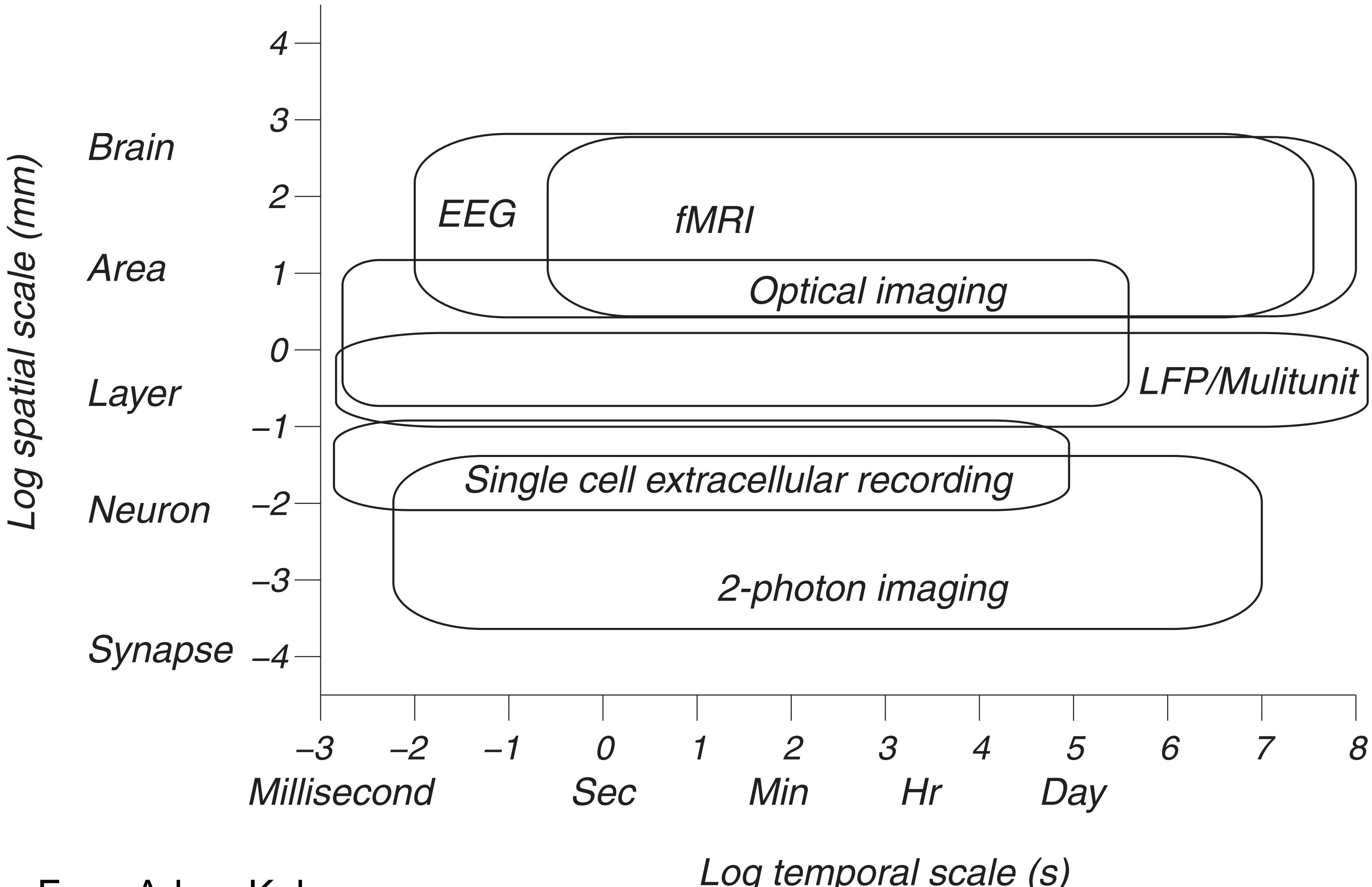
# *The Neural Code*

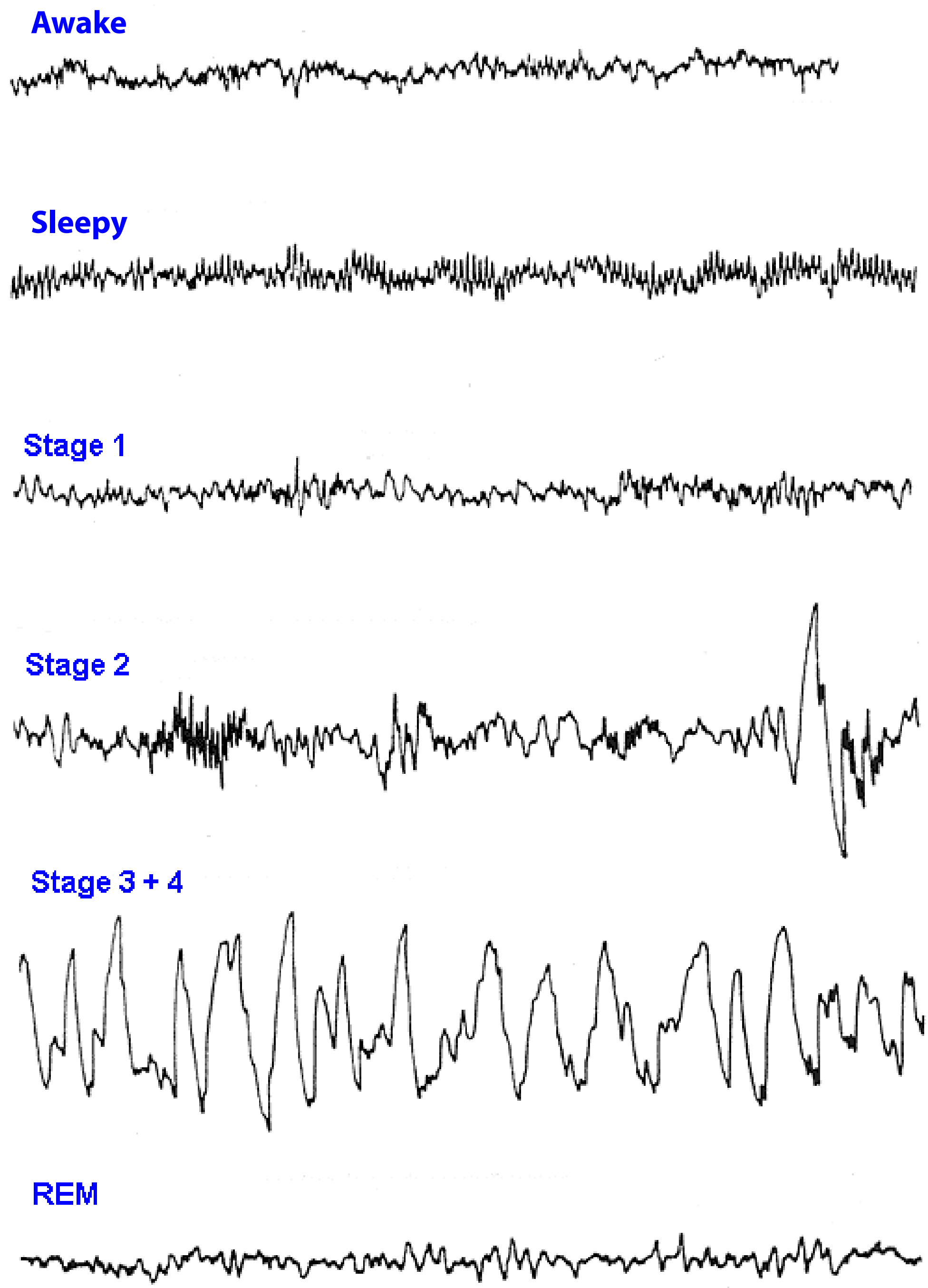
*Neurons communicate with action potentials. Understanding what they are communicating requires knowledge of their language: the neural code*

# Measuring neural activity



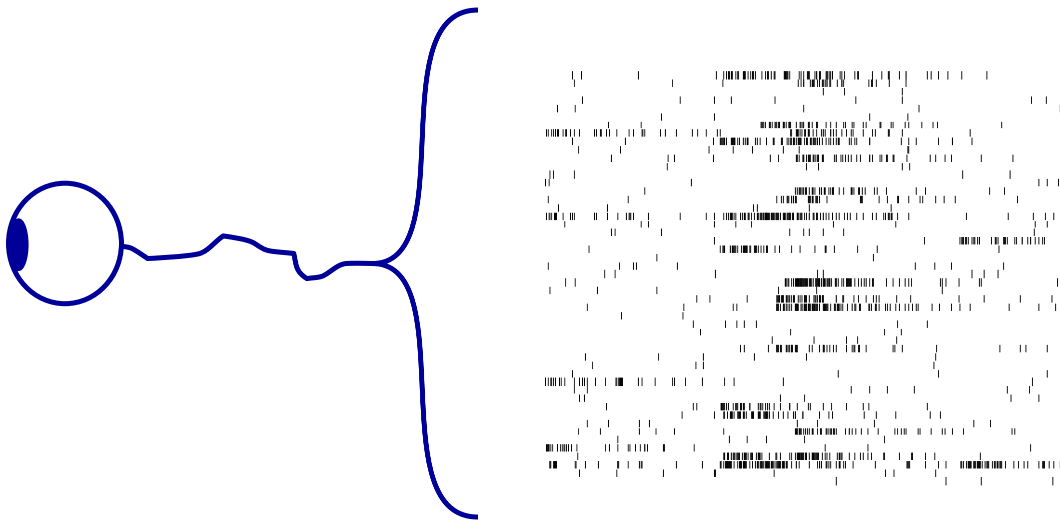

From Adam Kohn

# EEG



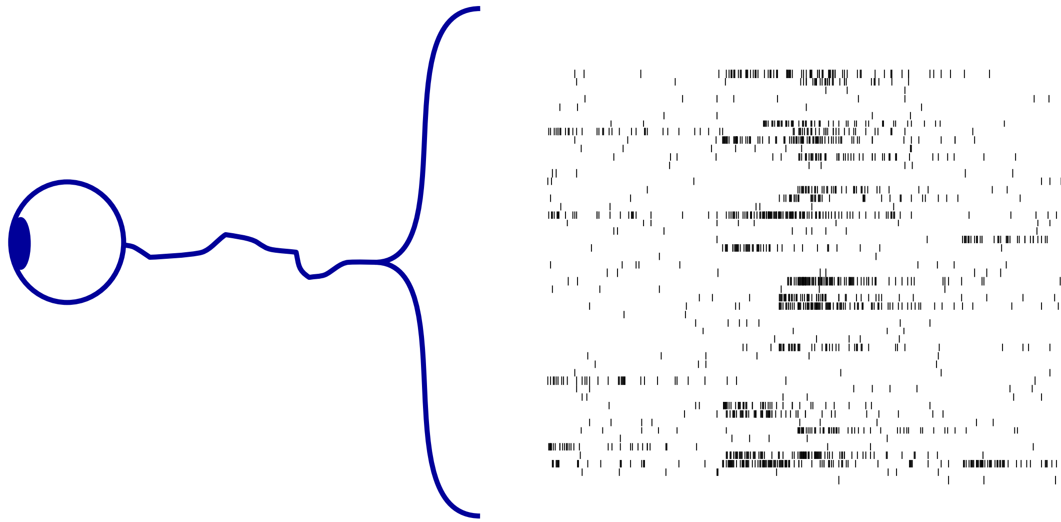

From Adam Kohn

# Population of neurons and spikes



Adapted from Gatsby Computational Neuroscience course

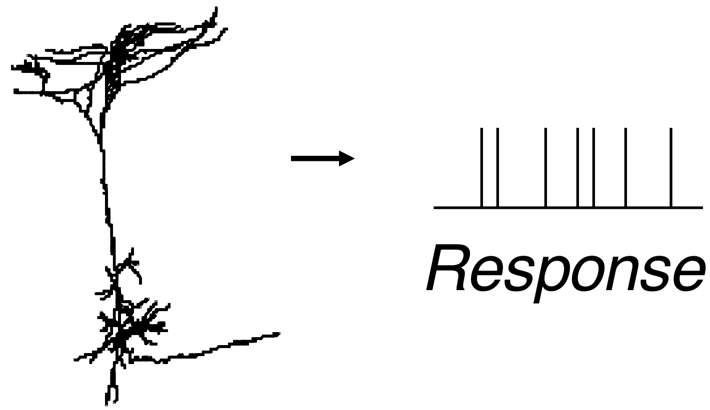
# What your brain "sees"

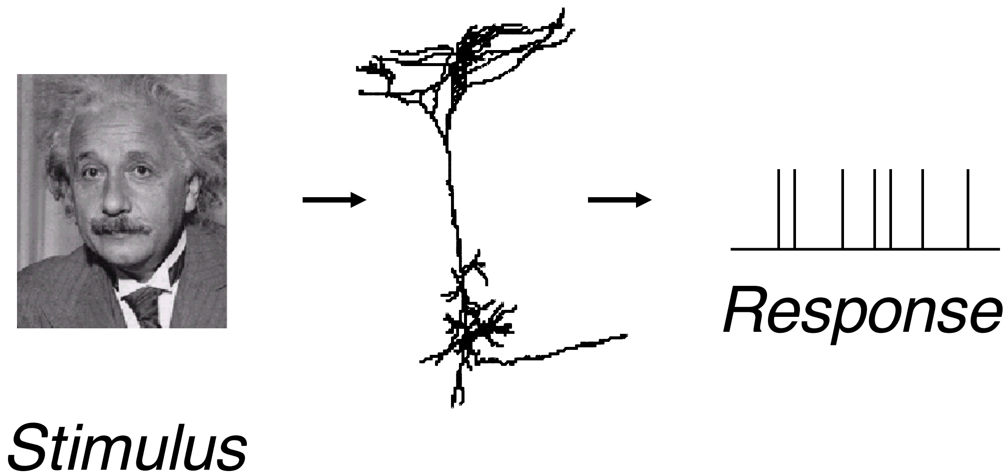


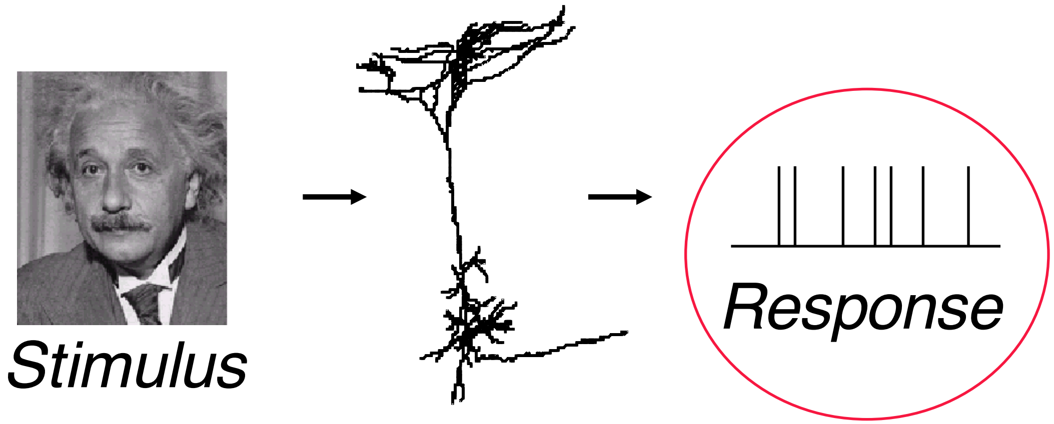
You infer…
Palm trees
UM Campus
Warm weather

Adapted from Gatsby Computational Neuroscience course

# Single neuron and spikes

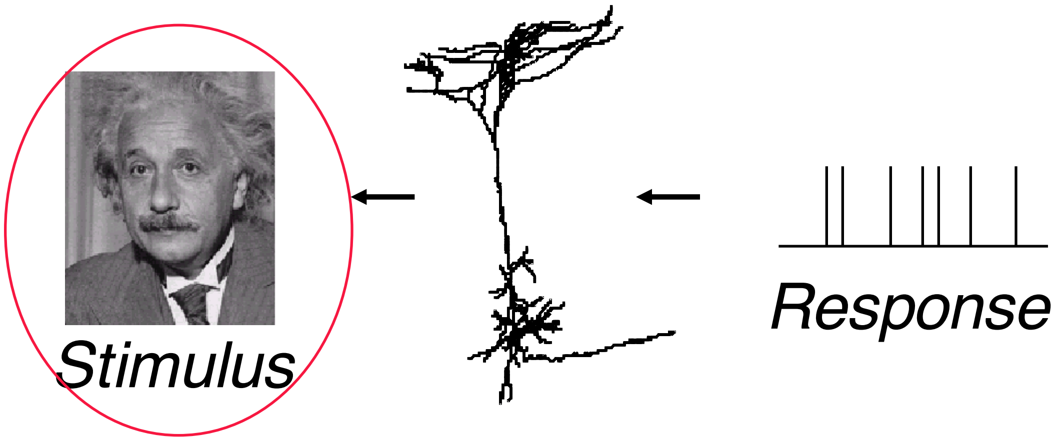



Stimulus
Response




*Encoding:* *Probability(Response | Stimulus)*

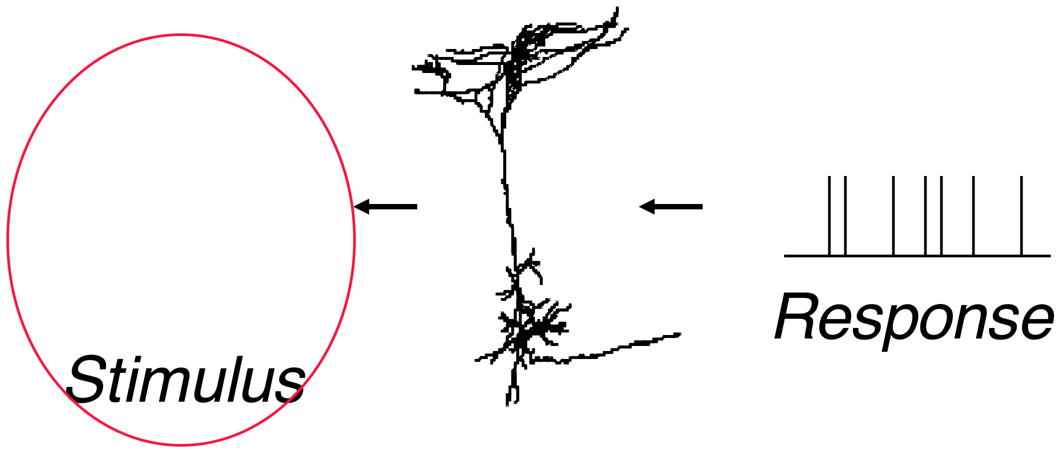
*As an experimenter, we can present stimuli and find what responses they lead to…*




