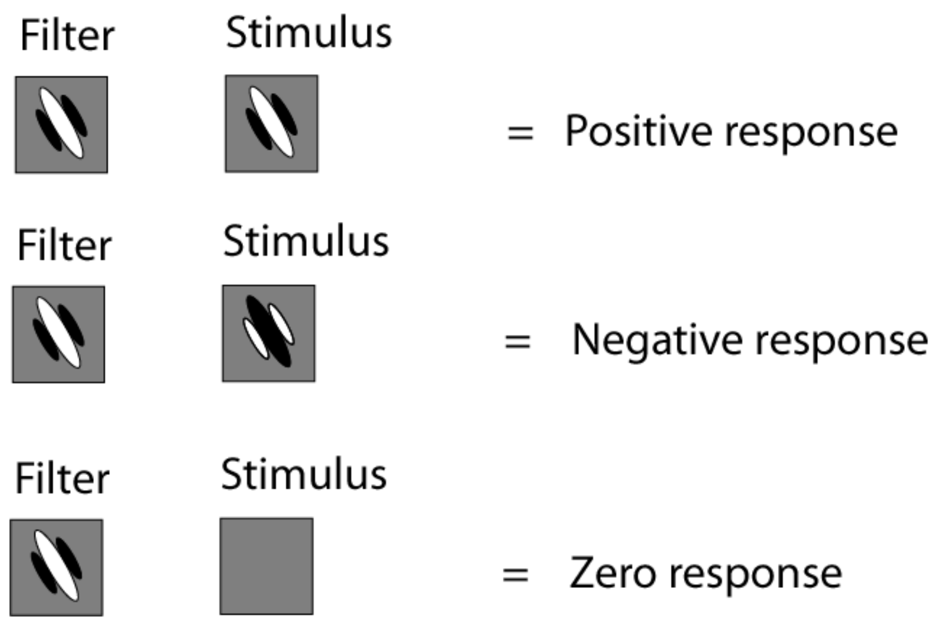
Hubel and Wiesel, 1959



REMINDER: RECEPTIVE FIELD

Primary Visual Cortex (V1)

RECEPTIVE FIELD



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

ROADMAP

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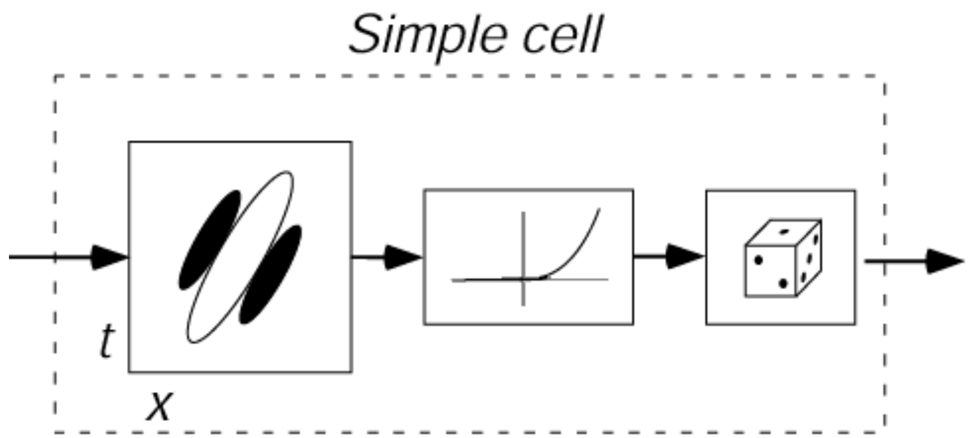
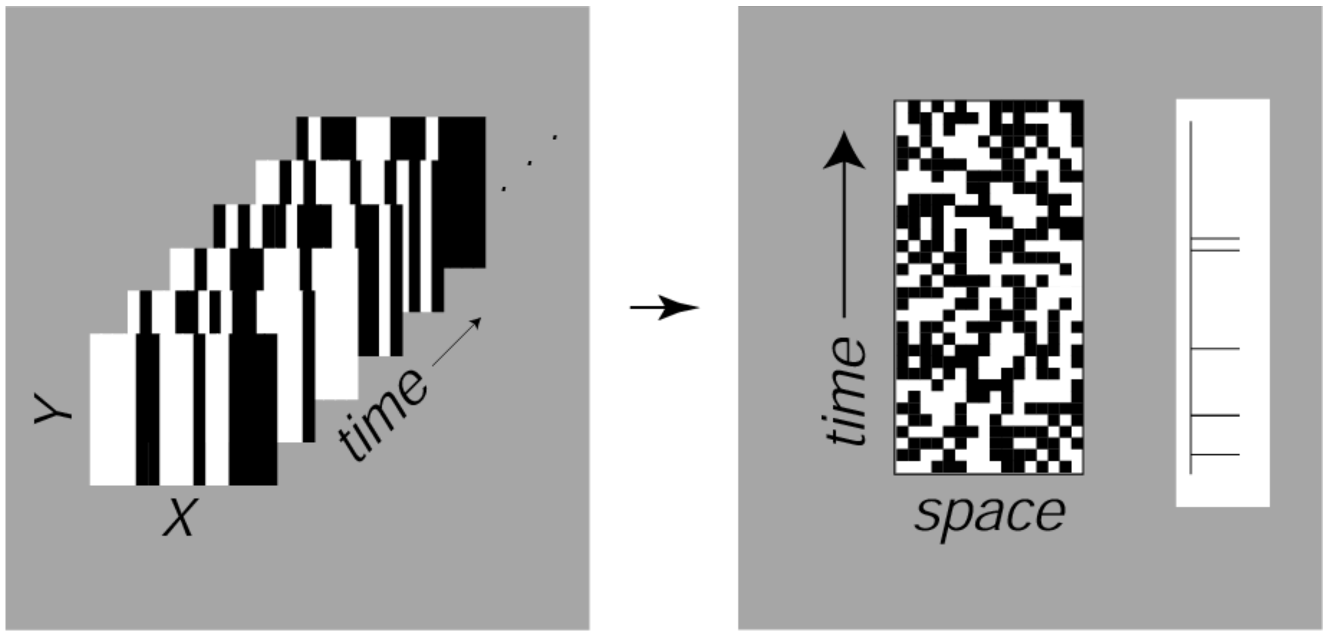
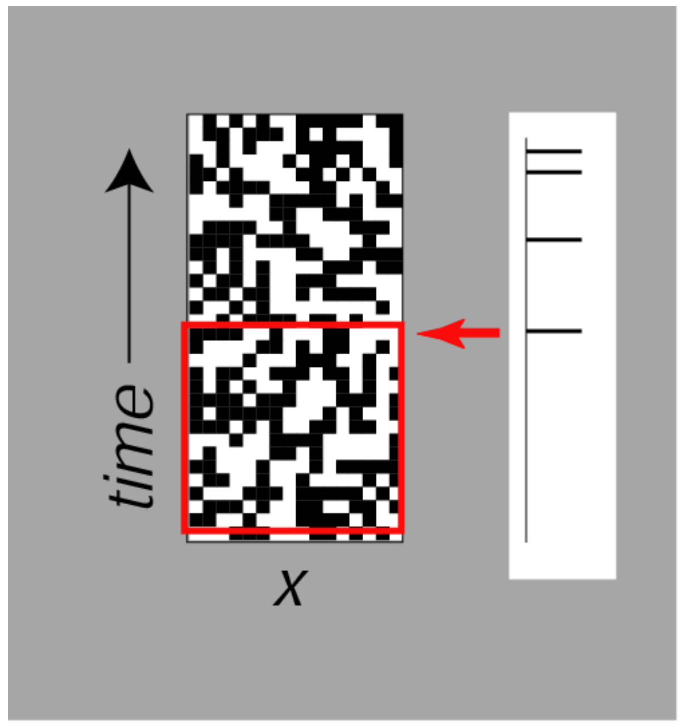