Decoding: the reverse problem…

*Probability(Stimulus | Response)*

*An organism receives sensory responses, and makes judgments about the stimulus*

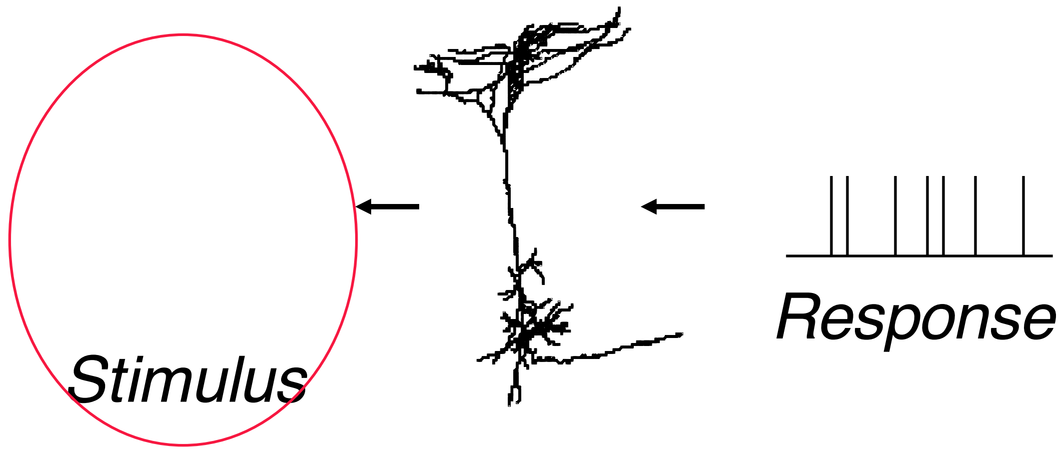



Decoding: the reverse problem…

Probability(Stimulus | Response)

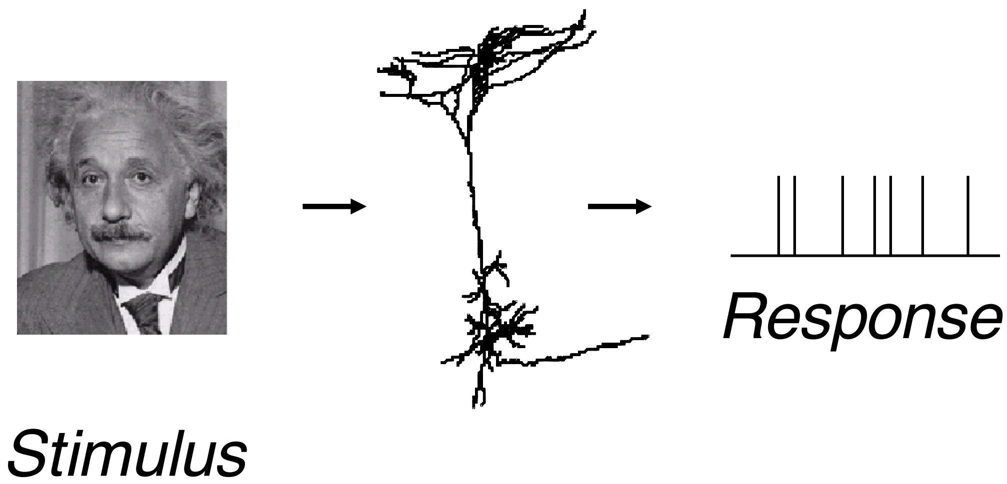
*An organism receives sensory responses, and makes judgments about the stimulus*

*Reconstruction*
*Orientation*
*Spatial location*
*Sound pitch*
*Discrimination*



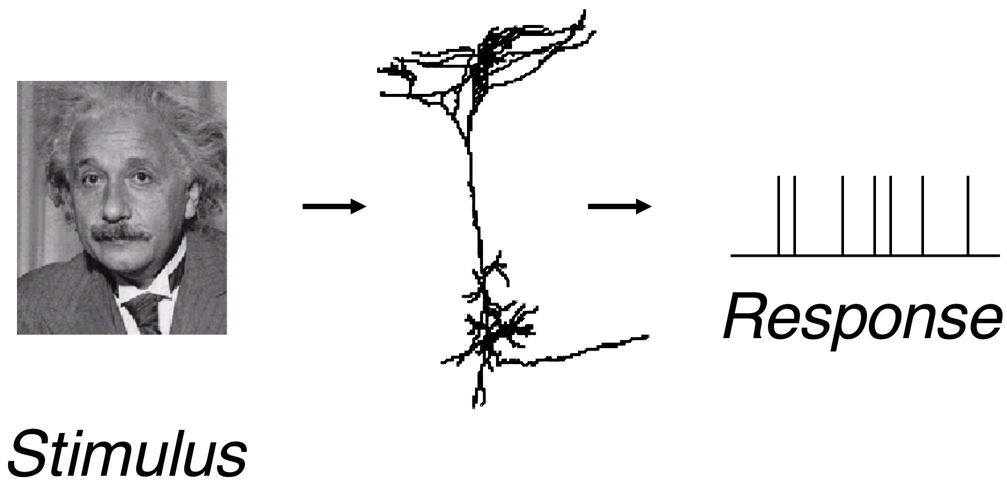

*Decoding: the reverse problem…*
*Probability(Stimulus | Response)*

*An organism receives sensory responses, and makes judgments about the stimulus*




*Ideally, for any input we'd like to know the response*
*And vice versa*

*Problems in deciphering the neural code?*




*Stimulus space huge*

*Response space huge*

# What kind of neural codes?

# *Rate codes*

*The only important characteristic of a response (spike train) is the number of spikes evoked/the response rate.*

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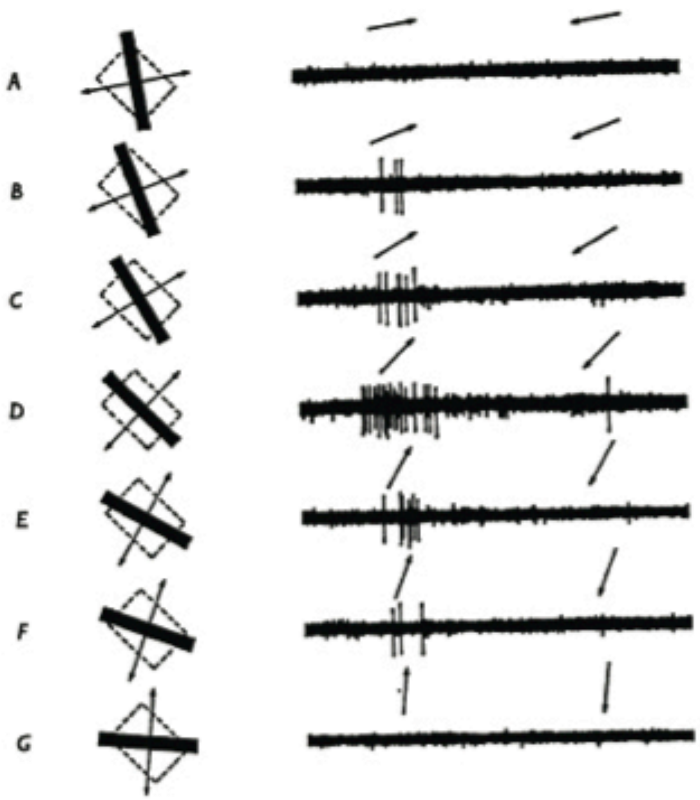
*Example 1:* *Orientation tuning in primary visual cortex*




# *Rate codes*

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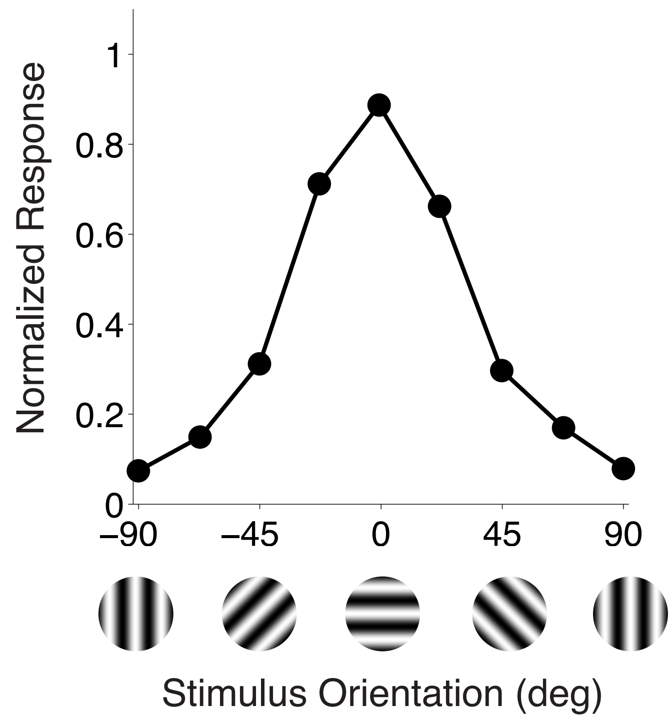
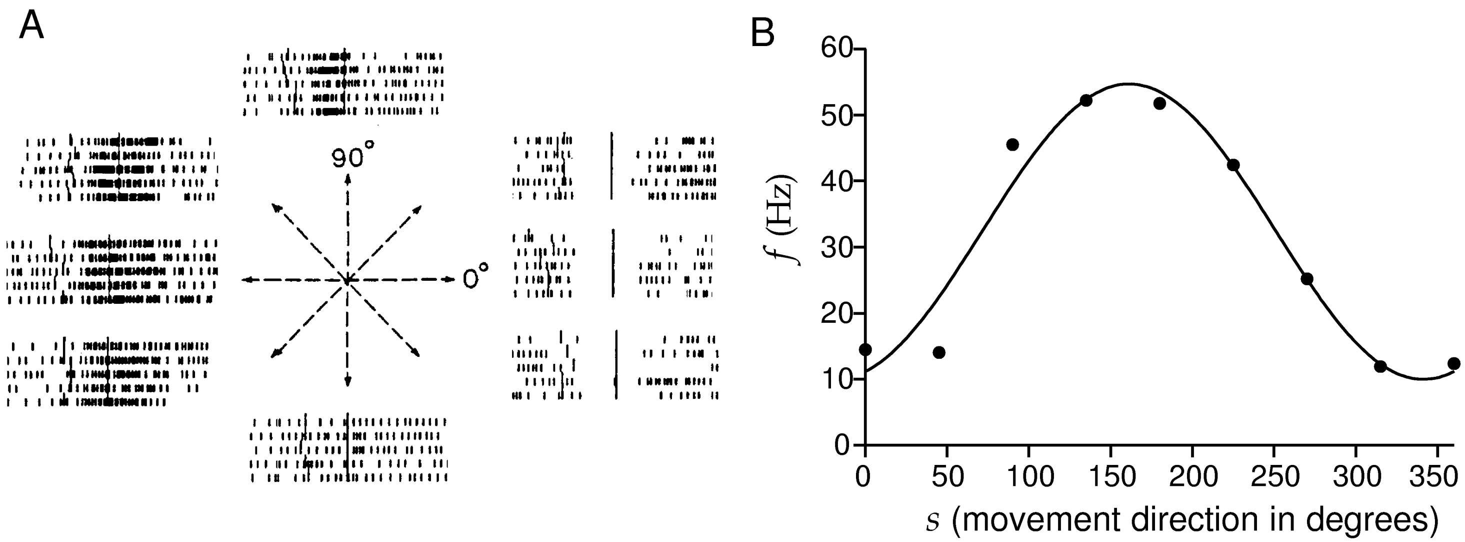
*Example 1:* *Orientation tuning in primary visual cortex*



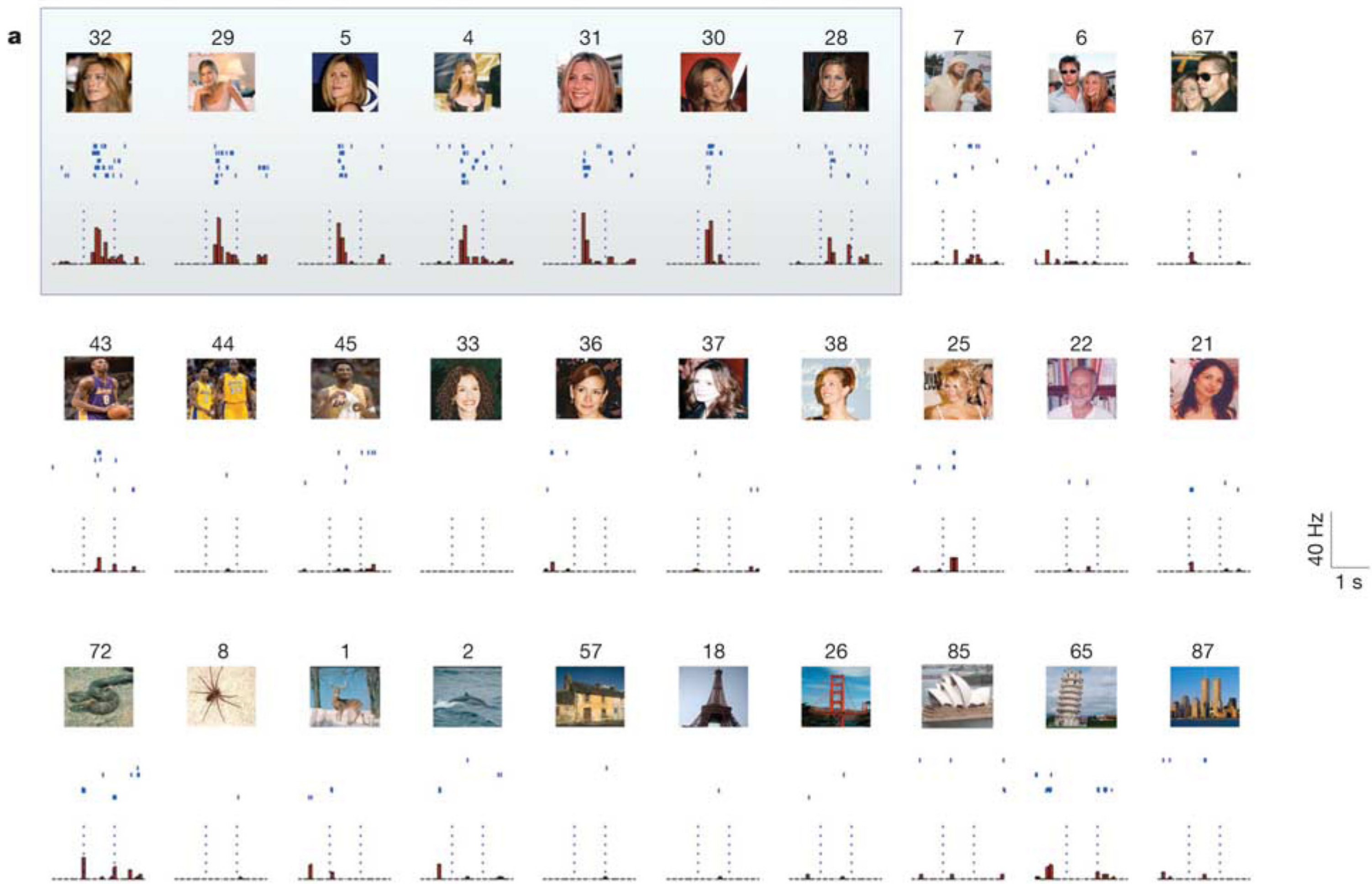

Wissig and Kohn 2012

# *Rate codes: example 2*




- Dayan and Abbott textbook; adapted from Georgopoulos et al. 1982

# *Rate codes: example 3*




- Quiroga et al. 2005 (Nature)

# *Rate codes*

- The only important characteristic of the spike train is the mean firing rate

- What other codes?