Simple cell
t
x

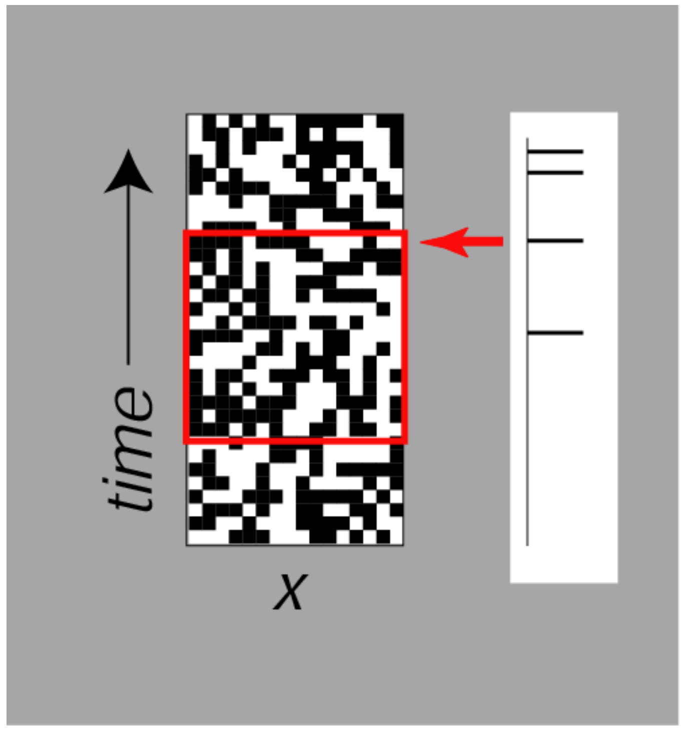
SPIKE-TRIGGERED AVERAGE



SPIKE-TRIGGERED AVERAGE



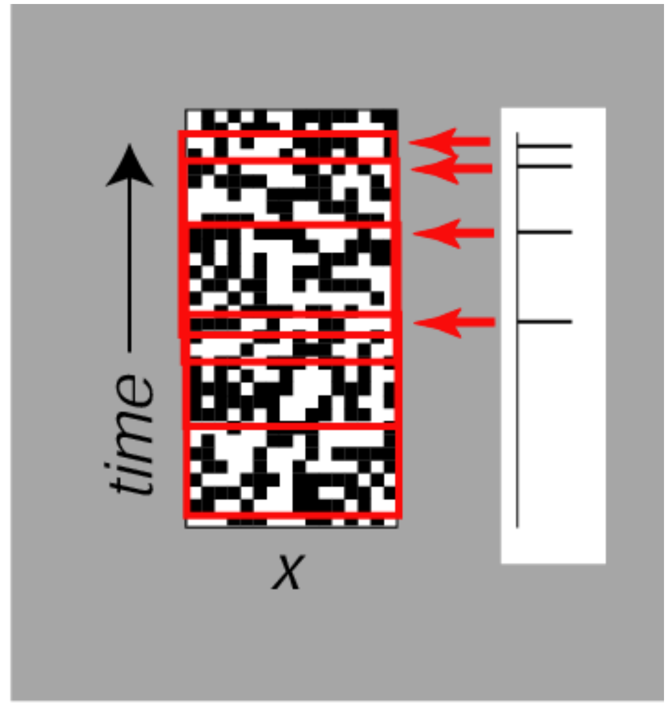
SPIKE-TRIGGERED AVERAGE



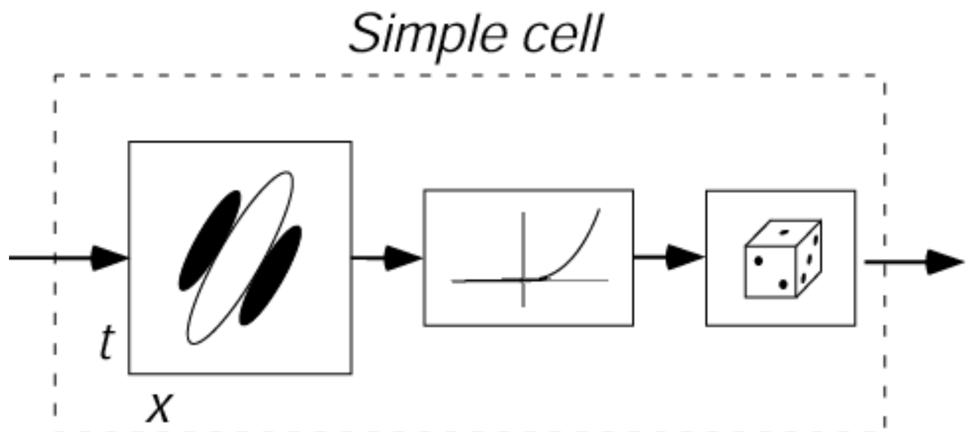
SPIKE-TRIGGERED AVERAGE

STA

Average of spike-triggered stimuli



EFFECT OF NONLINEARITY IN MODEL?



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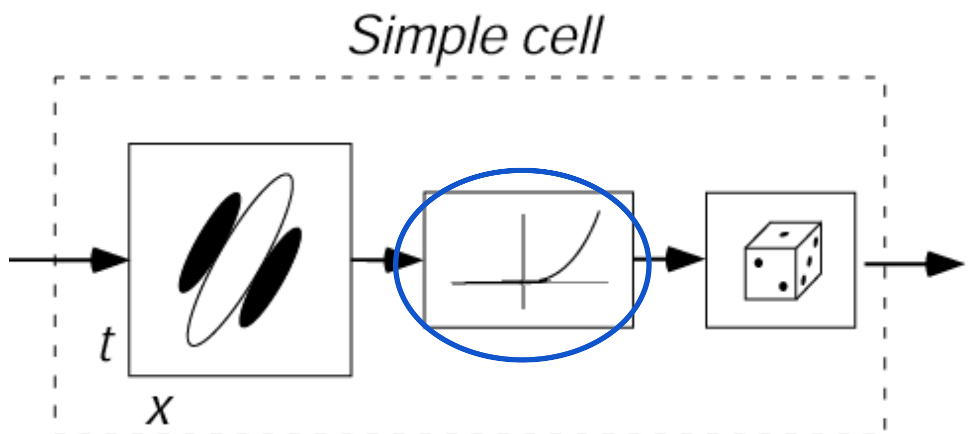
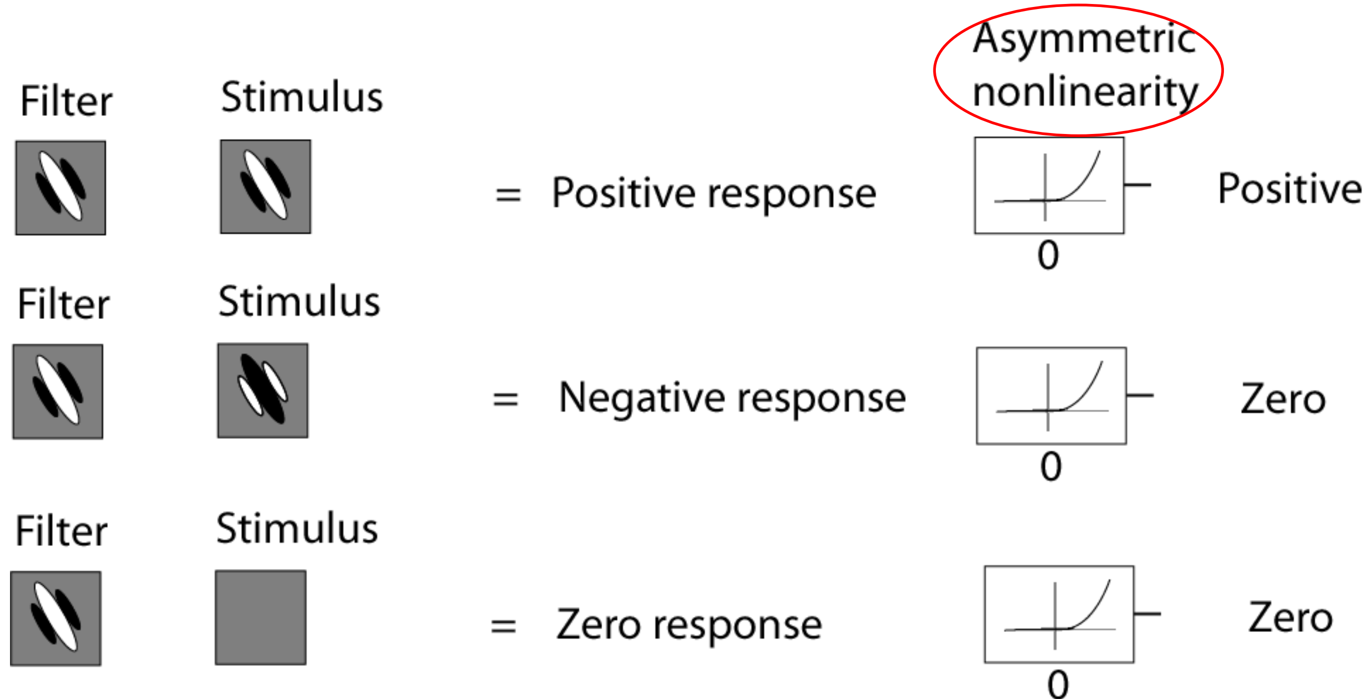
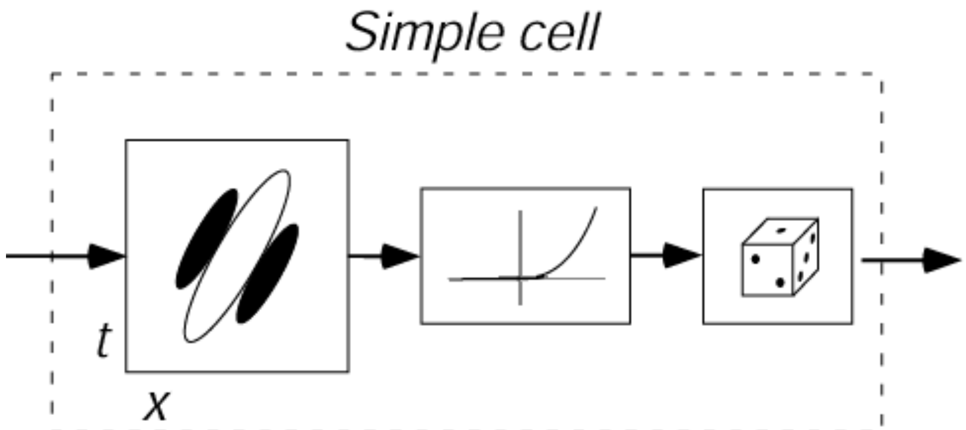


EFFECT OF NONLINEARITY IN MODEL?



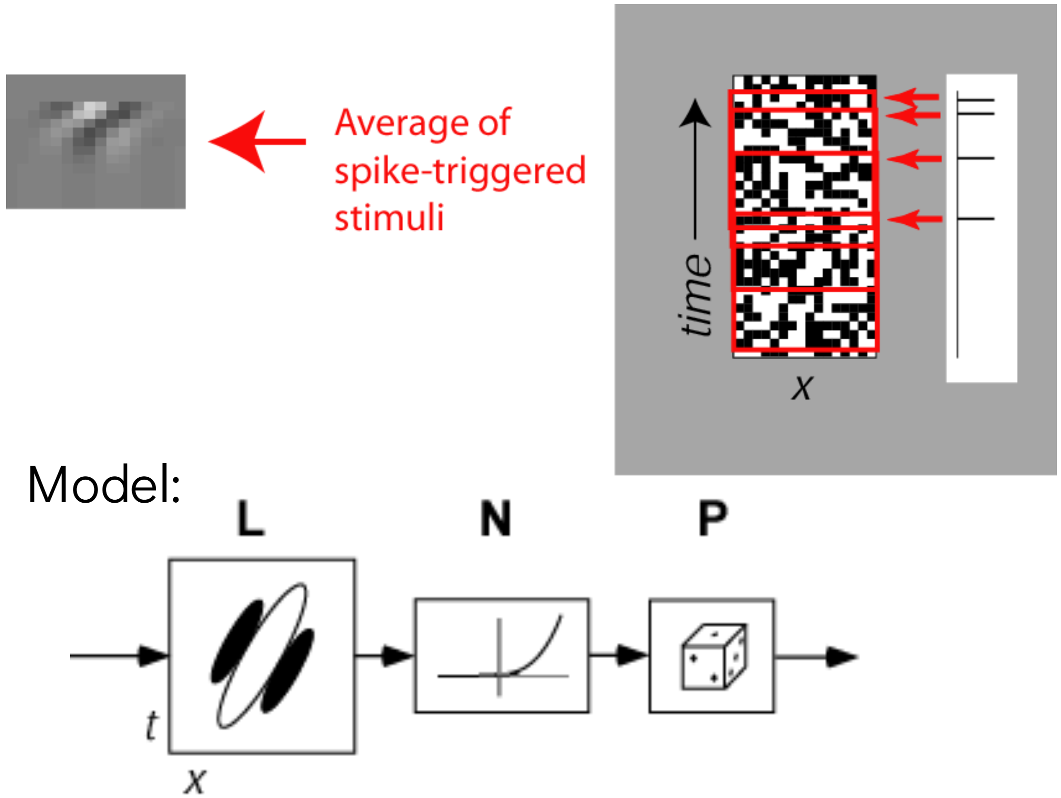
- Nonlinearity sets negative filter responses to zero (firing rates are positive)

SPIKE-TRIGGERED AVERAGE (STA)

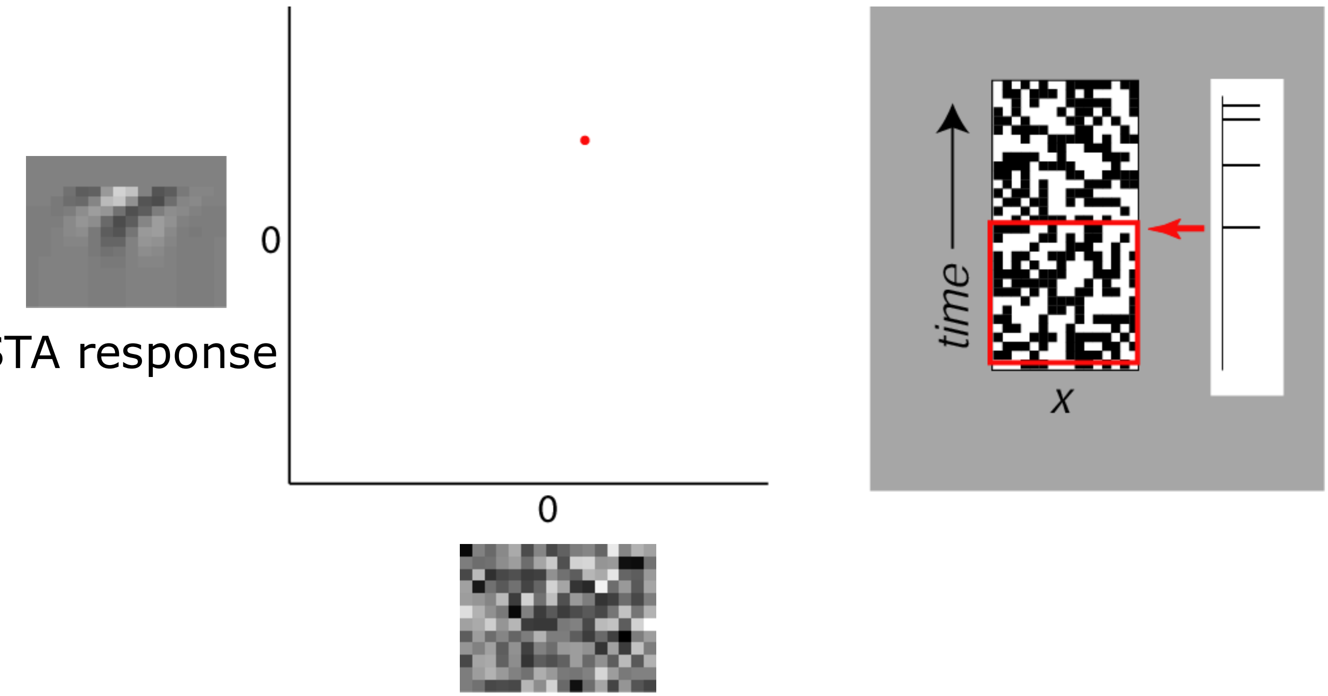


- Stimuli that are more similar to filter are more likely to elicit a spike…

SPIKE-TRIGGERED AVERAGE (STA)



SPIKE-TRIGGERED AVERAGE (STA)



STA response

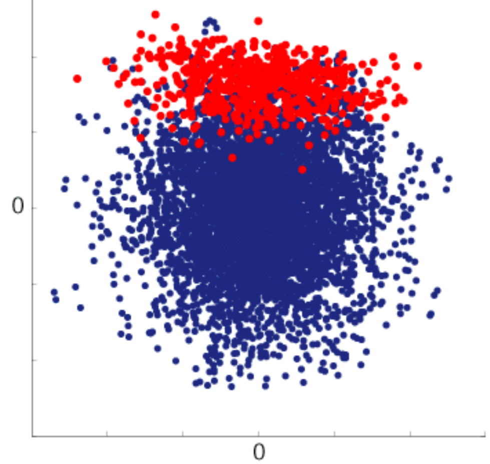
Random filter response

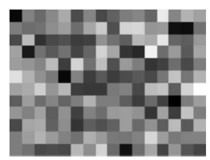
SPIKE-TRIGGERED AVERAGE (STA)

Geometrical view: change in the mean

Large filter response likely to elicit spike

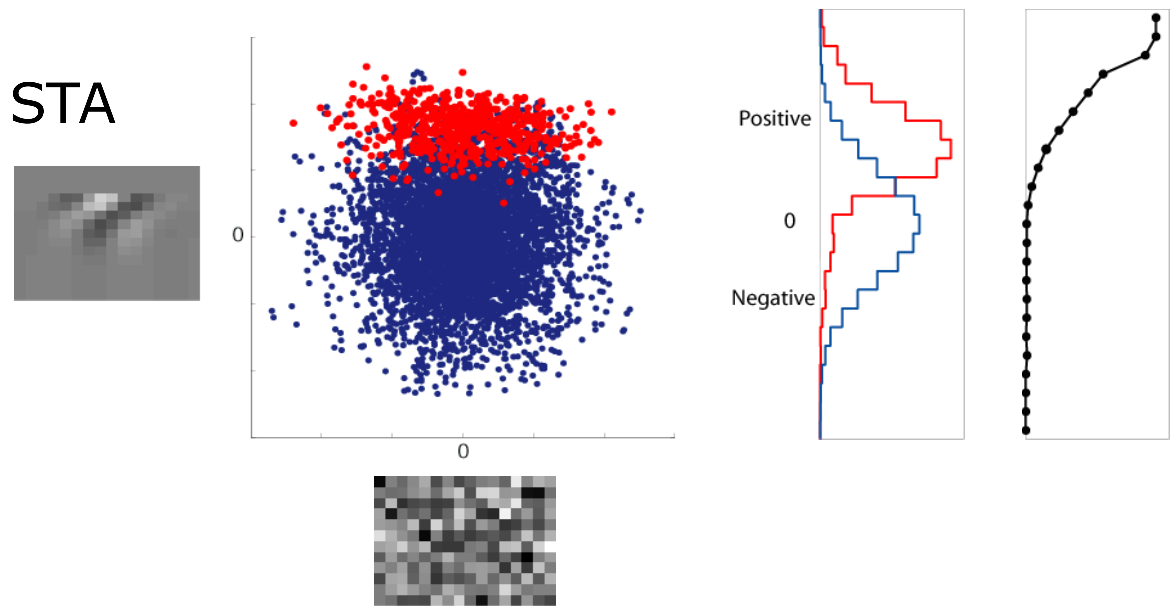
STA response





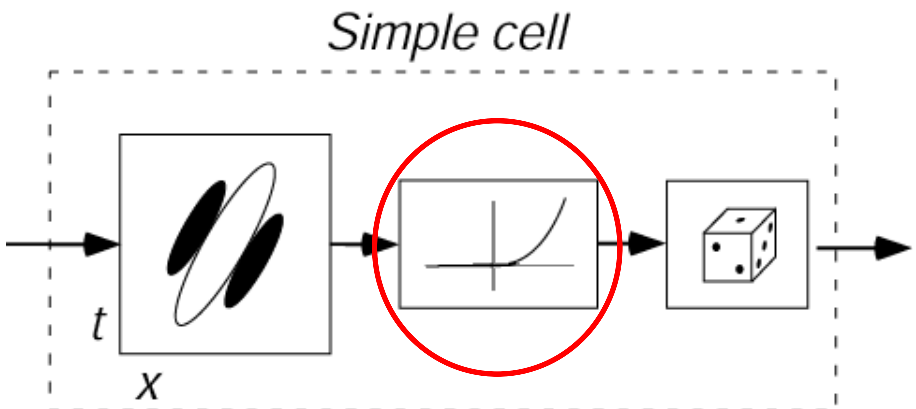
Random filter response

SPIKE-TRIGGERED AVERAGE (STA)



We can also recover the nonlinearity

SPIKE-TRIGGERED AVERAGE (STA)