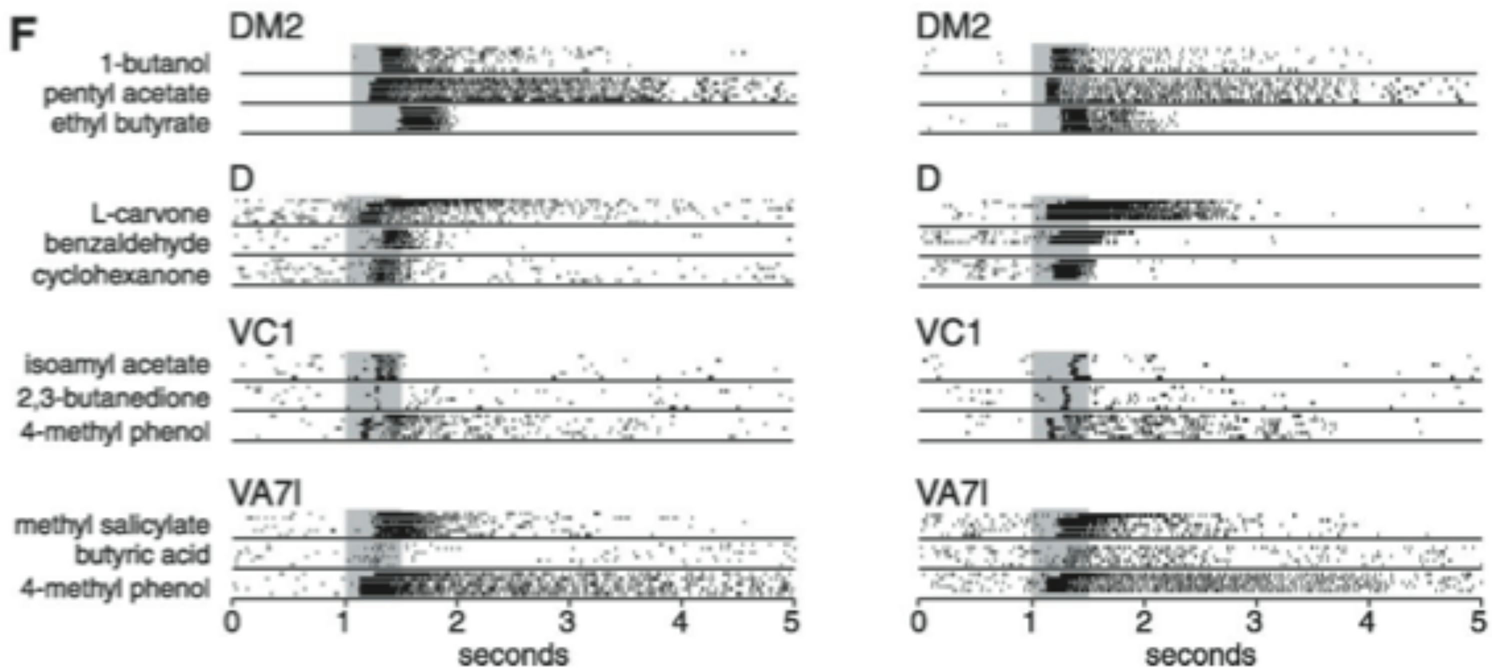
# *Rate codes*

- The only important characteristic of the spike train is the mean firing rate

- What other codes?
  Temporal codes: temporal structure of the spike train carries information about the stimulus beyond what is conveyed by the mean firing rate

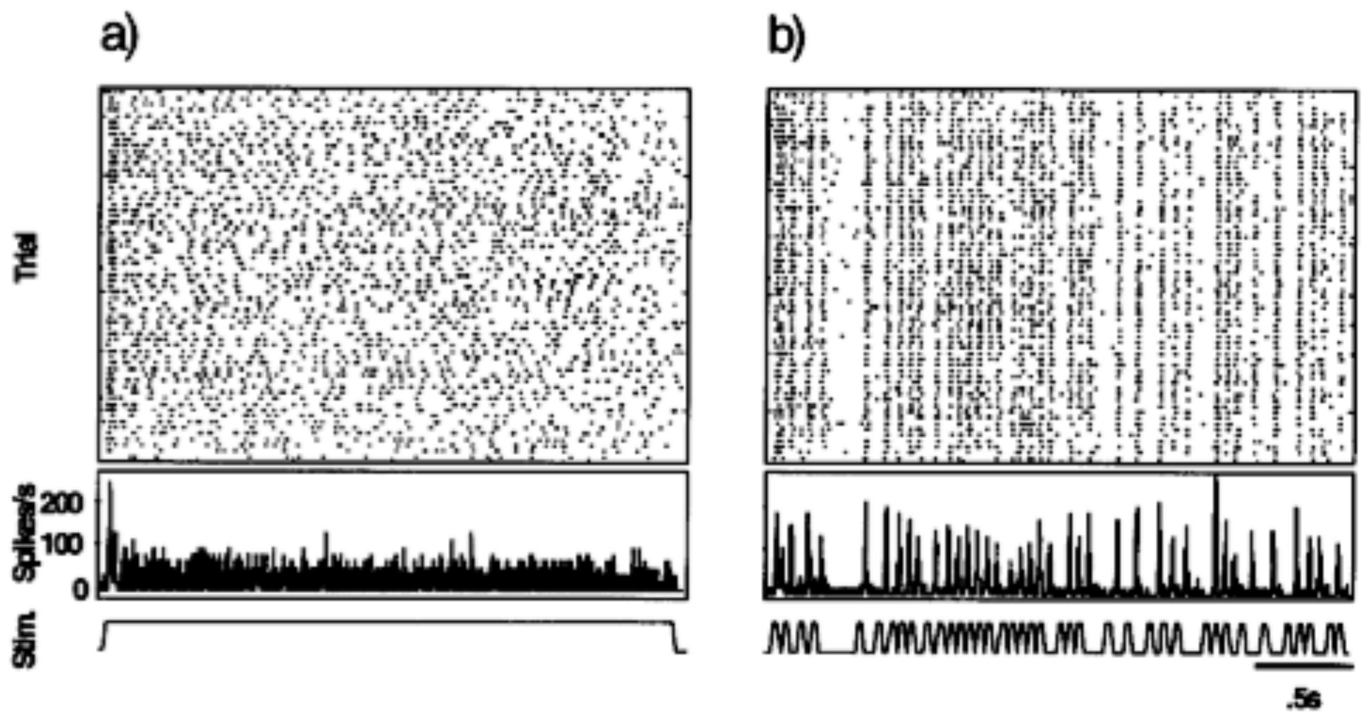
# *Temporal codes*

*Example 1: Coding of olfactory stimuli*




Neurons in the fly within a glomerulus: "Responses across flies were similar not just in intensity but also in temporal pattern, implying that odors elicit stereotyped dynamics in the antennal lobe network"; Wilson et al. 2004

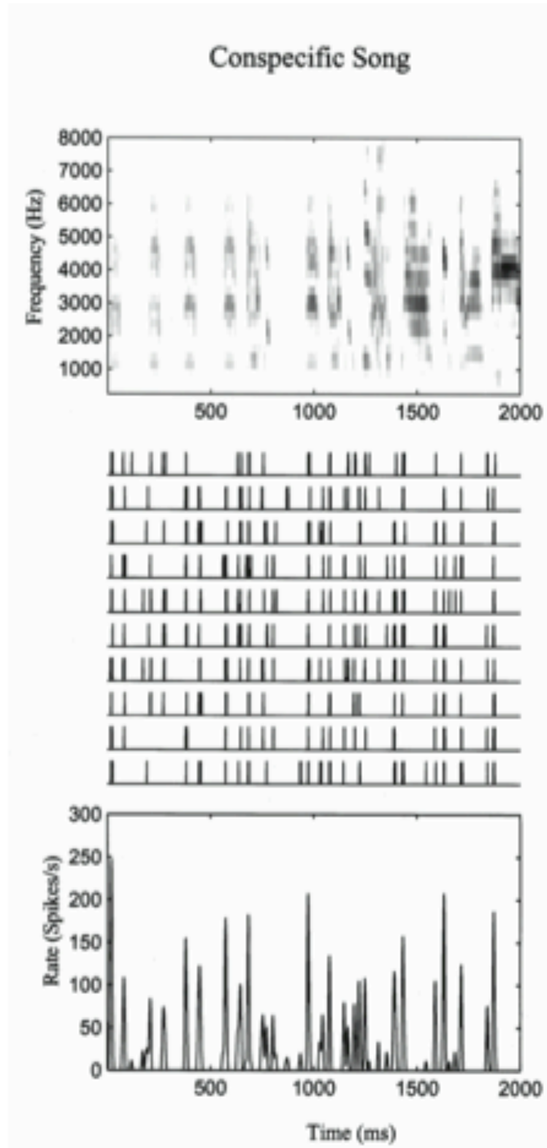
• Stimuli that change quickly typically generate rapidly changing firing rates regardless of coding strategy




*MT neurons, deCharms and Zador (after Buracas et al., 1998)*

# *Importance of timing*

*Zebra finch song learning*


*Theunissen et al. (2000) J Neurosci 20: 2315*

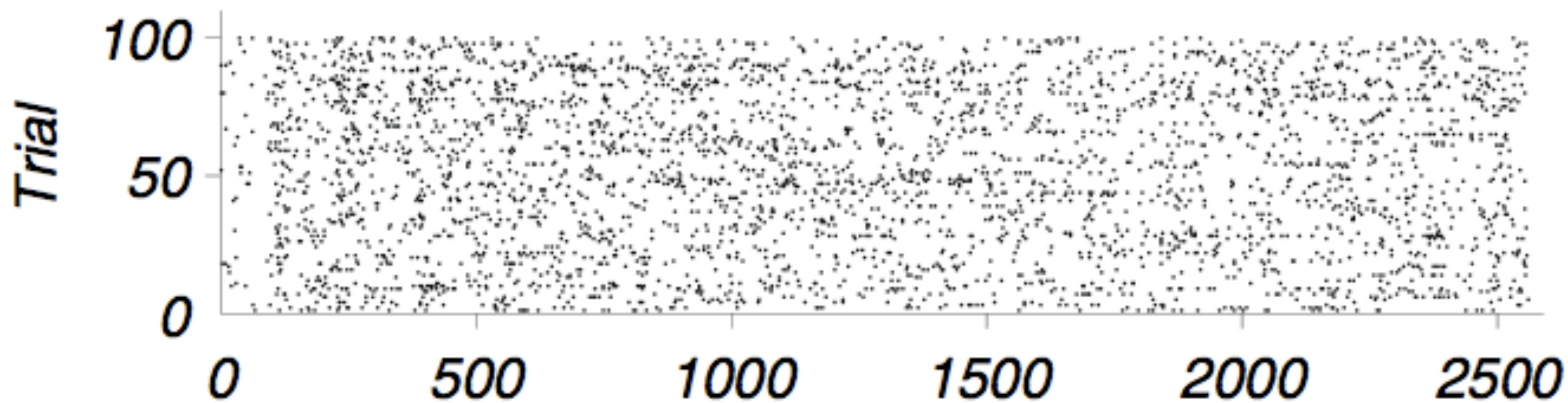
- Stimuli that change quickly typically generate rapidly changing firing rates regardless of coding strategy

- Temporal structure in spike trains carries information about temporal structure of stimuli

- More controversial: temporal structure in spike trains carries information not arising from dynamics of stimuli but due to some other stimulus property

# *Problems for both rate and temporal codes*

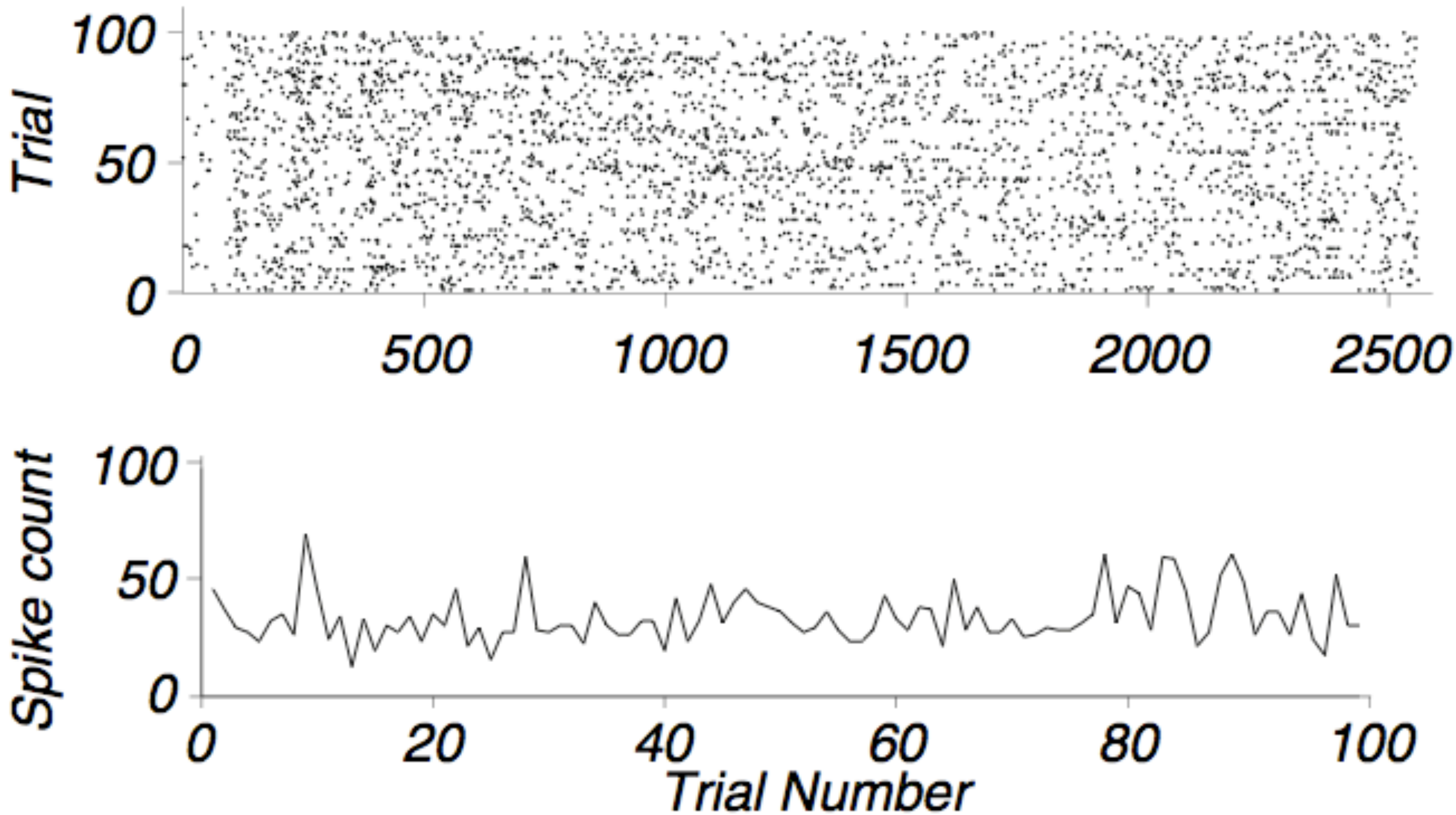
*Neuronal responses are "noisy"*




Same stimulus presented many times…

# Problems for both rate and temporal codes

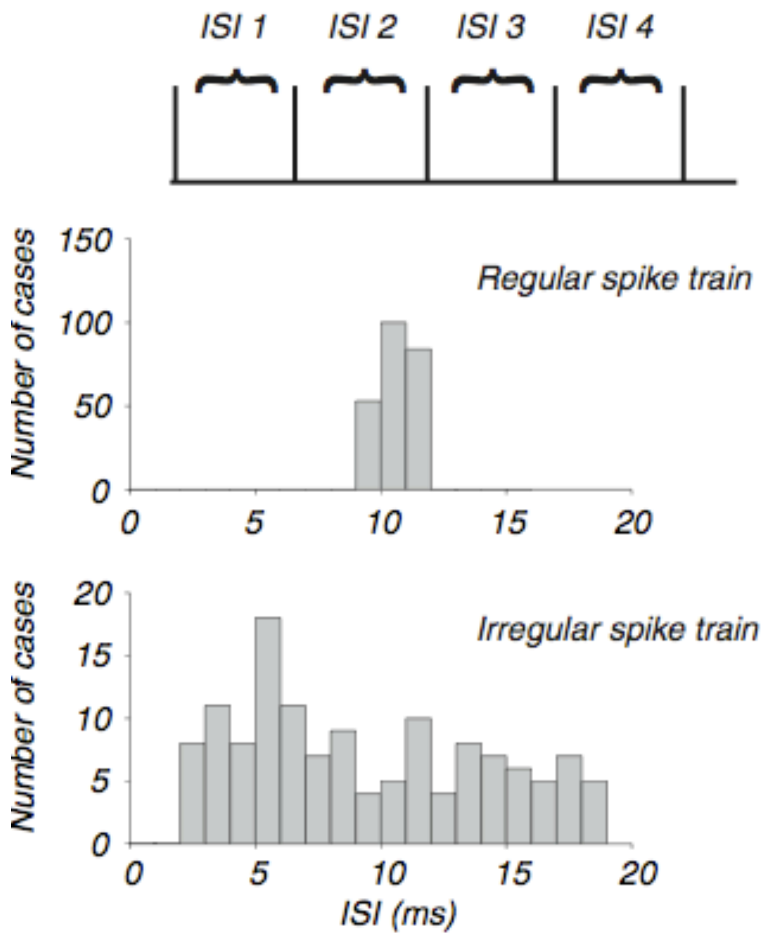
*Neuronal responses are "noisy"*



# Noise in temporal codes

*Difficult to measure:*

*Measure of spike train regularity*



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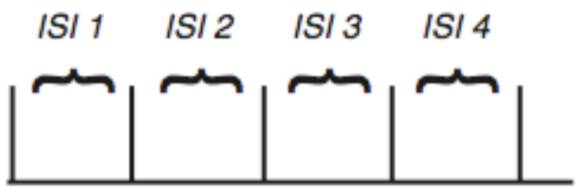
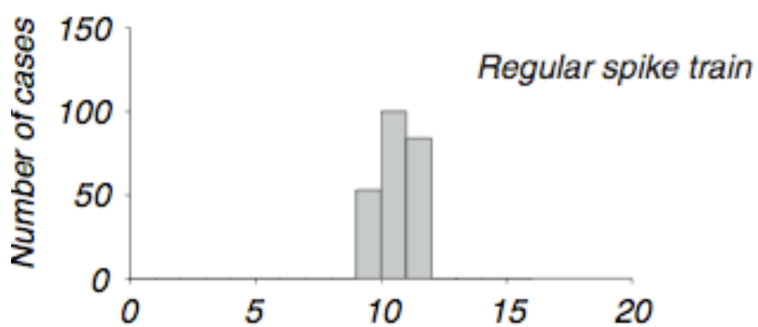
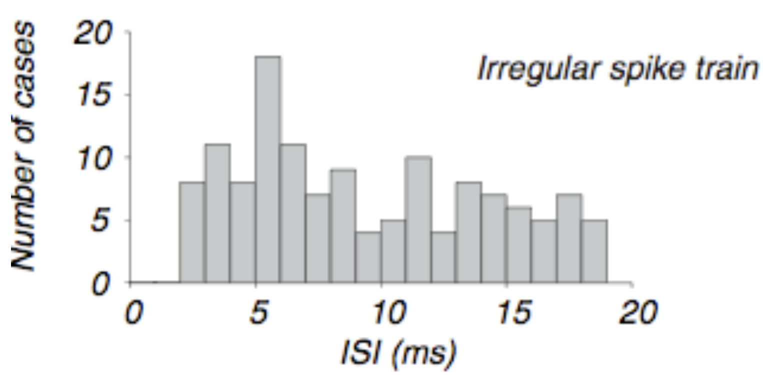