We can also recover the nonlinearity

STEPS

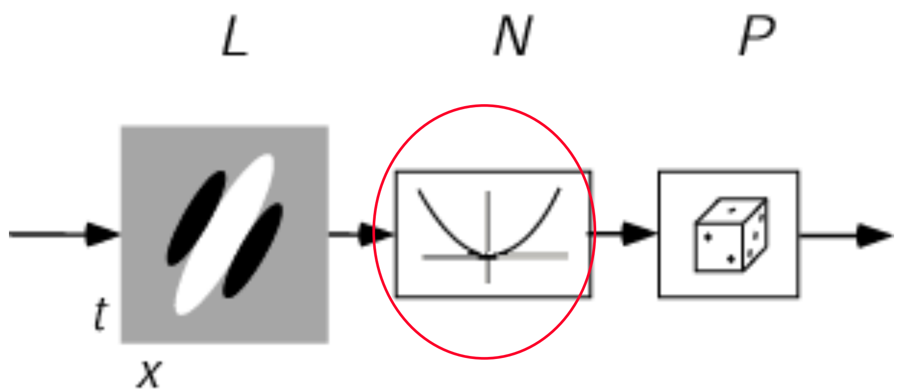
1. Assume a model (filter/s, nonlinearity)
   (we assumed one filter and asymmetric nonlinearity)

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

ROADMAP

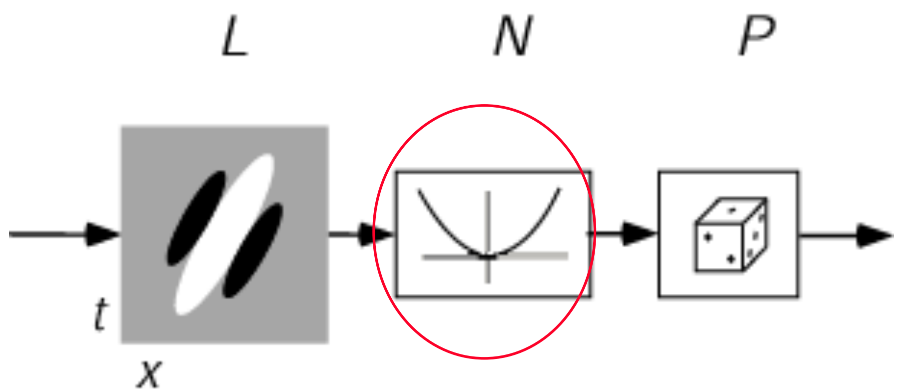
- Simple cell – traditional approach
- Simple cell (STA)
- When STA fails
- Complex cell (STC)
- Another example (STC)
- More generic model with multiple filters

BUT STA DOES NOT ALWAYS WORK



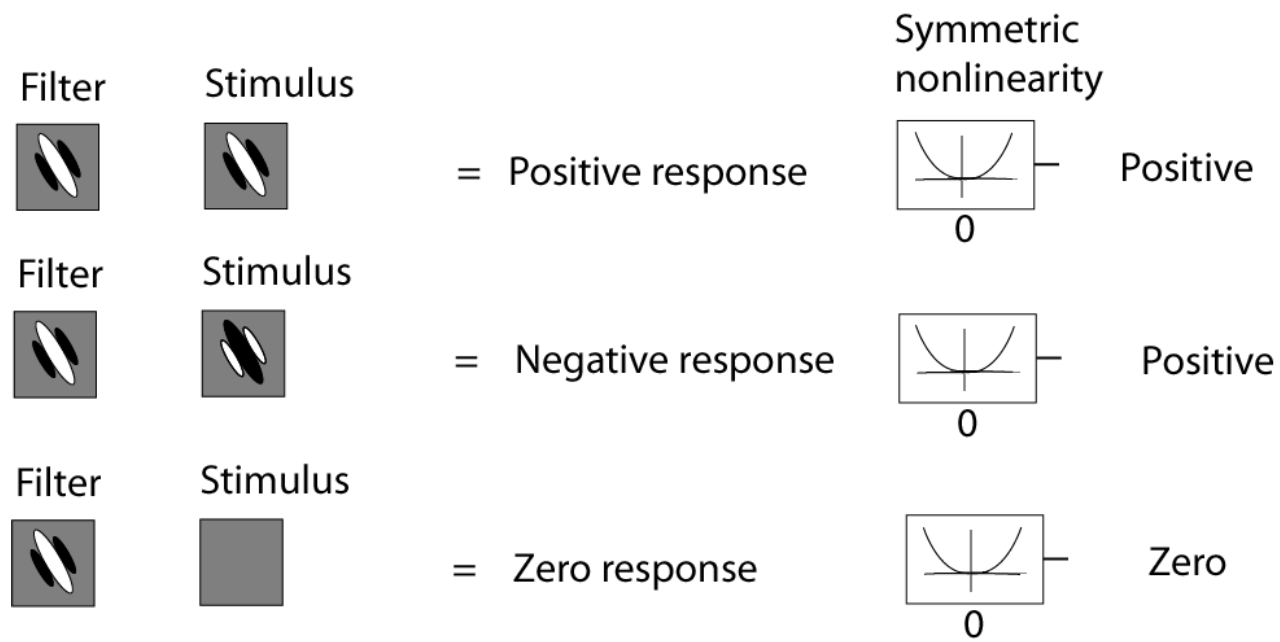
STA filter??

BUT STA DOES NOT ALWAYS WORK



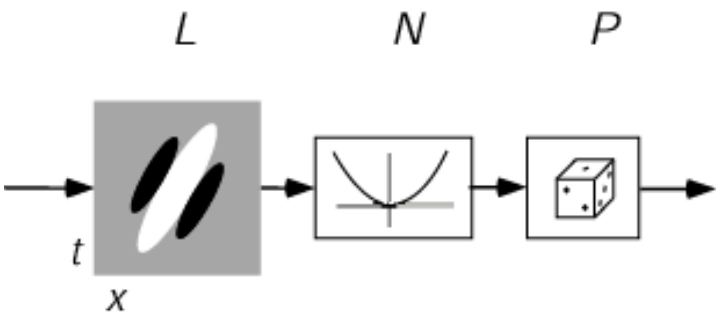
STA filter! 

WHAT HAPPENED??

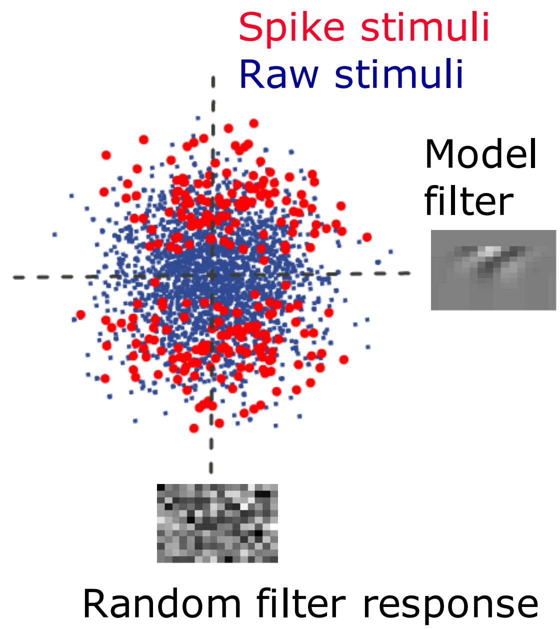


Nonlinearity sets negative filter responses to positive (firing rates are positive)

WHAT HAPPENED??

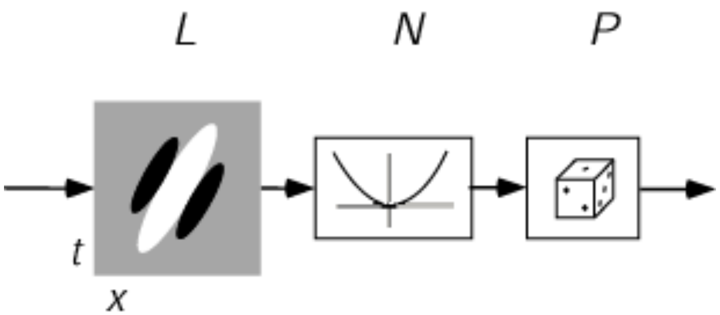


STA filter! 

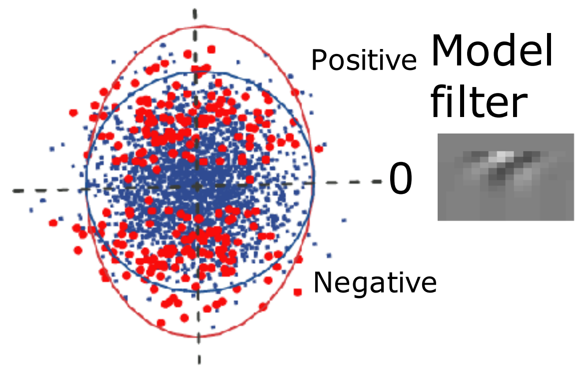


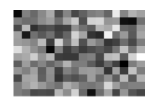
Large or small filter response likely to elicit spike
Mean stimuli eliciting spikes = 0

CHANGE IN THE VARIANCE



STA filter!

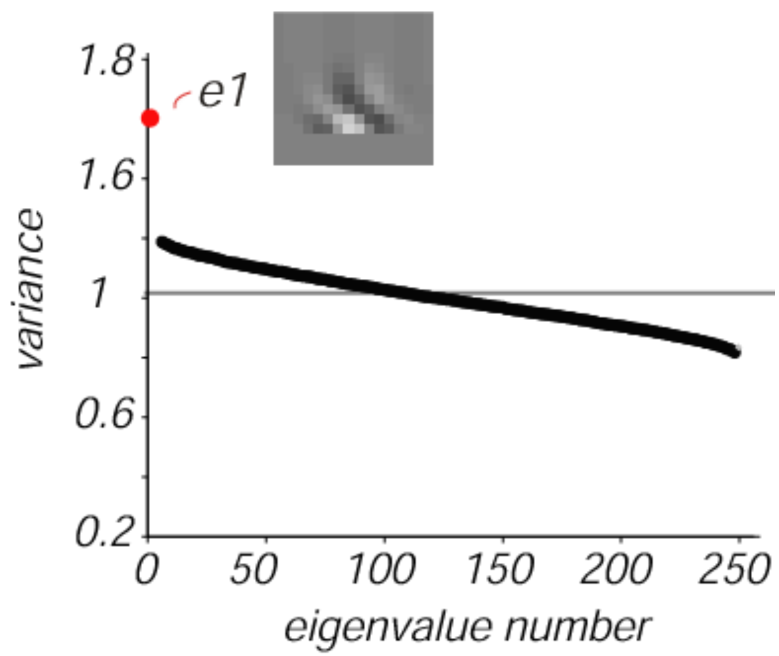


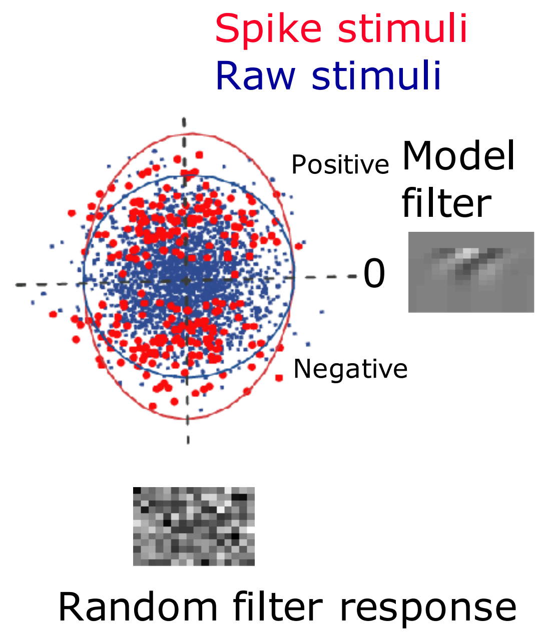


Random filter response

Large or small filter response likely to elicit spike

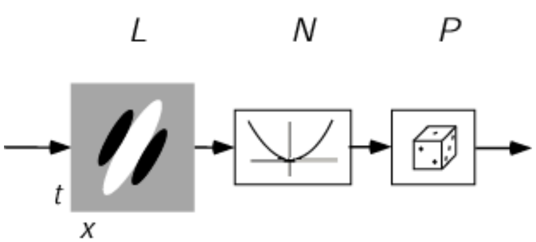
SPIKE-TRIGGERED COVARIANCE (STC)

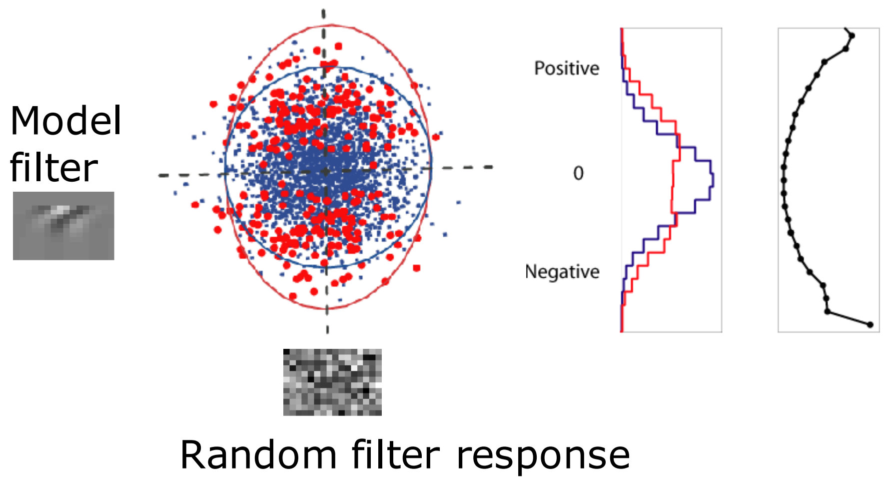




Standard algebra techniques (eigenvector analysis) recovers changes in variance

SPIKE-TRIGGERED COVARIANCE (STC)





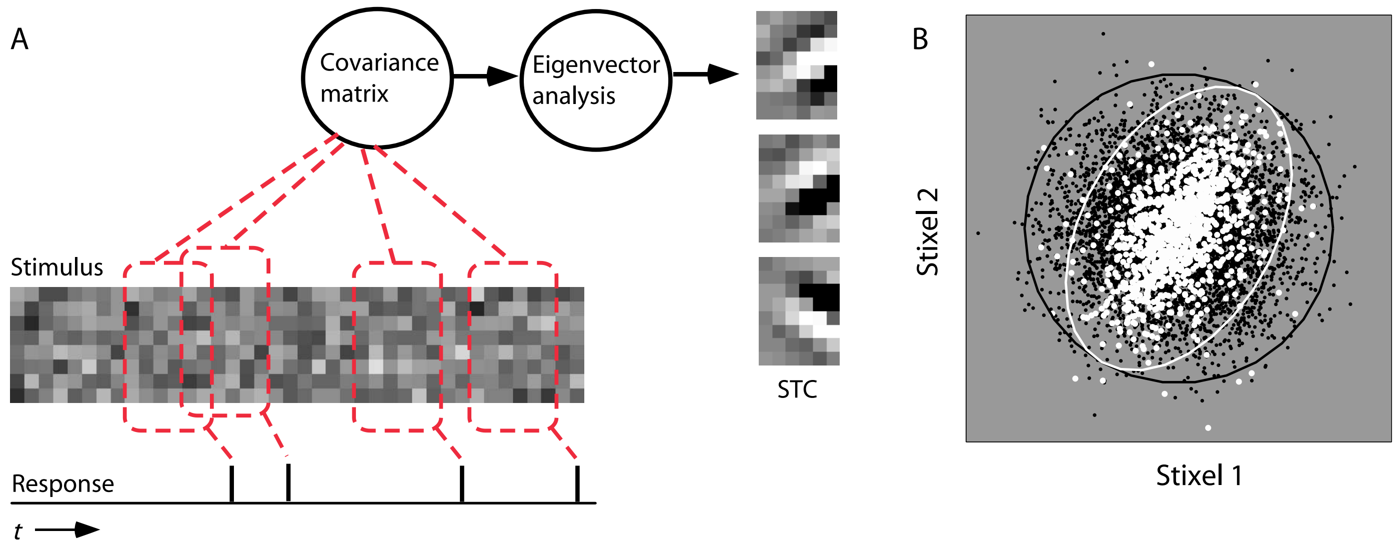
We can also recover the nonlinearity

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)

SPIKE-TRIGGERED COVARIANCE (STC)



- Figure from Schwartz et al. 2006; see also Rust et al. 2005, de Ruyter & Bialek 1988
- Approach estimates linear subspace and nonlinearity

ROADMAP

- Simple cell – traditional approach
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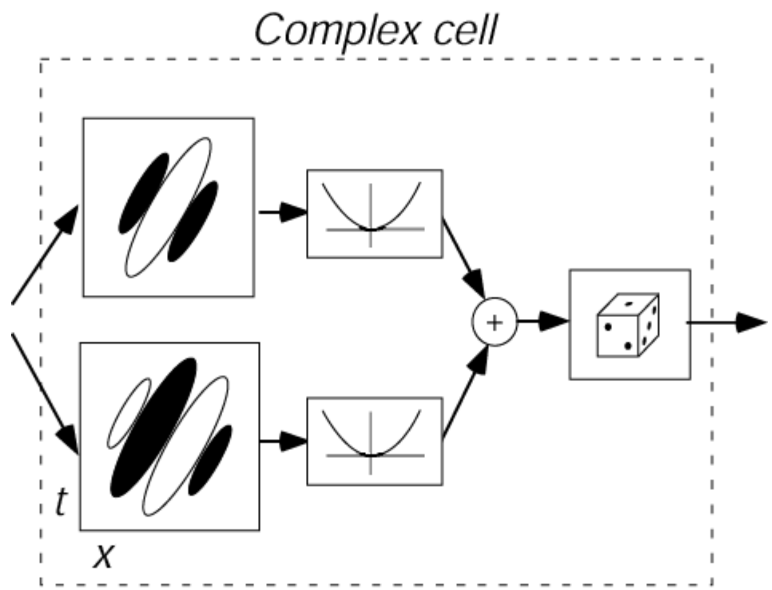
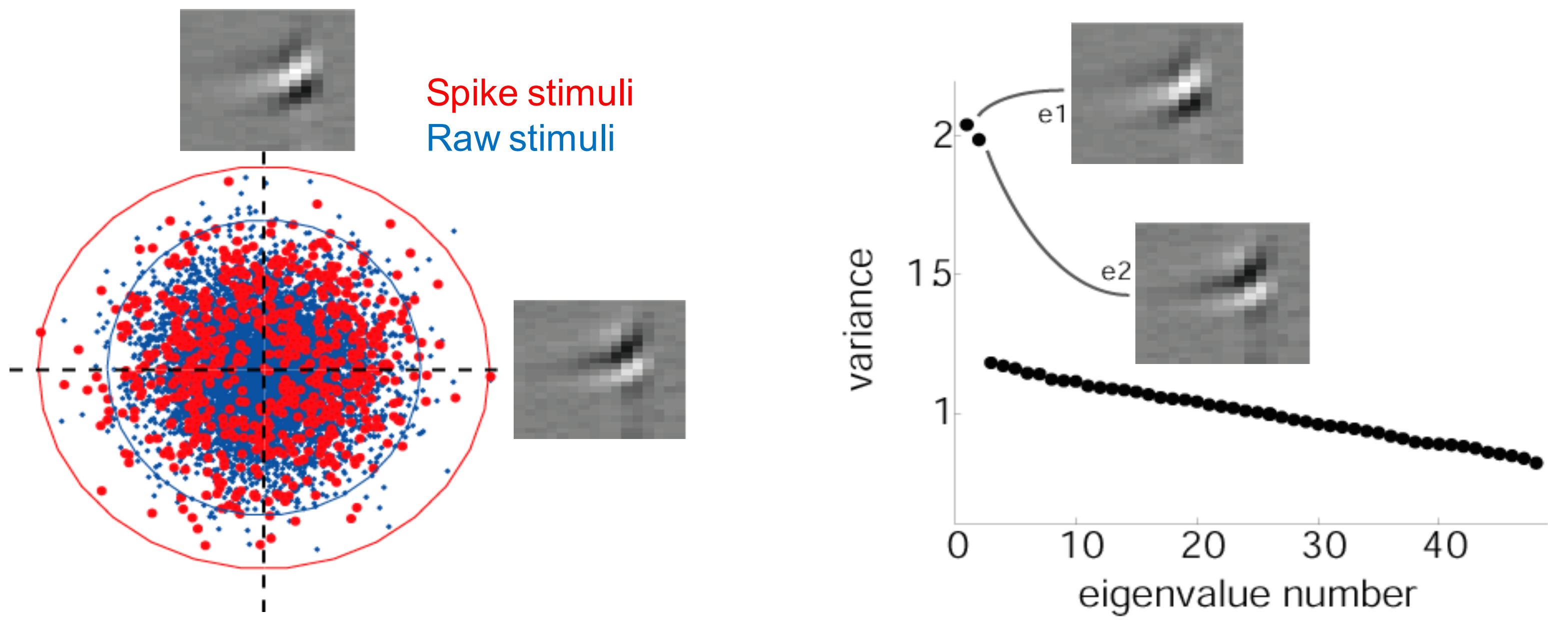
- Another example (STC)
- More generic model with multiple filters