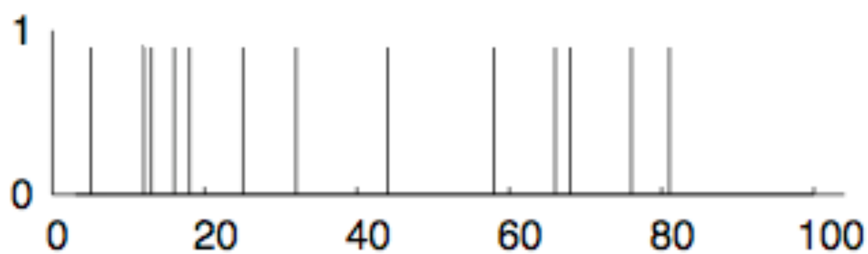

*Measure of pattern repeatability: Cost-based metric for transforming one spike train to another*


Victor JD (2005) Curr Opin Neurobiol. 15: 585-92.

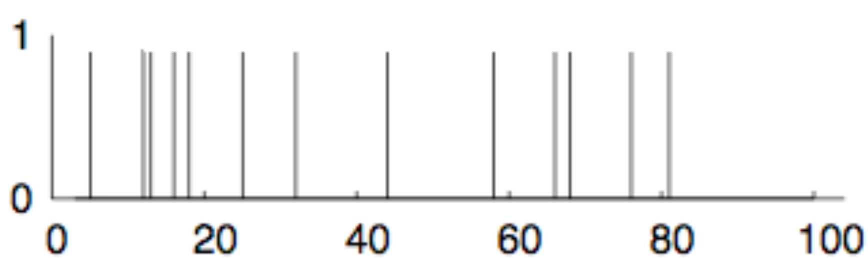
# *Poisson spike trains*

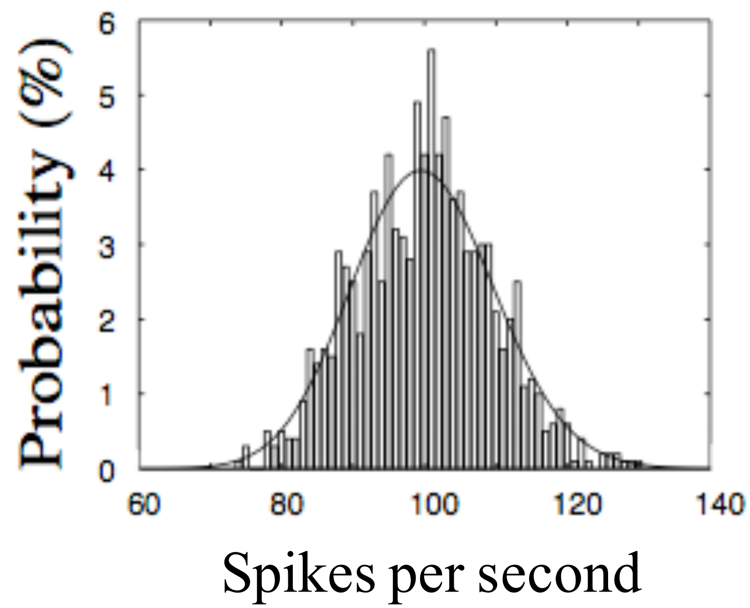
*Variability of neuronal spikes similar to a stochastic/random process, specifically a Poisson process*

*Process is defined by a single parameter—firing rate. The probability of a spike in any time interval is a random event (and independent of previous spikes)*



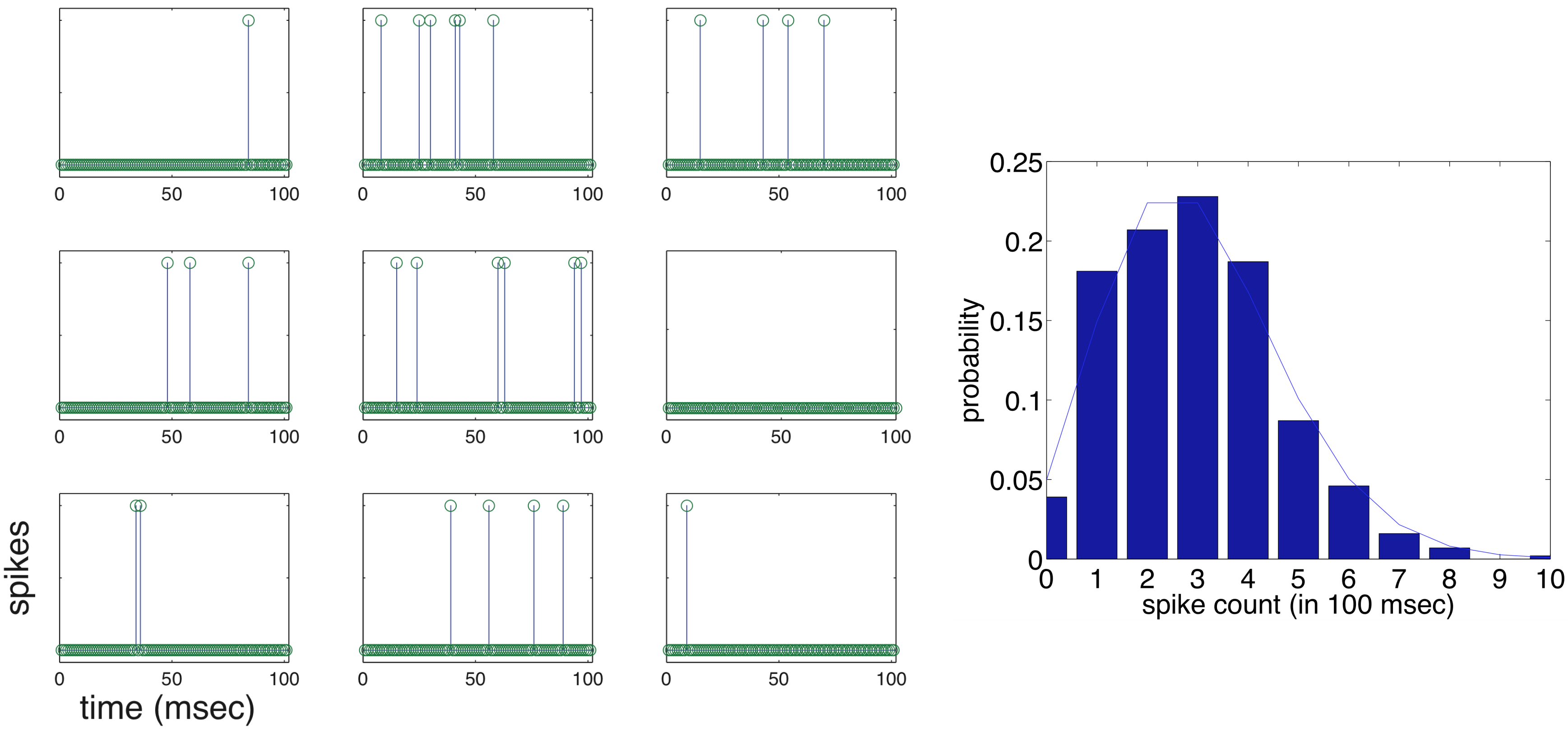
# *Poisson spike trains*



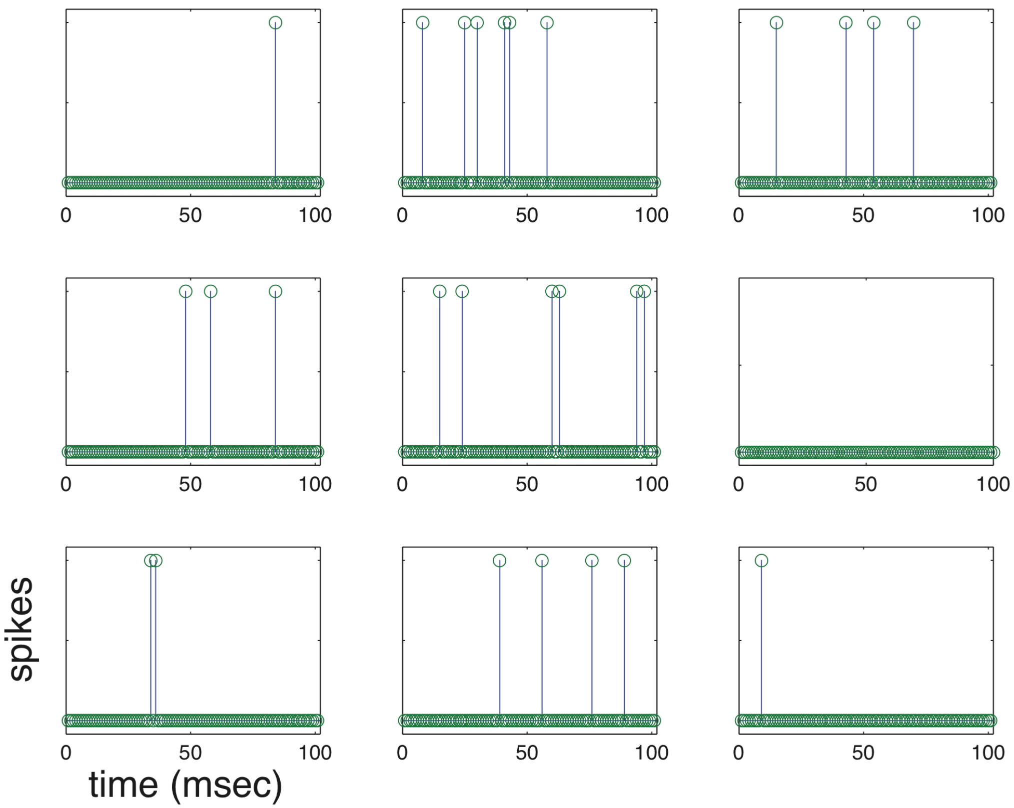

*Fano factor: var(count)/mean(count) = 1*

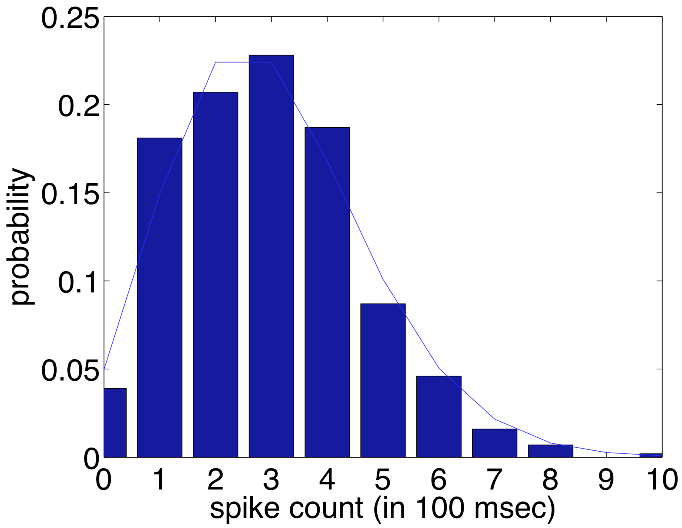
# *Poisson spike trains*




*Fano factor: var(count)/mean(count) = 1*

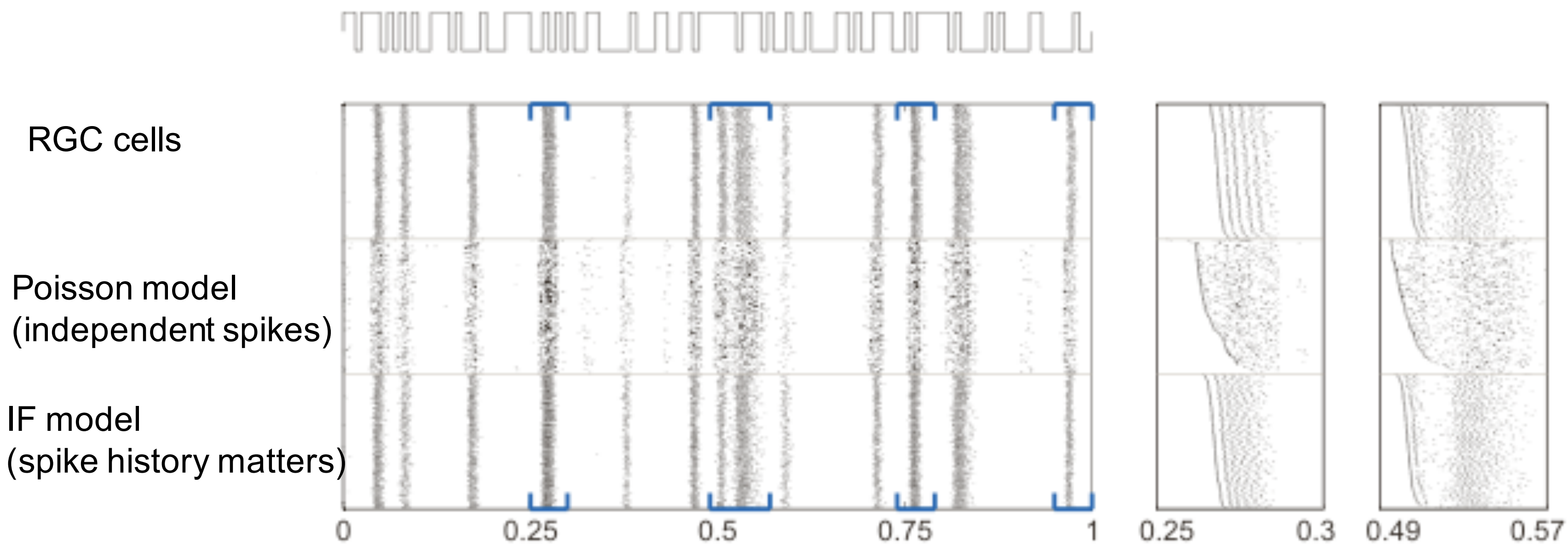
# *Poisson spike trains*




We'll generate Poisson spikes
in the computer lab…

# Less variability than Poisson




*Retinal Ganglion Cells, Pillow et al., 2006*

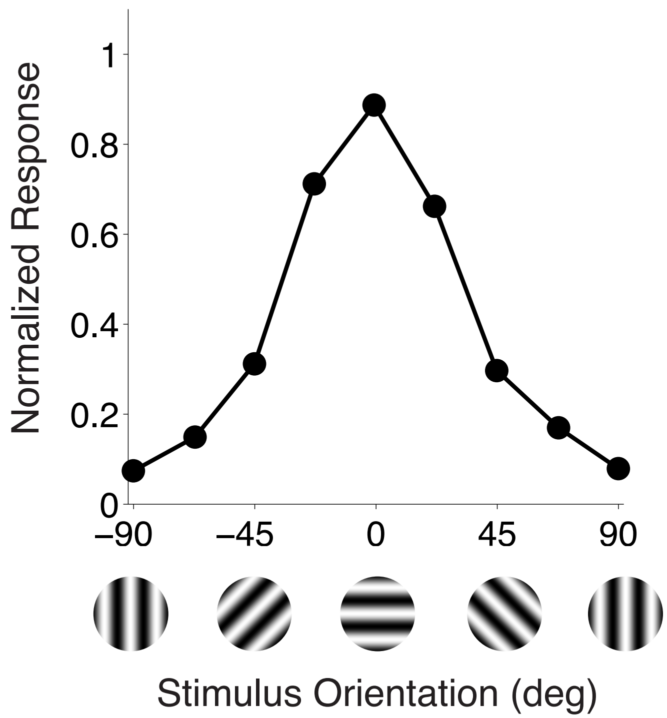
## Summary so far…

- Rate and temporal codes
- Neurons are “noisy”
- We’ve seen one way to generate spike trains: Poisson model
- We’d now like to look at a simple encoding model (inputs and Poisson spiking outputs) and estimate the response properties of a neuron

How do we characterize the response properties of neurons for a given encoding model?

# *We've already seen…*

- Tuning curves characterize the average firing rate response of a neuron to a given stimulus property




Wissig and Kohn 2012

## *We've already seen…*

- Tuning curves characterize the average firing rate response of a neuron to a given stimulus property (orientation; reaching direction; etc)

- But we've decided in advance on a stimulus dimension (such as orientation)!
  Experimentalists did too when they used spots of light or bars…
  That seems pretty biased or lucky…

# *We've already seen…*

- Tuning curves characterize the average firing rate response of a neuron to a given stimulus property (orientation; reaching direction; etc)

- But we've decided in advance on a stimulus dimension (such as orientation)!

- Instead: Can we "blindly" figure out what a neuron cares about??

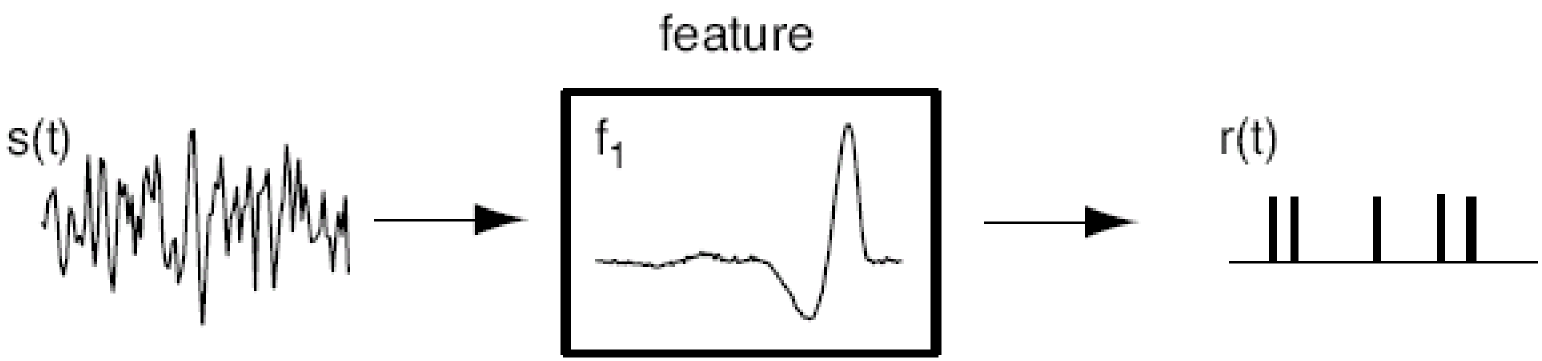
## *Characterizing response properties of neurons*

- Cool idea: Explicitly consider an encoding model (Linear filter, Nonlinearity, Poisson spiking)

- Estimate the missing pieces (eg, the Linear filter)

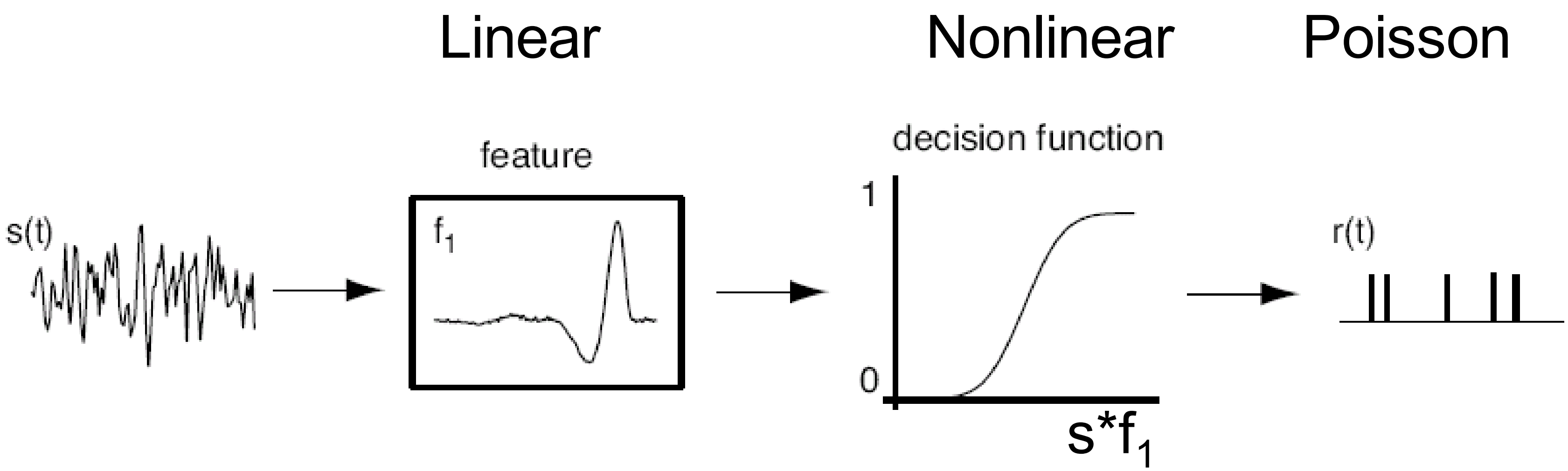
- Here we'll use a simple approach known as spike-triggered average (or reverse correlation)

# Basic coding model: temporal




- This can also be seen as a descriptive model!

# Basic coding model: temporal

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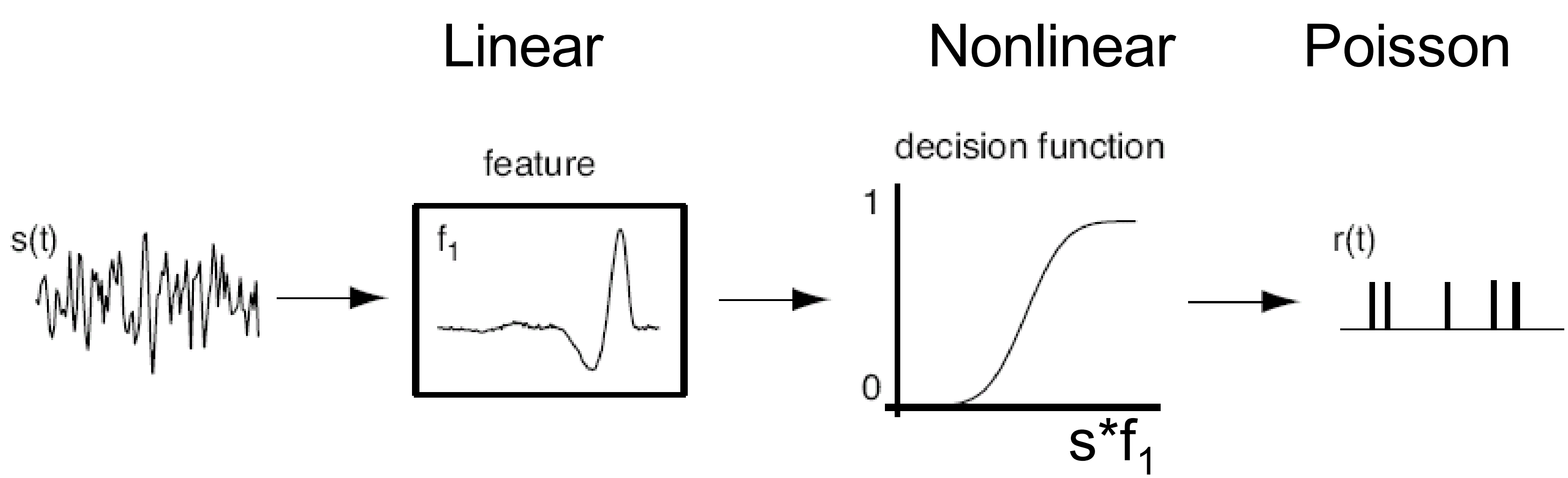


**In an experiment:**

- We know the input stimuli
- And we measure the corresponding spike trains

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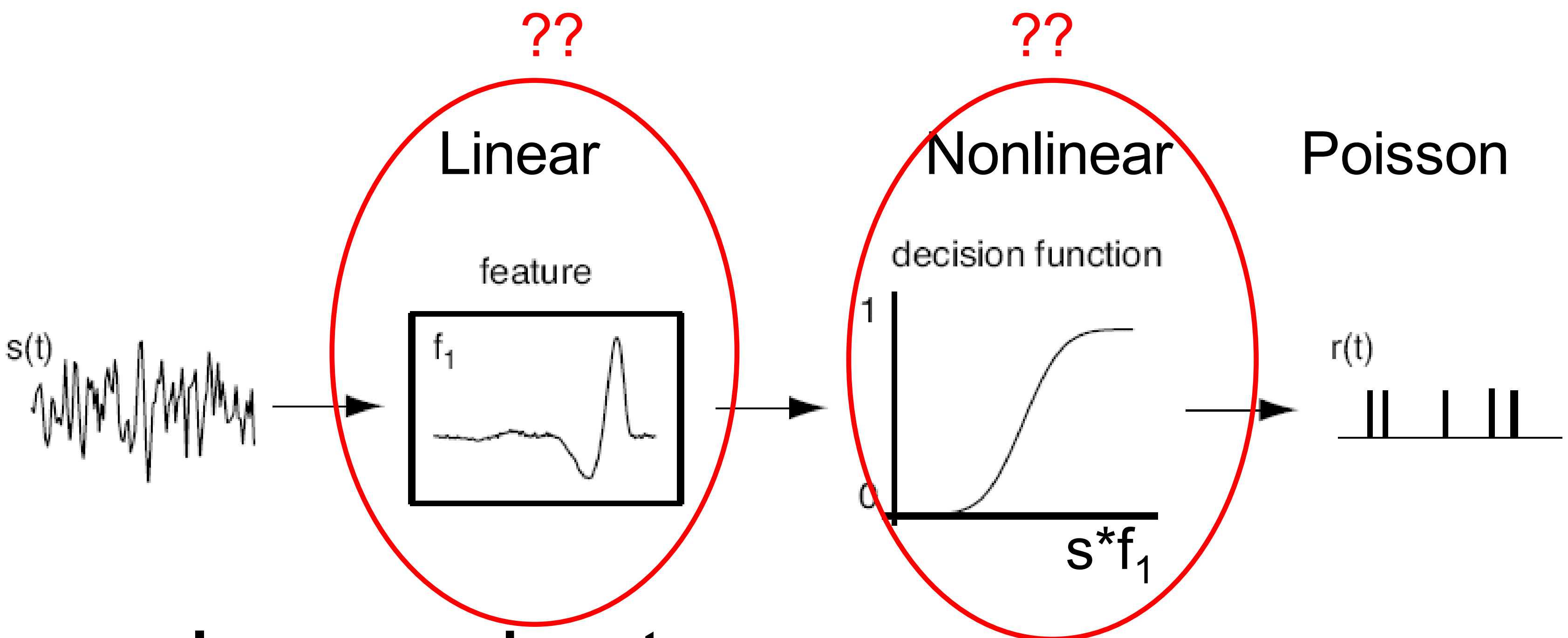


**In an experiment:**

- We know the input stimuli
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- We don't know the Linear or Nolinear boxes!

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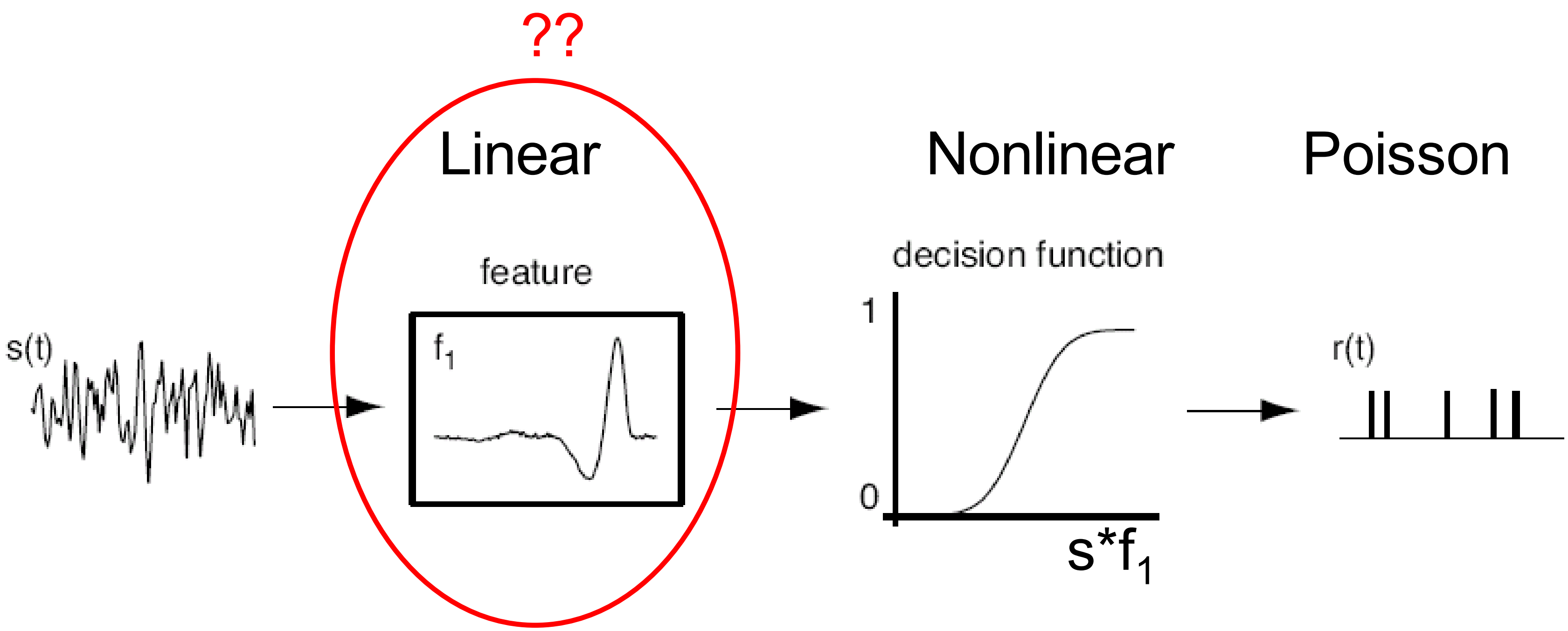
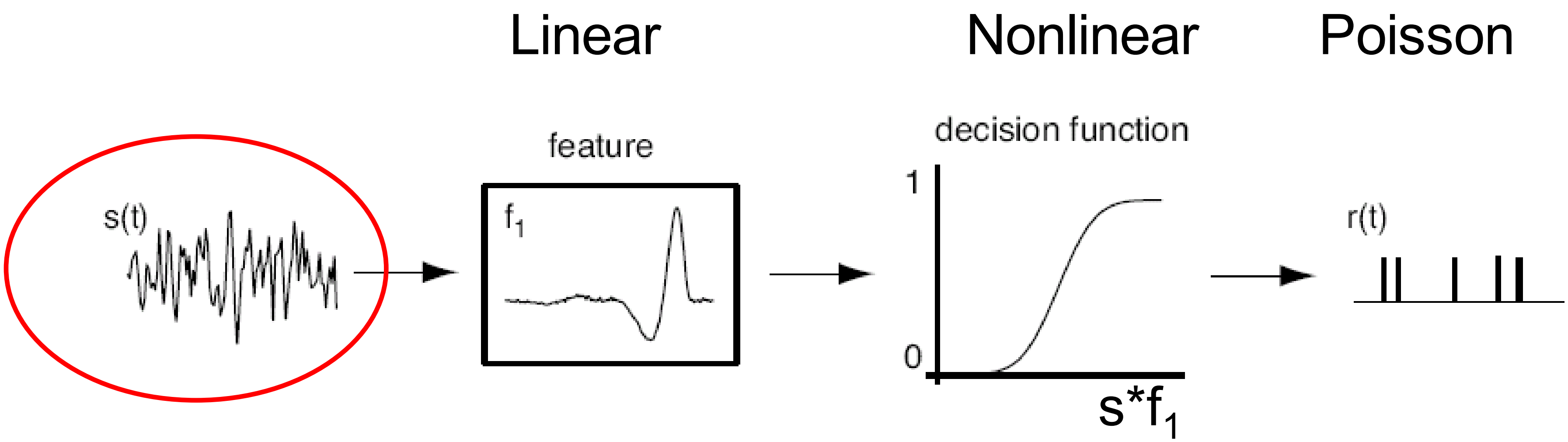



**In an experiment:**

- We know the input stimuli
- And we measure the corresponding spike trains
- We don't know the Linear or Nolinear boxes!
- Here we will show how to find the Linear

# Basic coding model: temporal

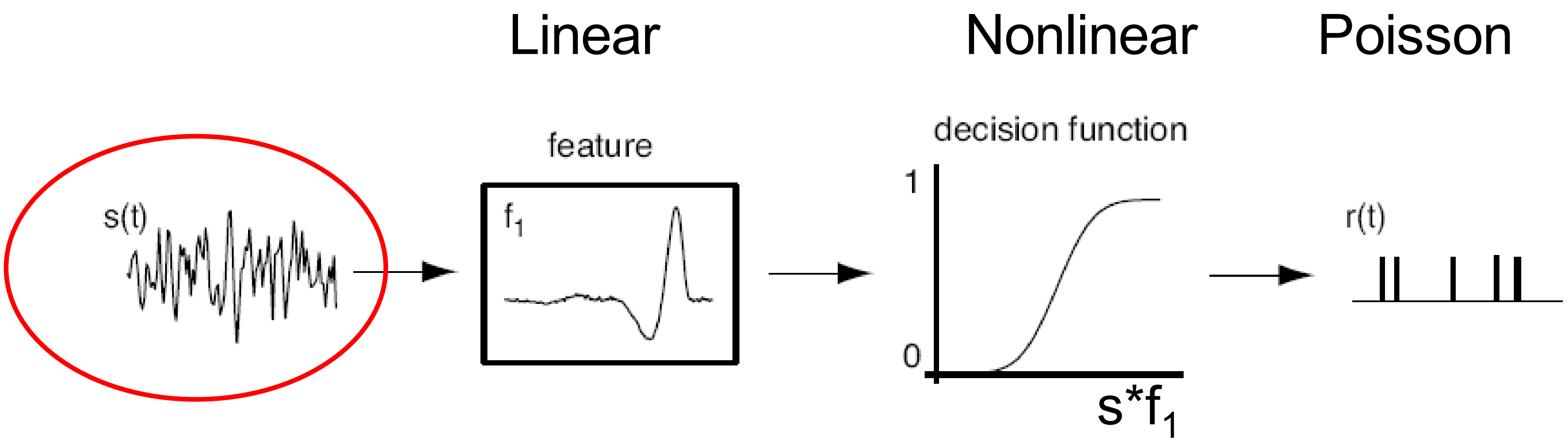



**In an experiment:**

- We know the input stimuli

Or at least we have control over input stimuli.
What should we use???