SPIKE-TRIGGERED COVARIANCE (STC)

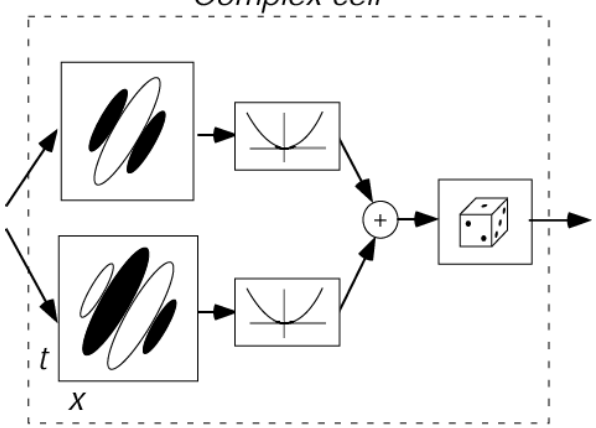


Adelson & Bergen (1985)

CHANGE IN VARIANCE (STC)



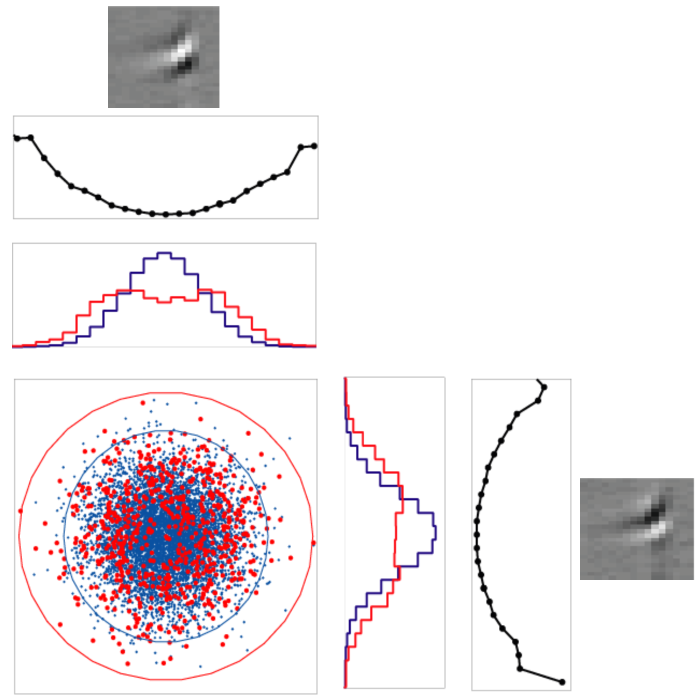
CHANGE IN VARIANCE (STC)



Adelson & Bergen (1985)

STA filter!

CHANGE IN 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)
(STA failed)
(we looked for changes in variance: STC)

ROADMAP

- Simple cell – traditional approach
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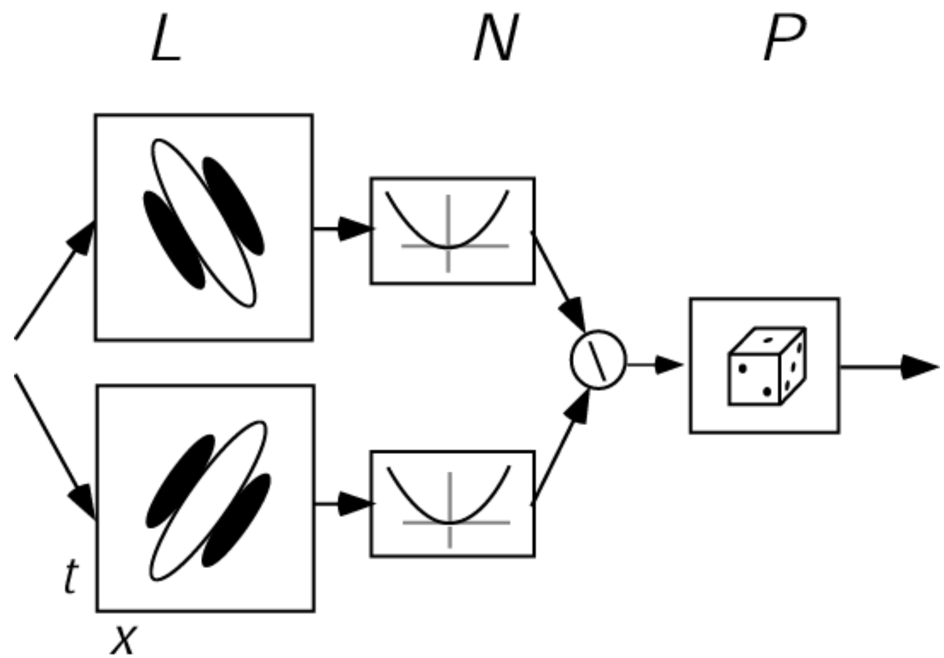
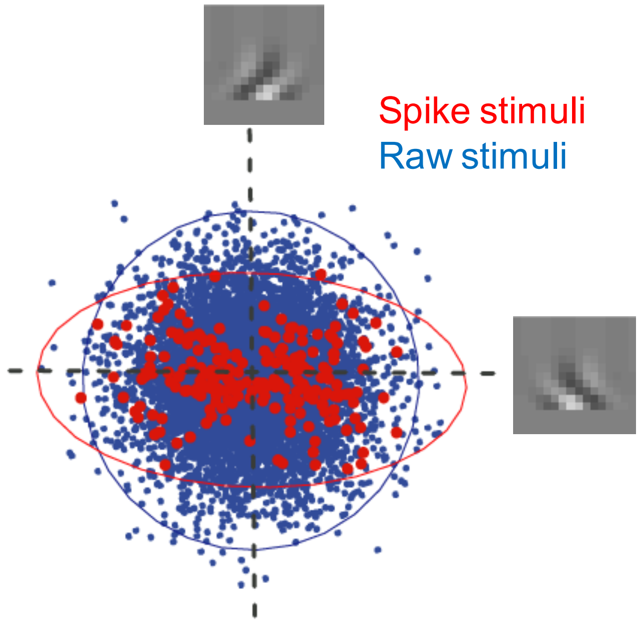
- More generic model with multiple filters

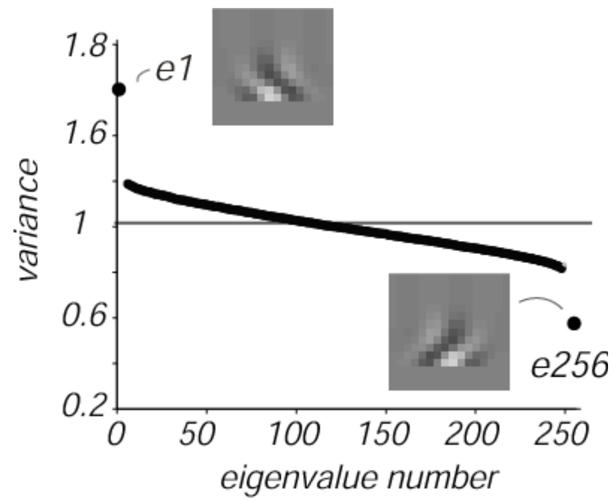
SECOND FILTER SUPPRESSIVE (E.G., DIVISIVE)



SECOND FILTER SUPPRESSIVE (E.G., DIVISIVE)

Second filter brings about reduction in variance!