# Basic coding model: temporal



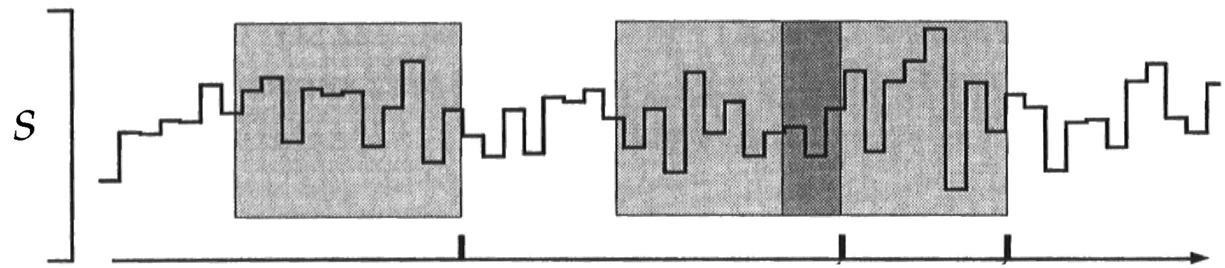

**In an experiment:**

- We know the input stimuli

Or at least we have control over input stimuli
What should we use??? Random stimuli

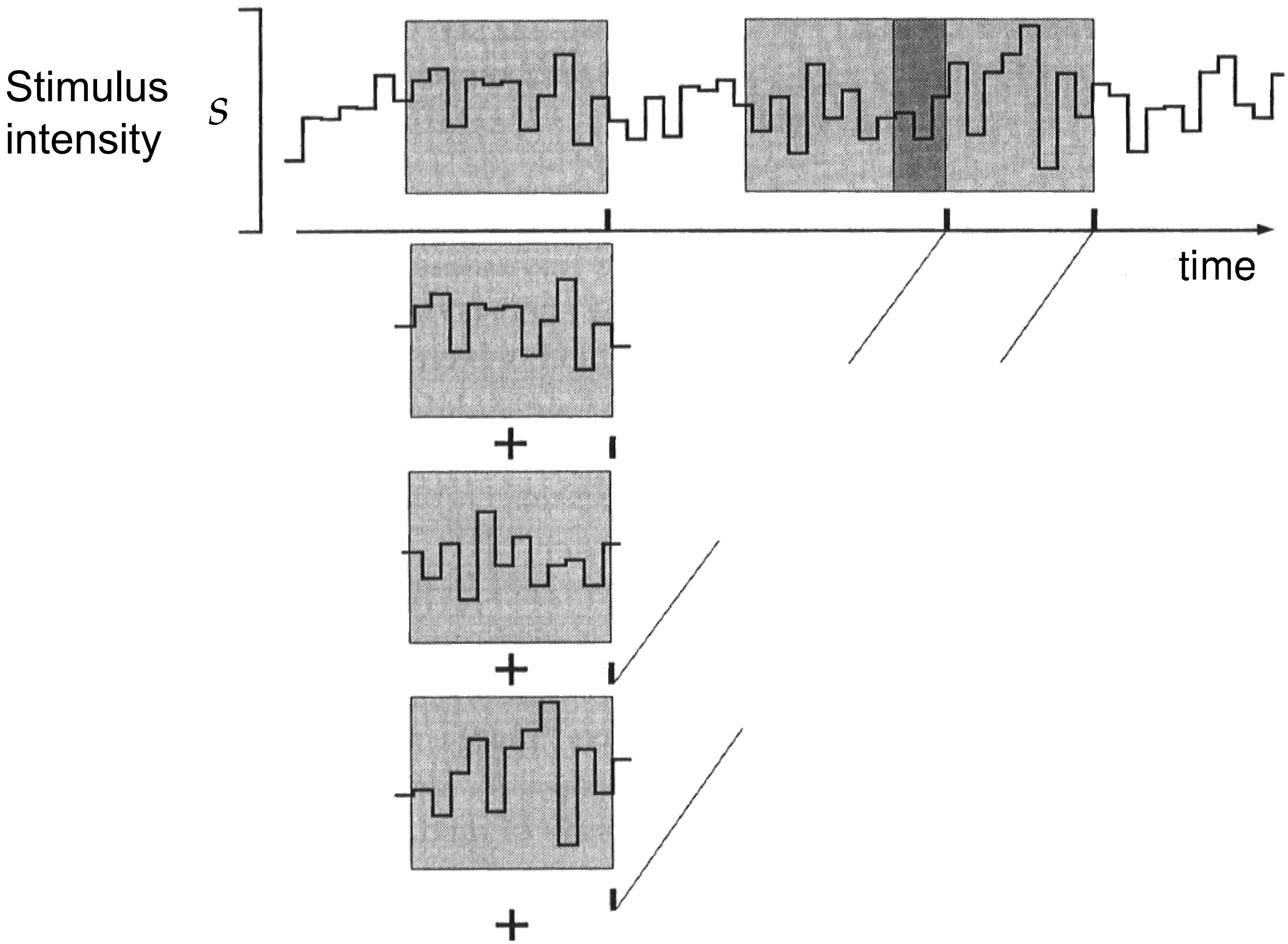
# Spike-triggered Average (STA)

Stimulus intensity




From Dayan and Abbott textbook; 2001

# Spike-triggered Average (STA)

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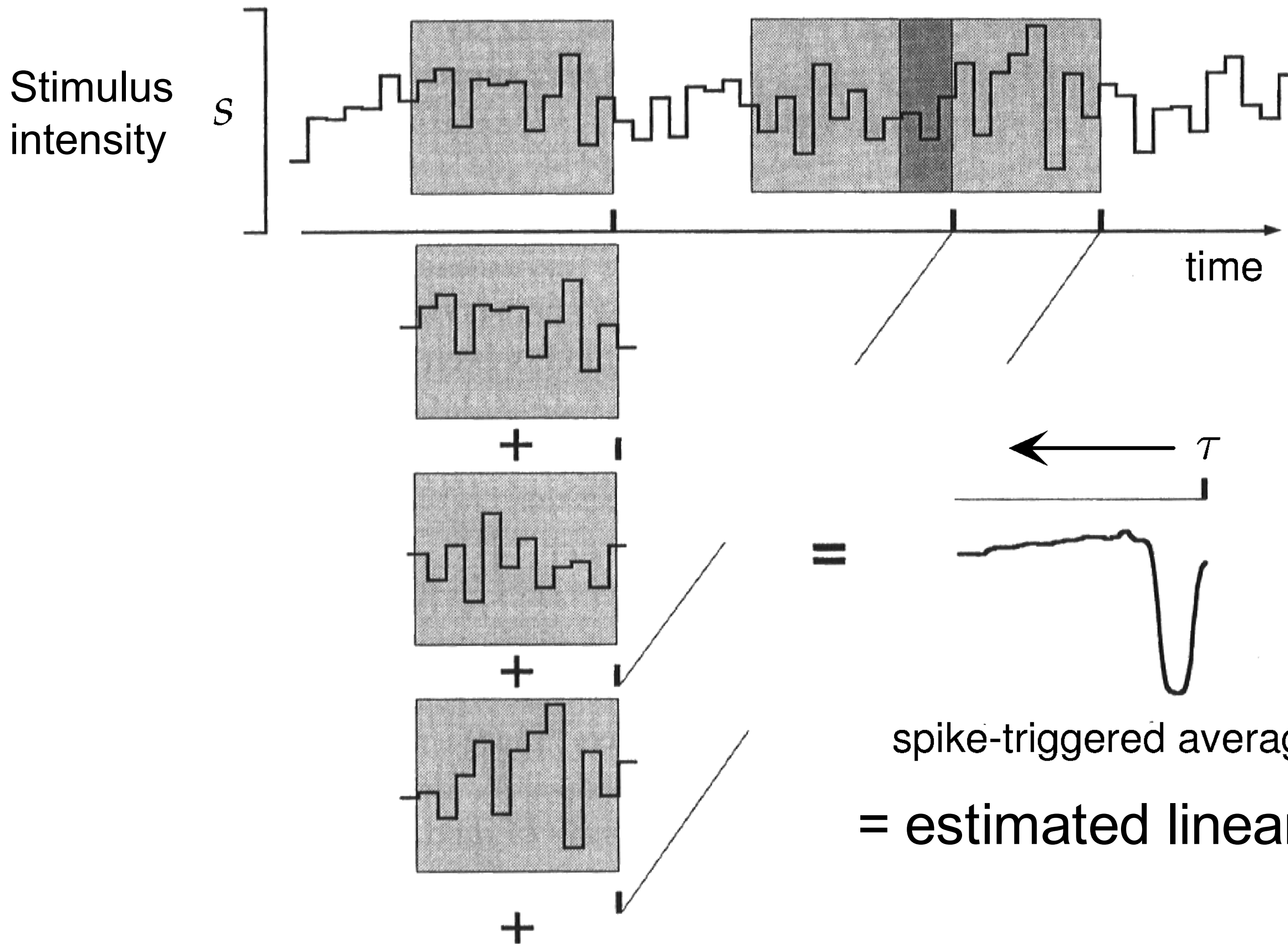
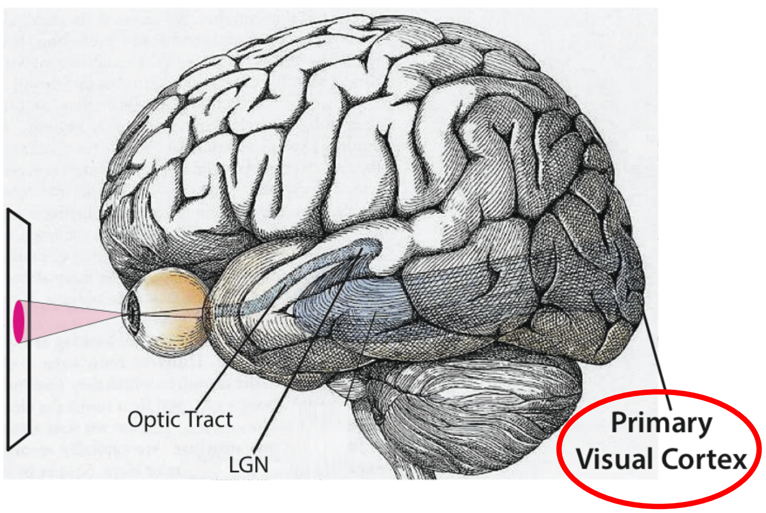
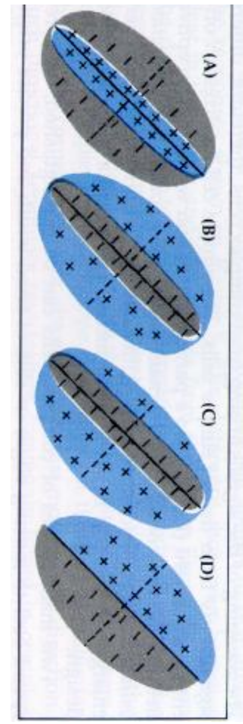



= estimated linear filter

From Dayan and Abbott textbook; 2001

# Primary Visual Cortex Receptive Fields

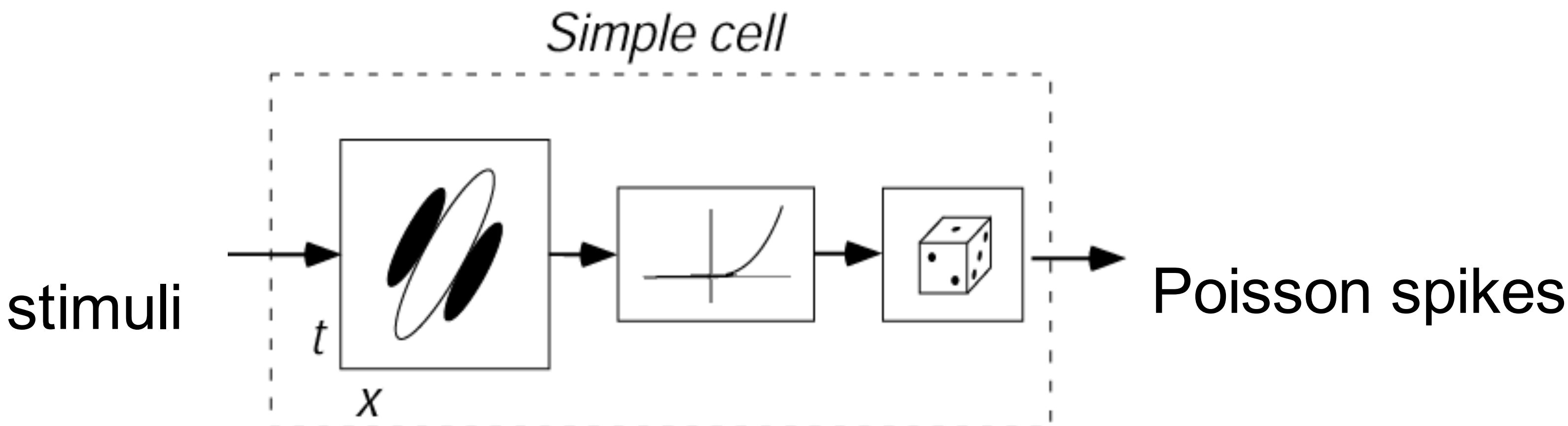



Examples of receptive fields in primary visual cortex (V1)

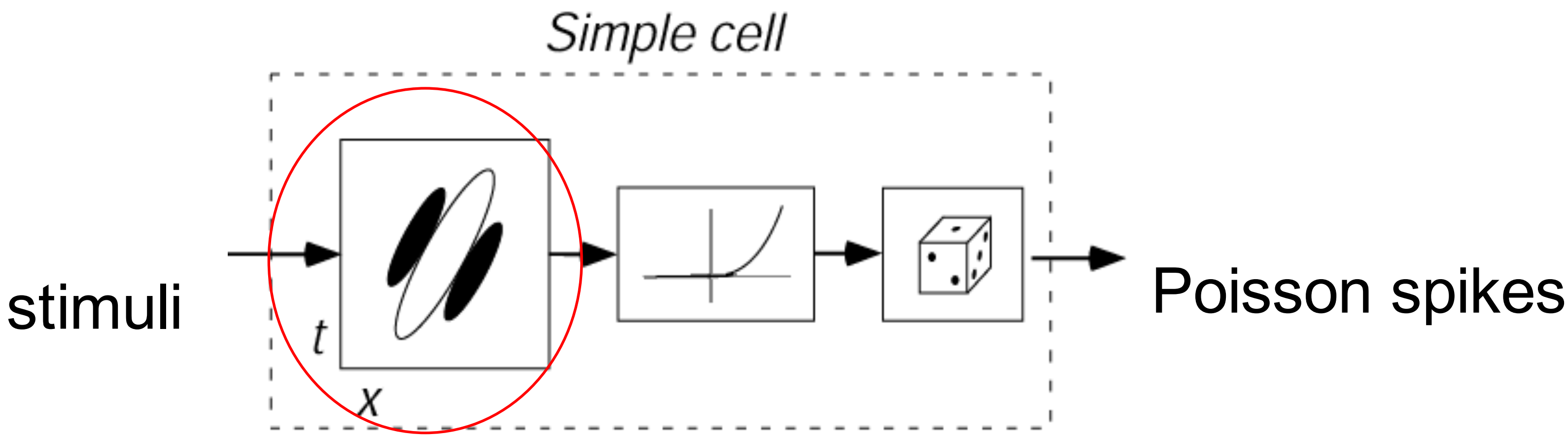
(From Nicholls et al., 1992)