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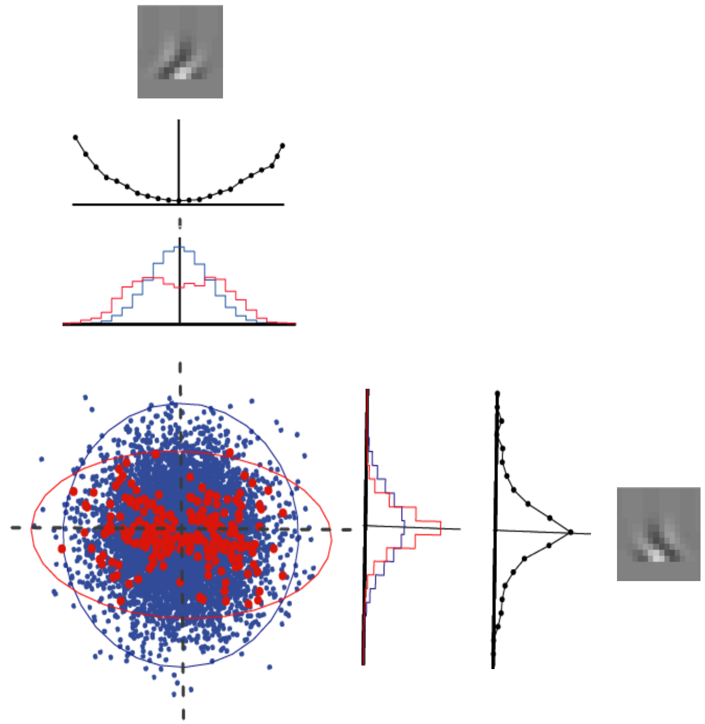


STEPS

1. Assume a model (filter/s, nonlinearity)

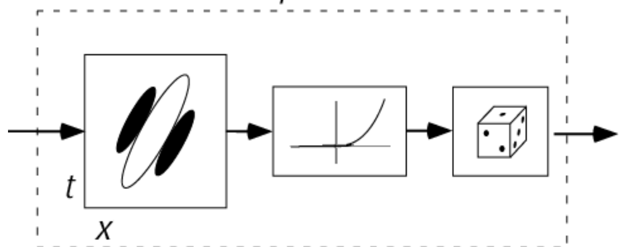
(we assumed more than one filter and symmetric nonlinearity)

2. Estimate model components (filter/s, nonlinearity)

(we looked for changes in variance, this time reduced variance: STC)

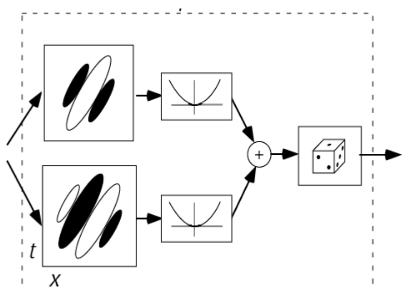
SPIKE TRIGGERED APPROACES

Simple cell

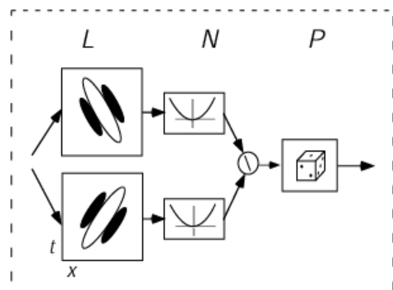


Change in the mean (STA)

Complex cell



Divisive normalization



Adelson & Bergen (1985)

Changes in the variance (STC)

ROADMAP

- Simple cell – traditional approach
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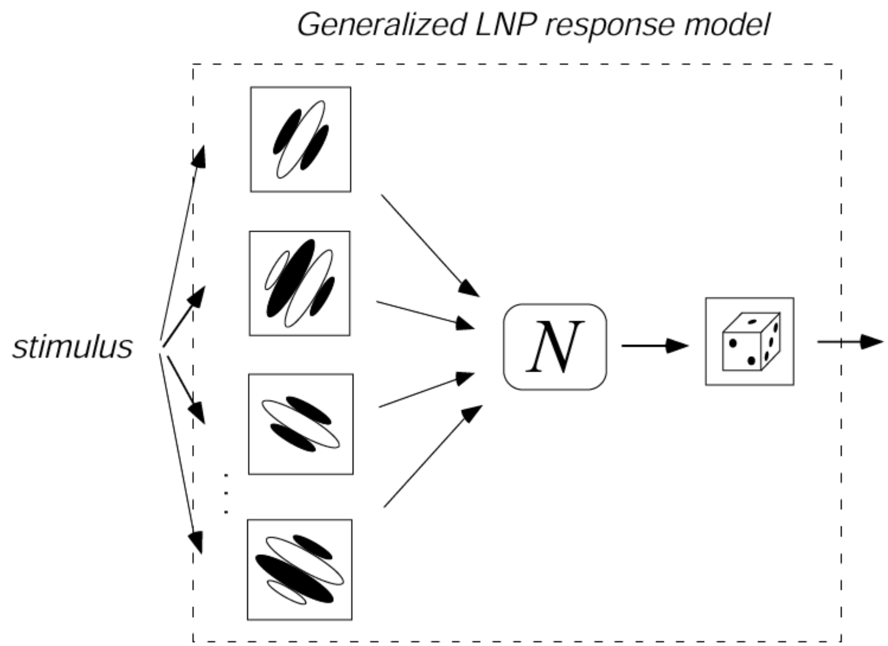
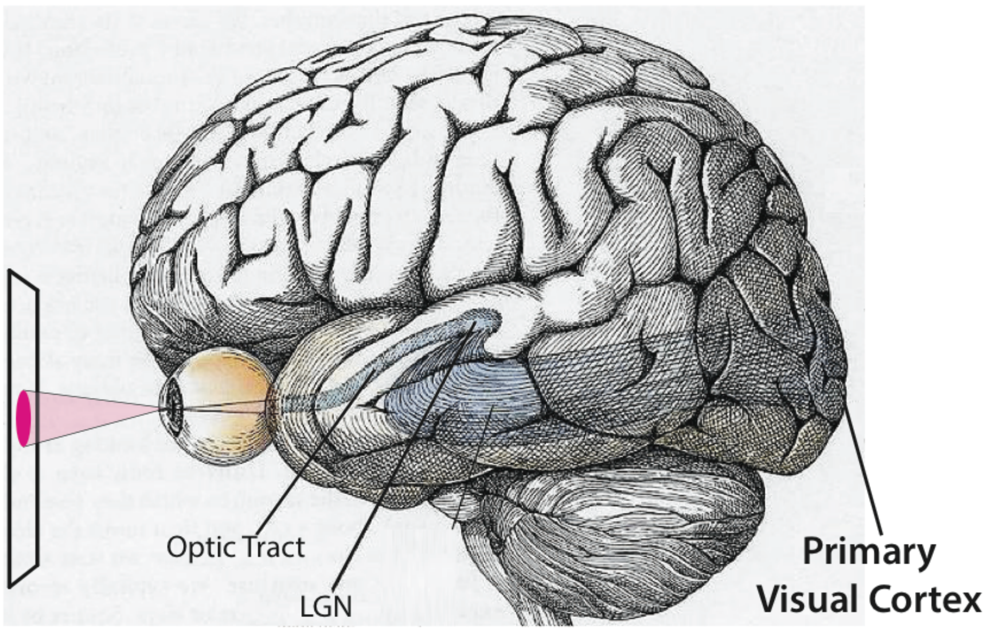
- More generic model with multiple filters

MORE GENERAL CLASS OF MODEL

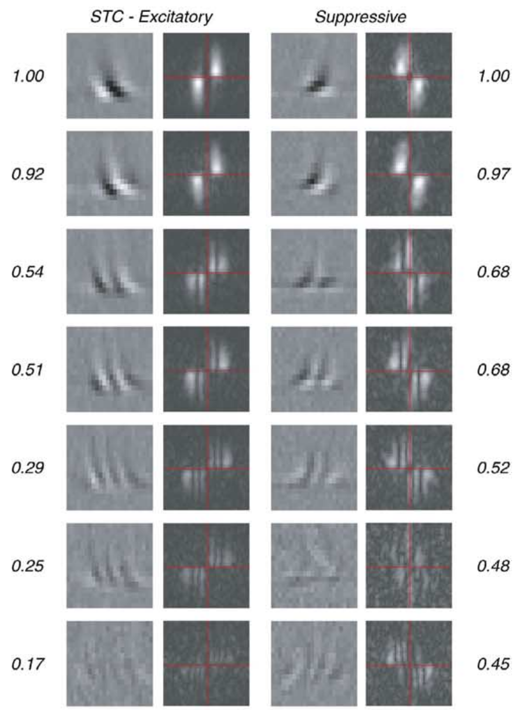
Look for changes in both the mean and the variance…



APPLICATION: V1 EXPERIMENT

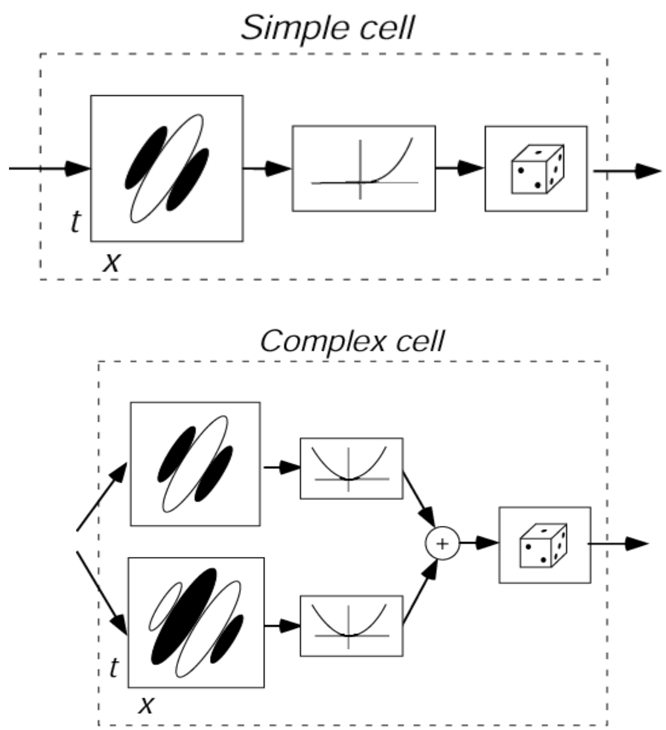


V1 NEURAL DATA: SPIKE-TRIGGERED COVARIANCE



- Example V1 neuron estimated filters from Rust et al. 2005

V1 NEURAL DATA: RECALL THE STANDARD MODELS



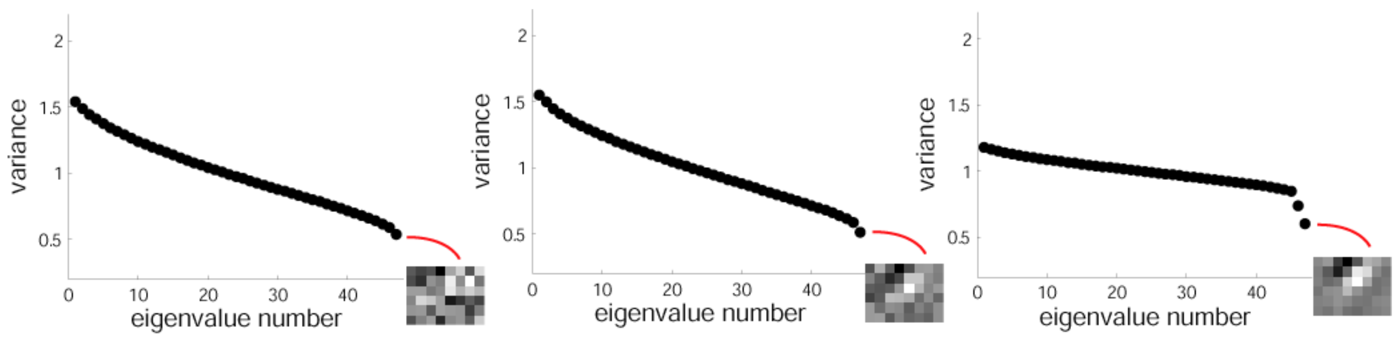
Adelson & Bergen (1985)

But…

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

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

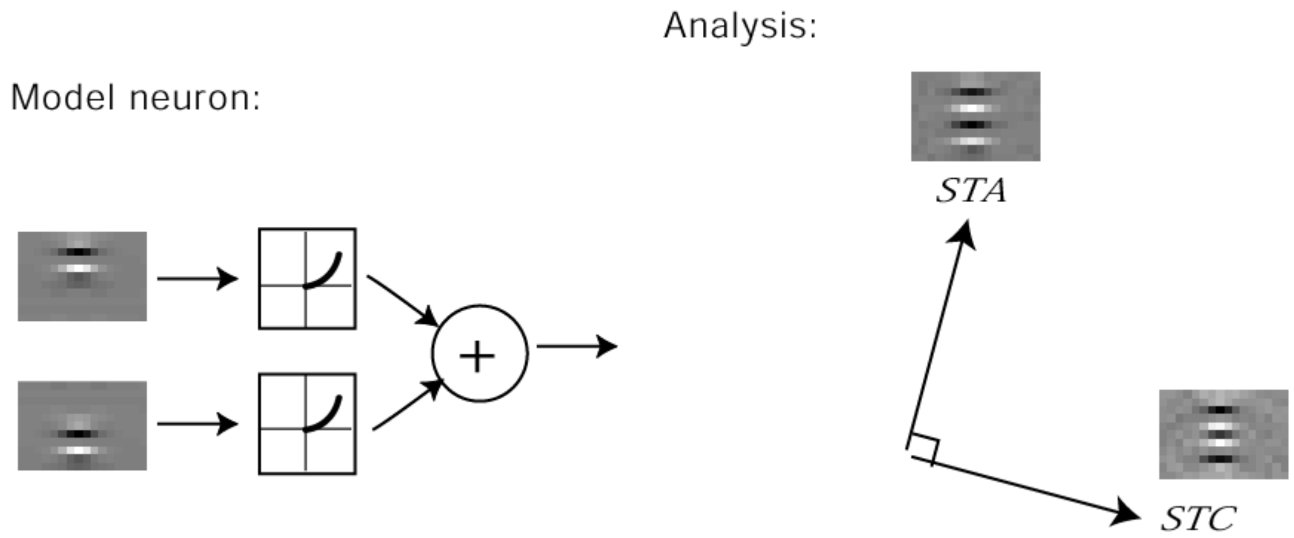
STC ISSUES: HOW MANY SPIKES?



Filter estimate depends on:

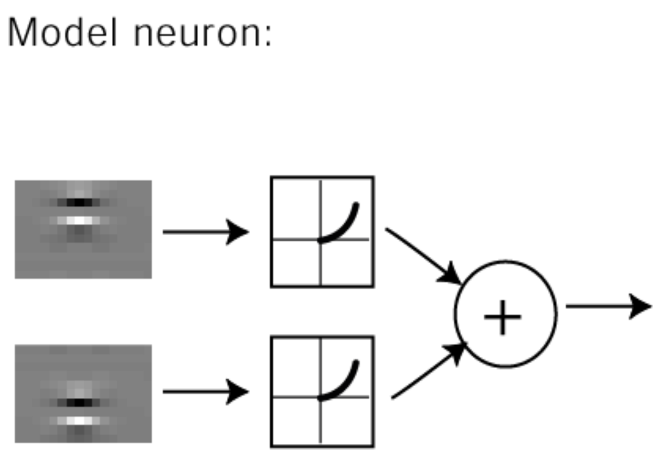
- Spatial and time dimensionality of input stimulus
  (smaller = better estimate)
- Number of spikes
  (more = better estimate)

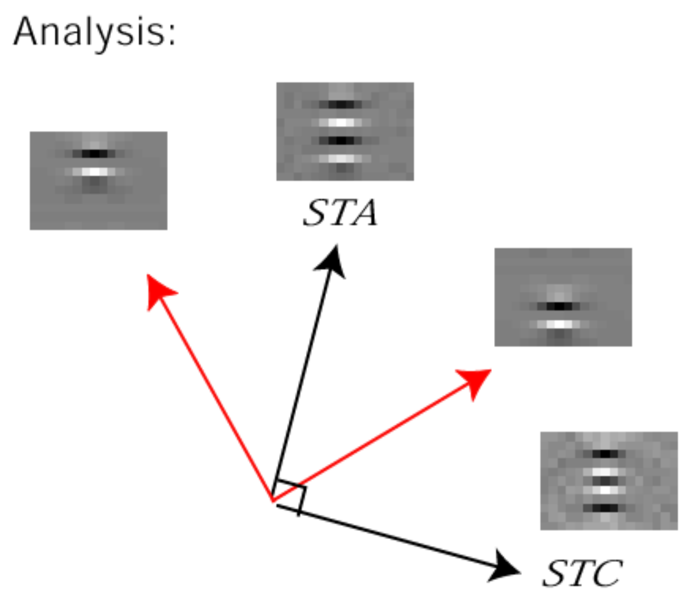
STC CAVEATS



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

STC CAVEATS





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

STC CAVEATS

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

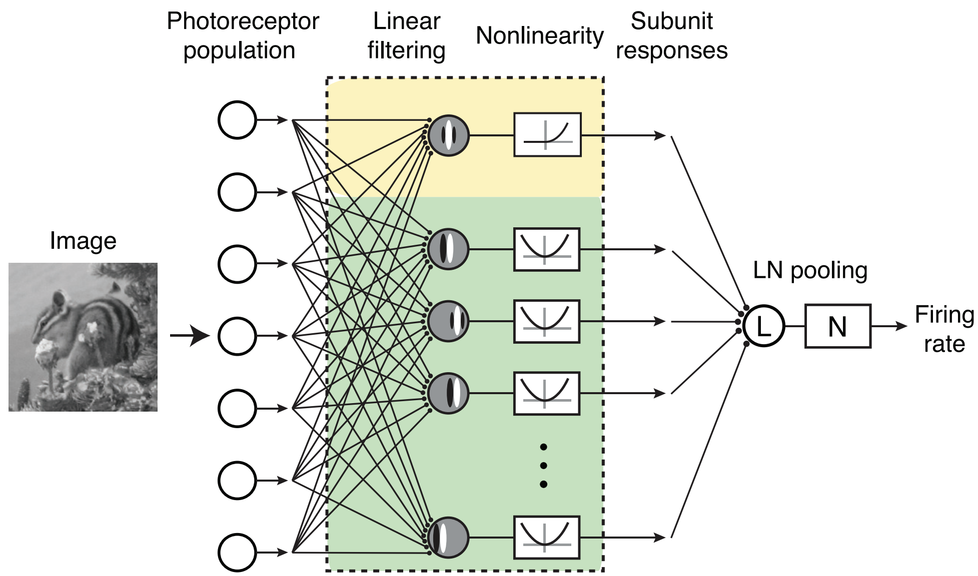
- Spiking in neuron may be non Poisson (bursts; refractory period; etc.)
  Filters should not be taken literally as physiological mechanisms

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

- STC guaranteed to work only for Gaussian stimuli

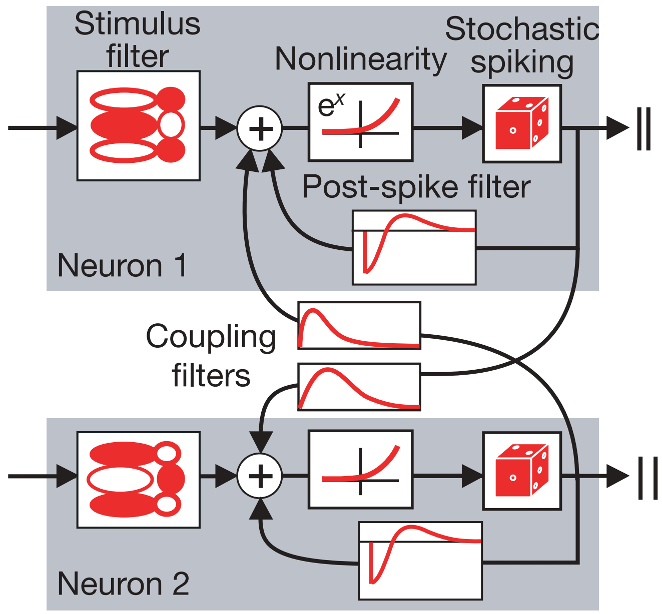
- There might be changes that are not in the mean or variance (other approaches; e.g., info theory)

EXAMPLE: FITTING LN-LN MODEL



- Figure from Pagan et al. 2015 describing retina and V1 with subunits (see Rust et al. 2005; Vintch et al. 2015)
- In Pagan et al. 2015 addressing higher level brain areas
- See also Rowekamp et al. 2017 addressing area V2

EXAMPLE: GENERALIZED LINEAR MODEL



- Figure from Pillow et al., 2008, describing retina