# Spike-triggered average (STA)




Linear, Nonlinear, Poisson encoding model

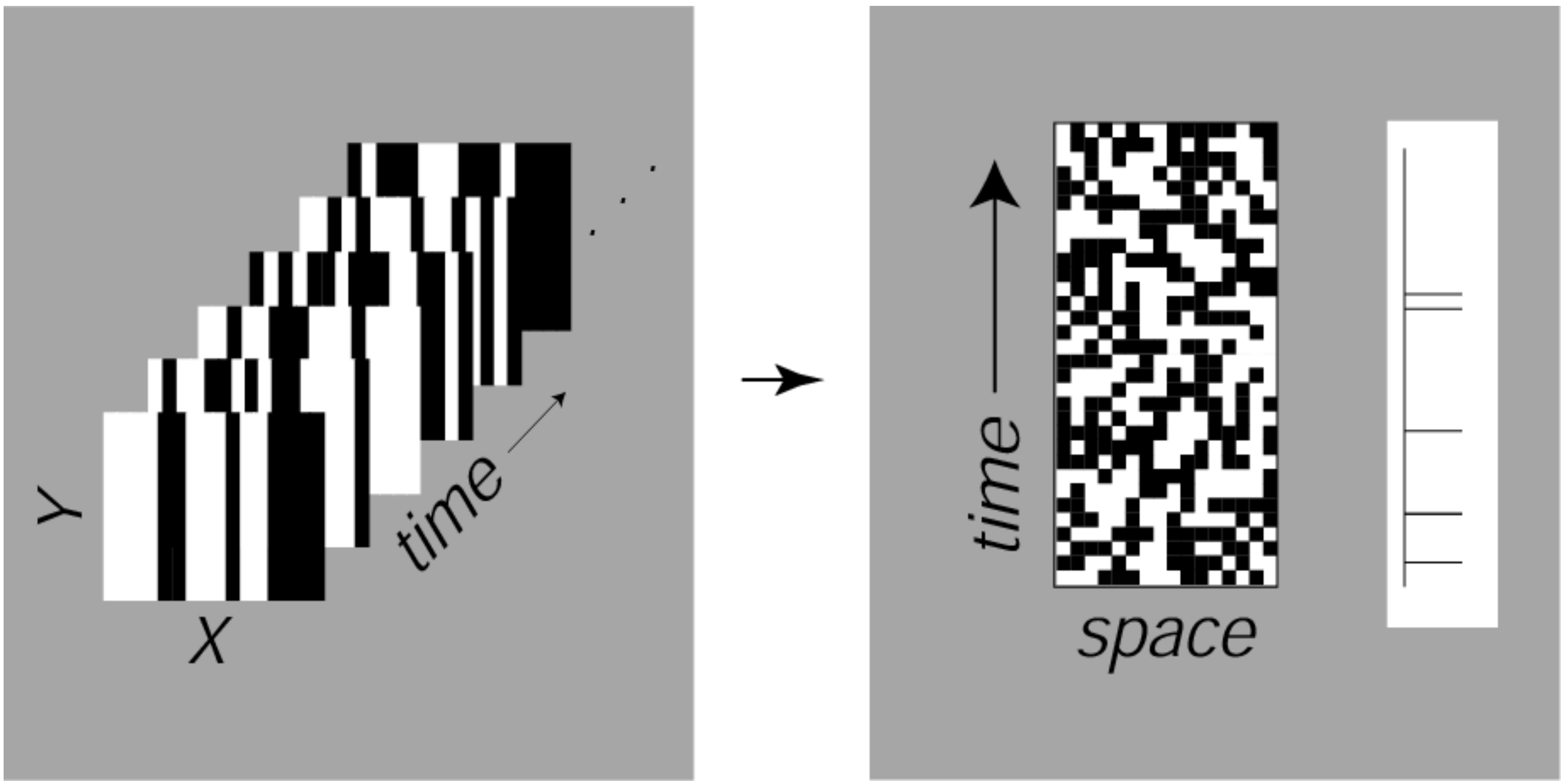
# Spike-triggered average (STA)




Linear, Nonlinear, Poisson (LNP) encoding model

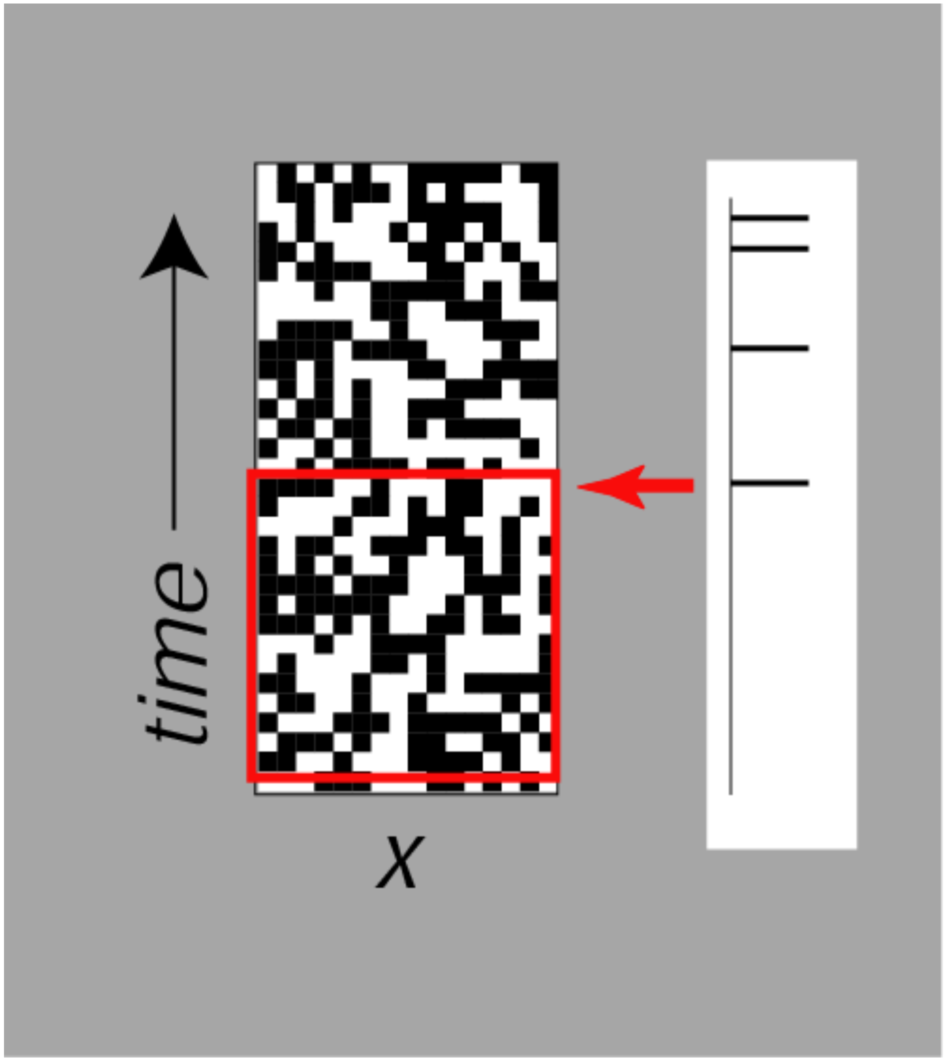
We would like to characterize the linear receptive field or filter (and the nonlinearity; later) for a neuron…

# Spike-triggered Average (STA): example



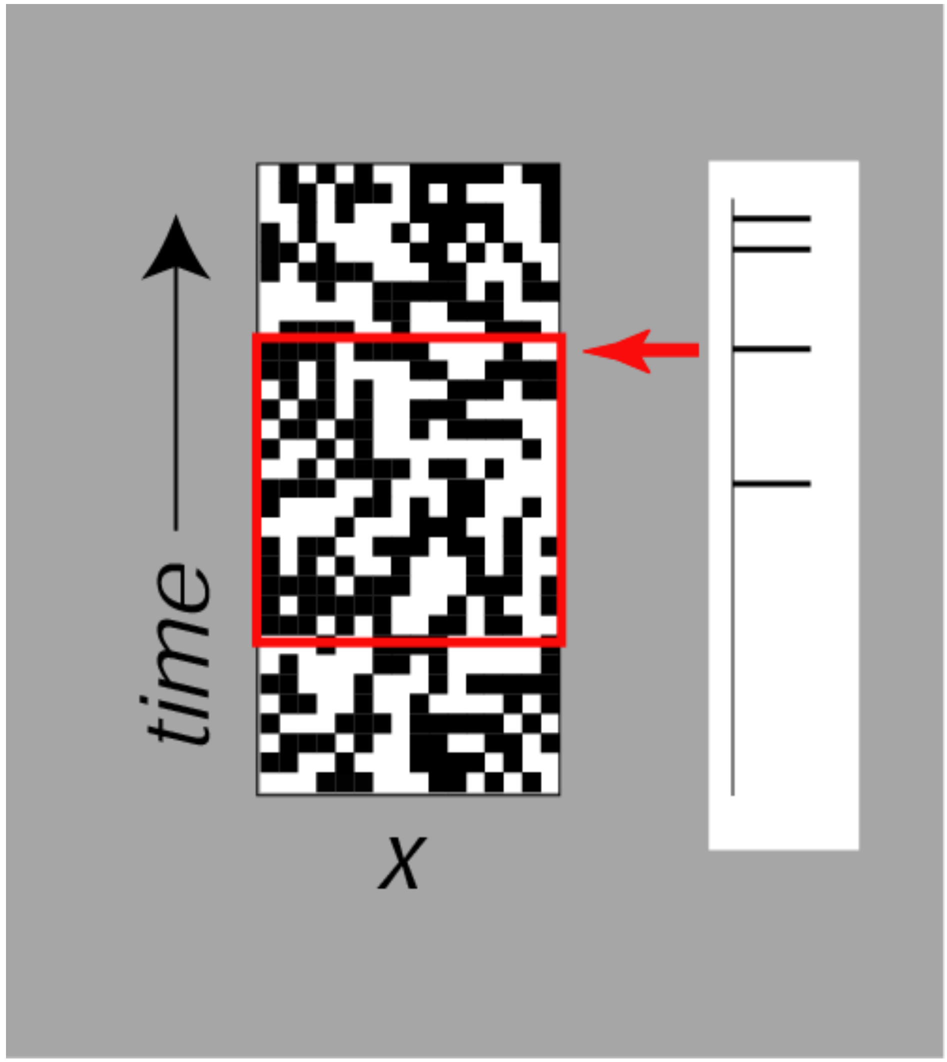

From Nicole Rust

# Spike-triggered Average (STA): example




From Nicole Rust

# Spike-triggered Average (STA): example

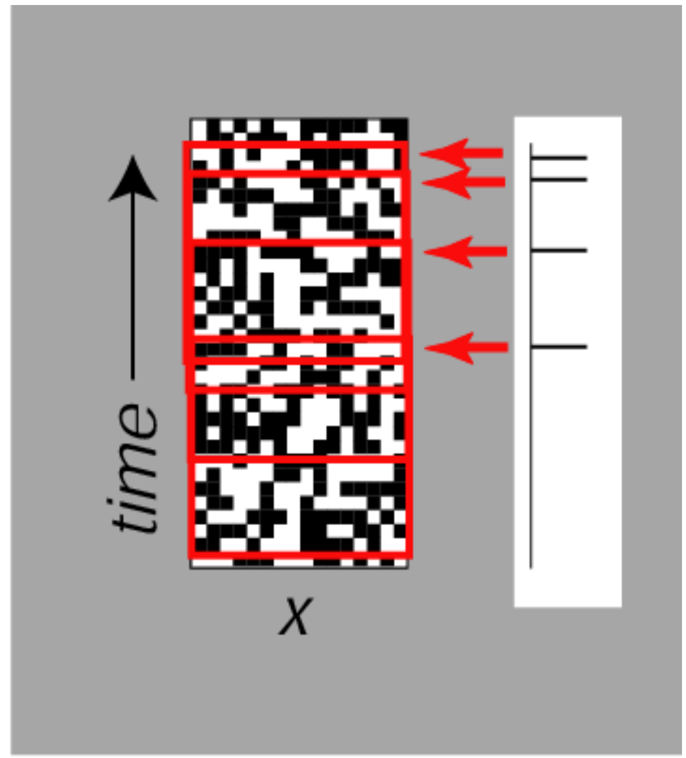



From Nicole Rust

## Spike-triggered Average (STA) : example

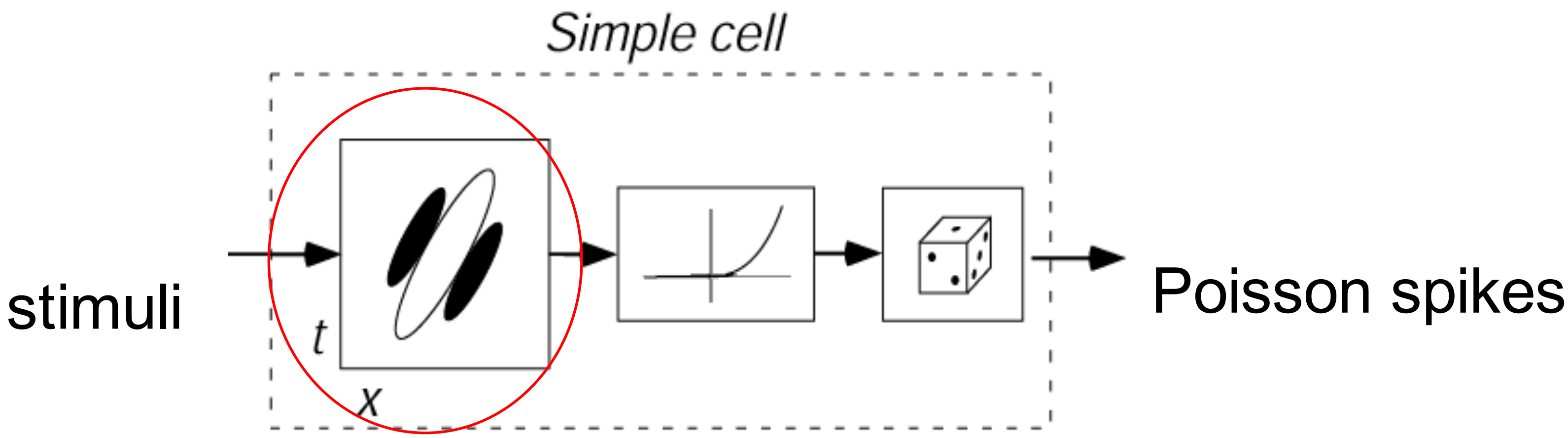
STA

Average of spike-triggered stimuli




From Nicole Rust

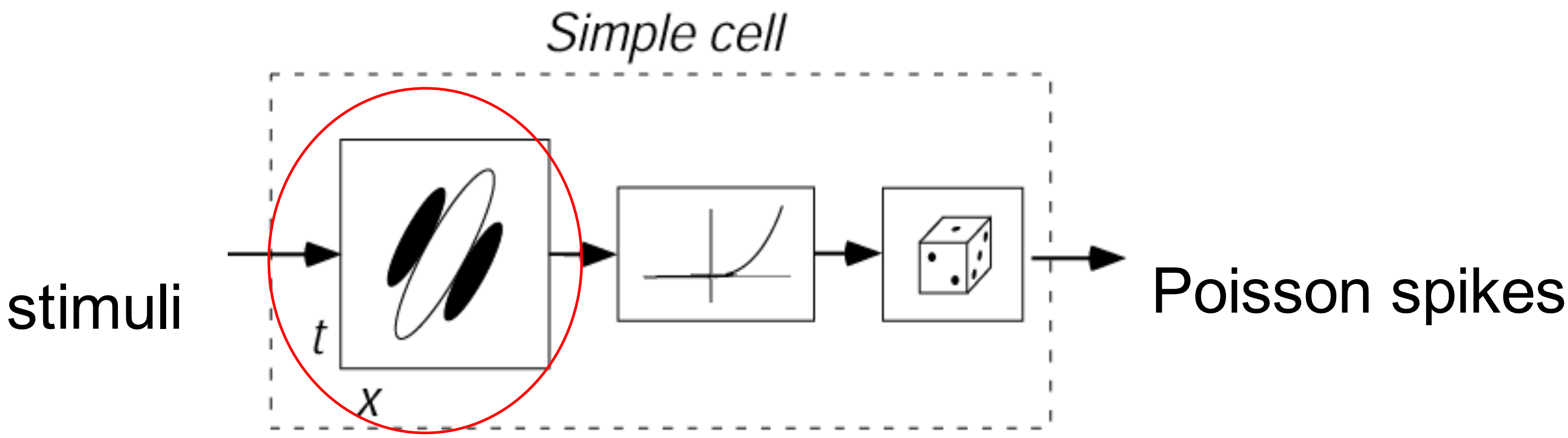
# Spike-triggered average (STA)




Linear, Nonlinear, Poisson (LNP) encoding model

Will estimate of Linear always work??

# Spike-triggered average (STA)




Linear, Nonlinear, Poisson (LNP) encoding model

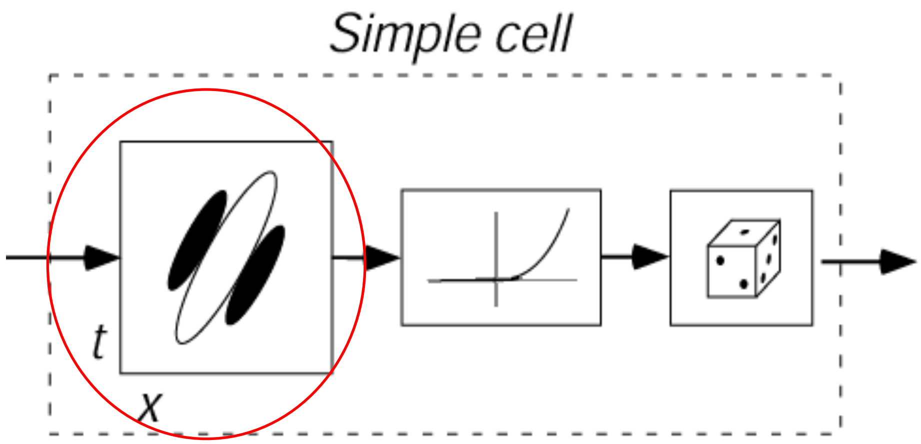
When can this estimation fail?

- Non Poisson spiking
- Input stimuli not spherically symmetric (Chichilnisky)
- Form of nonlinearity

(geometric view and more on later)

# Spike-triggered average (STA)

stimuli




Poisson spikes

Linear, Nonlinear, Poisson (LNP) encoding model

Can we generalize the model?

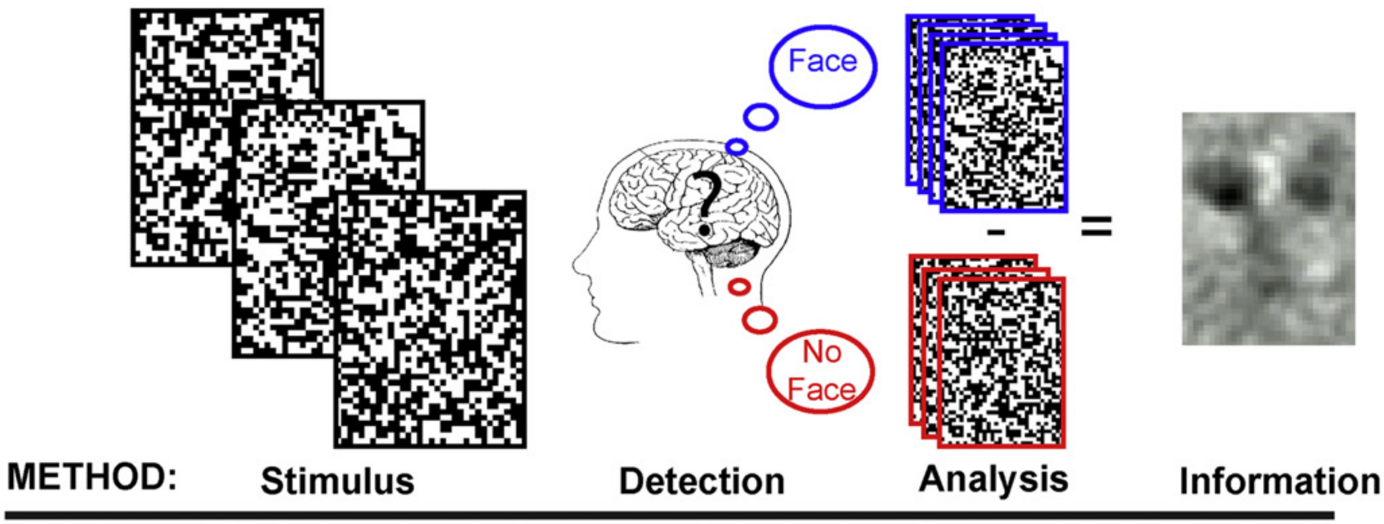
- More filters
- Other metrics of spike versus non spike ensemble beyond the mean

(more on later)

**So far: To Spike or not to Spike!**

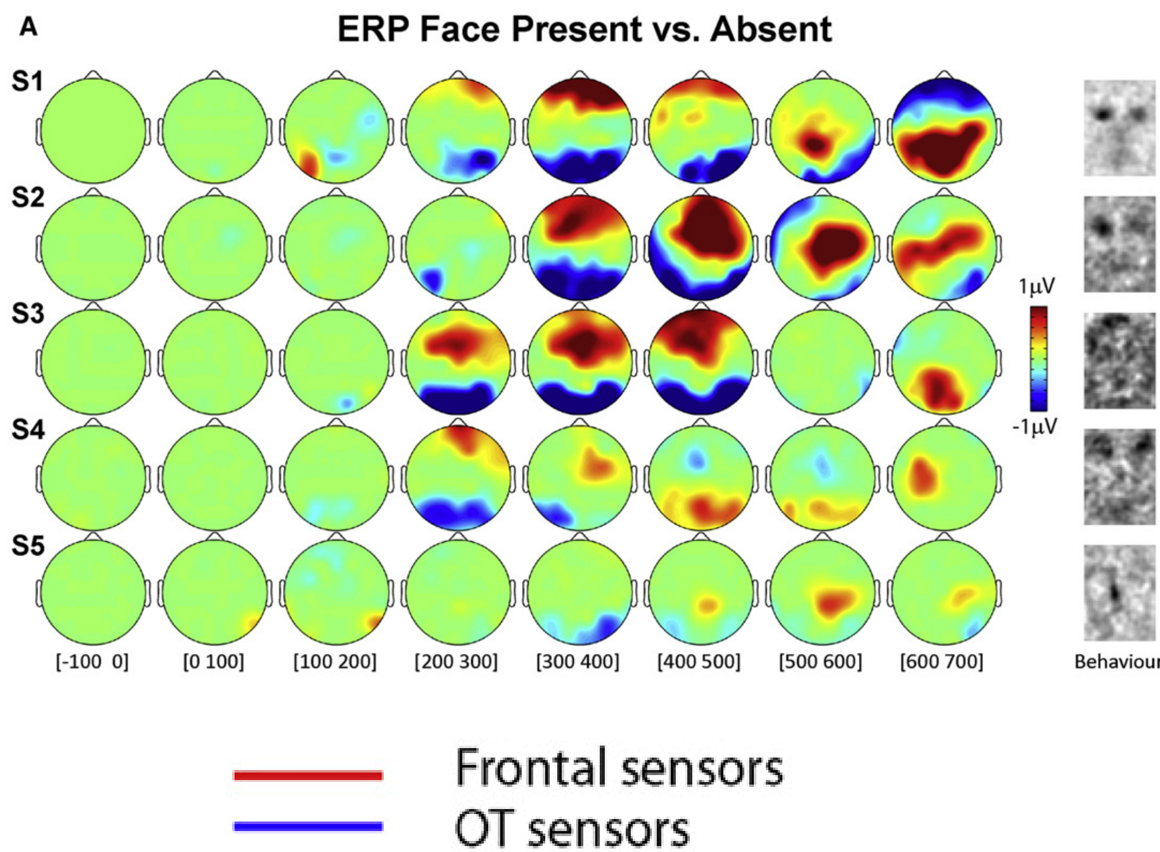
But can we also partition according to other properties of interest and other signal types??

In Psychology: termed
“Classification Images”

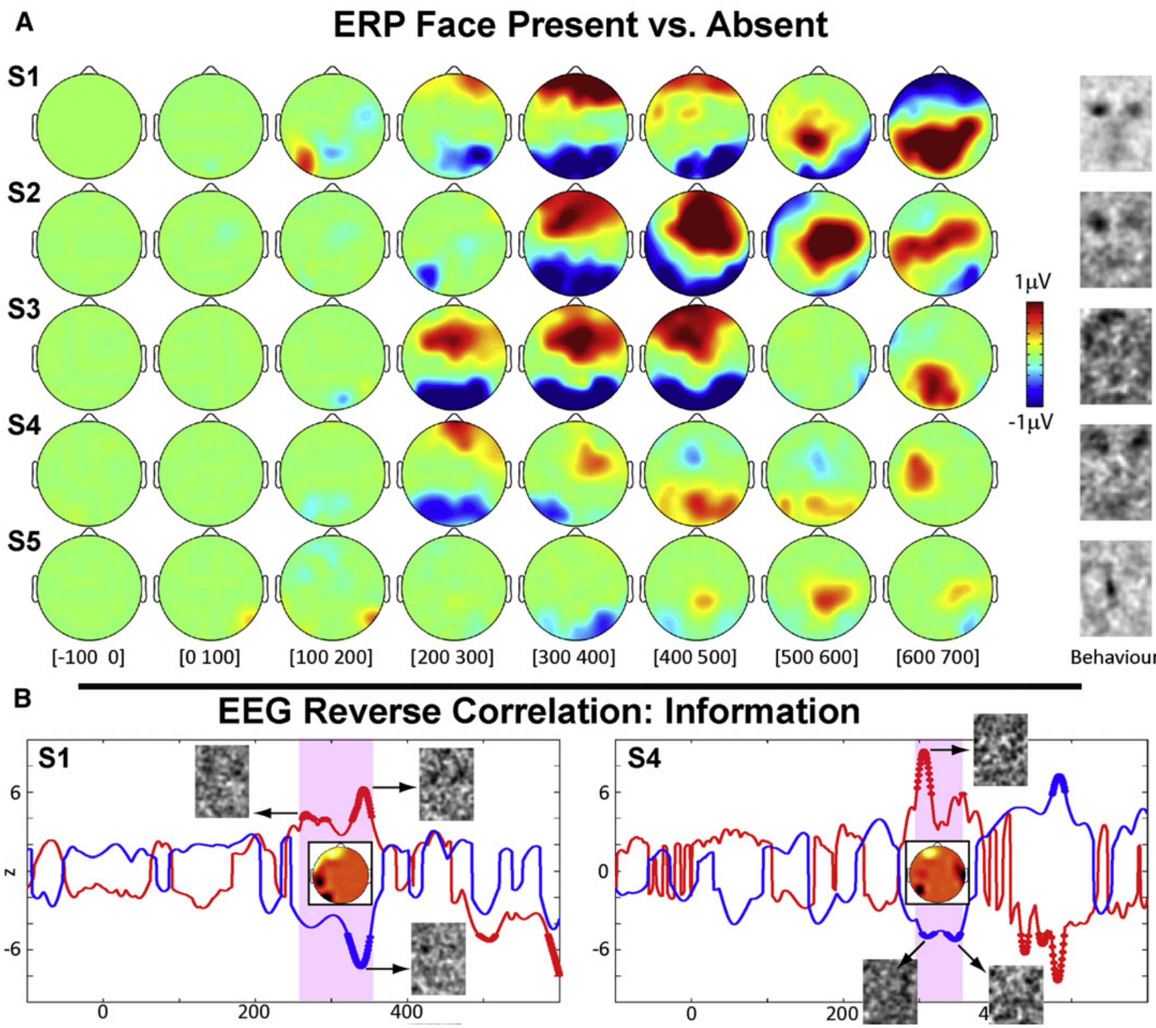



Smith et al. Current Biology 2012:
Subjects told that half the noise stimuli contain faces, although there are no faces…

# In Psychology: termed "Classification Images"

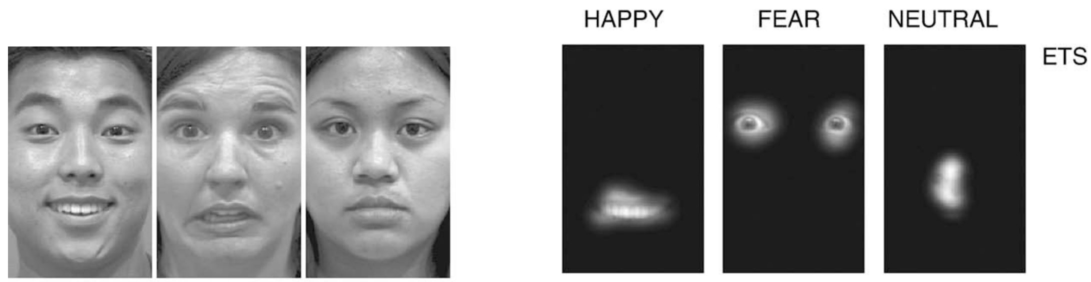


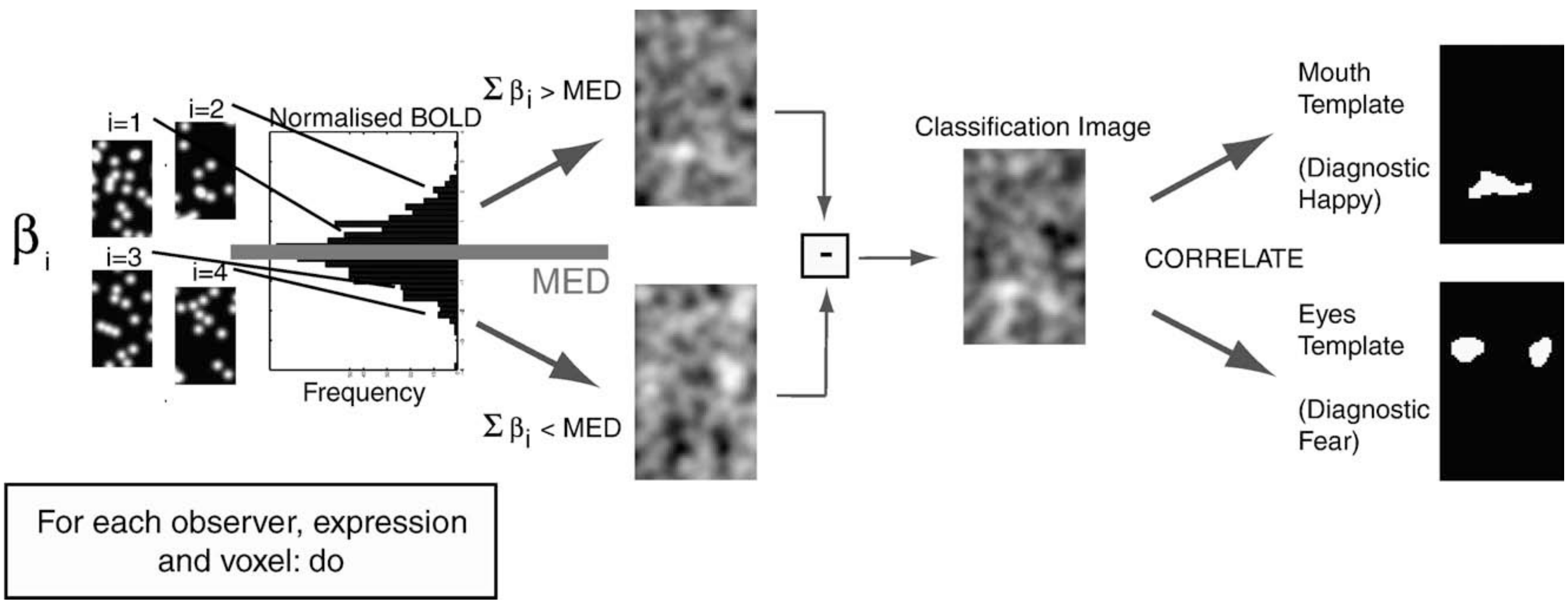
# In Psychology: termed "Classification Images"



# fMRI: Voxel triggered

# fMRI: Voxel triggered




Smith it el. 2008

# fMRI: Voxel triggered

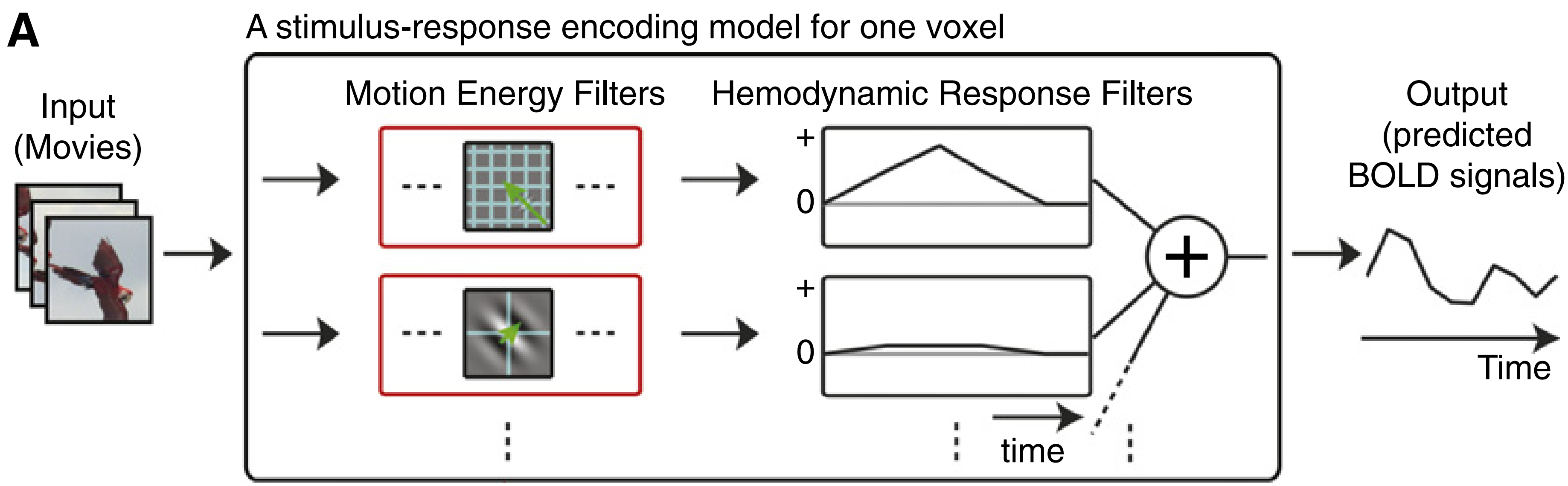



**Figure 1. Schematic Diagram of the Motion-Energy Encoding Model**

(A) Stimuli pass first through a fixed set of nonlinear spatiotemporal motion-energy filters (shown in detail in B) and then through a set of hemodynamic response filters fit separately to each voxel. The summed output of the filter bank provides a prediction of BOLD signals.

Nishimito, et al., Gallant 2011: Current Biology

## Summary

- Simple encoding model: Linear, Nonlinear, Poisson
- It’s a descriptive model of a neuron
- We’ve looked at estimating the Linear with Spike Triggered Average (later: limitations)
- Approach useful beyond single neurons to other types of data (EEG, fMRI)
- Next: population codes
  Later: more sophisticated encoding models