The Neural Code

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

Population of neurons and spikes
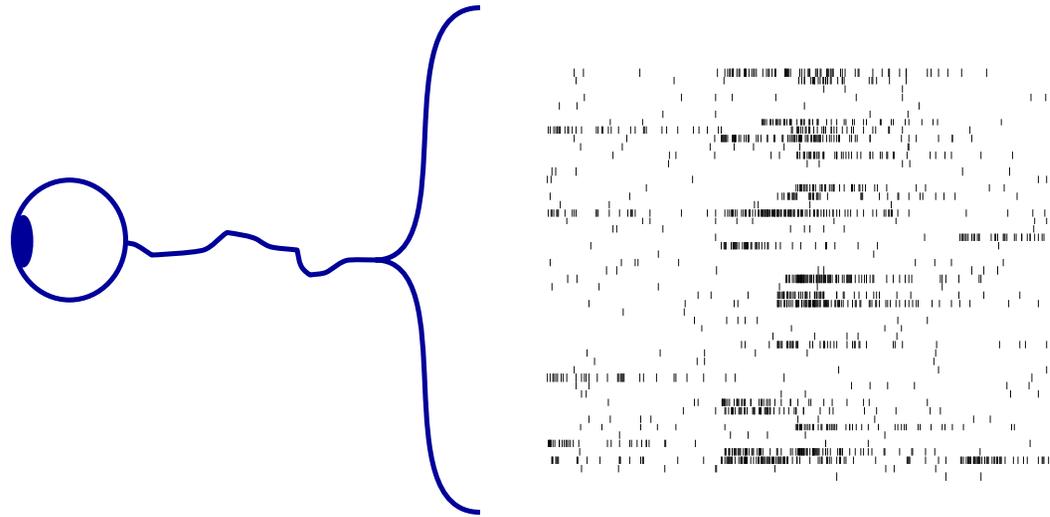
Adapted from Gatsby Computational Neuroscience course

What your brain "sees"
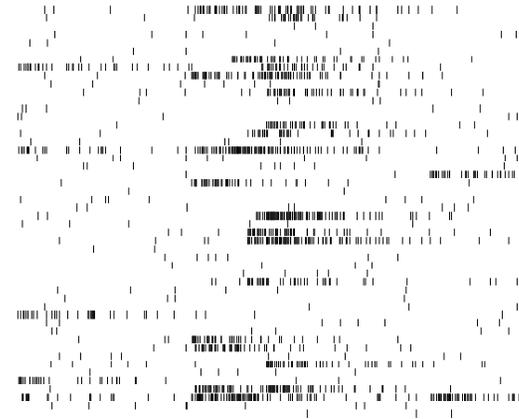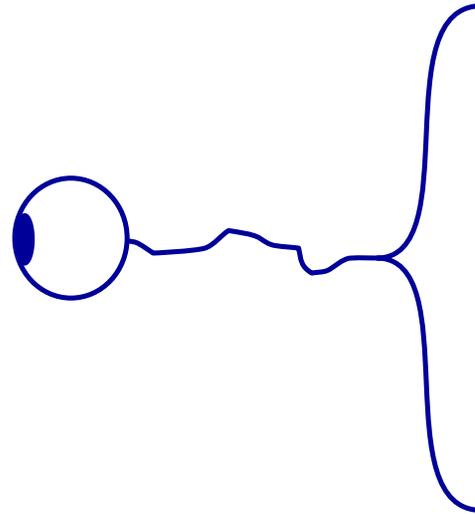
You infer…
Palm trees
UM Campus
Warm weather

Adapted from Gatsby Computational Neuroscience course

Single neuron and spikes

Response
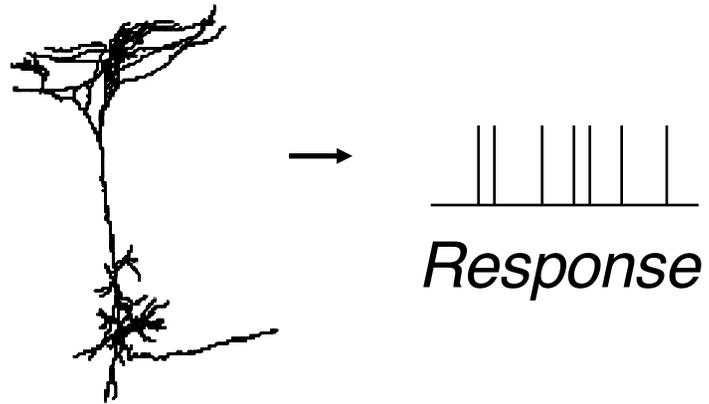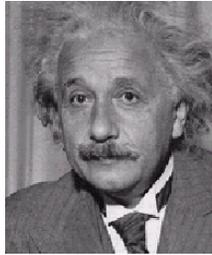
Stimulus → → Response
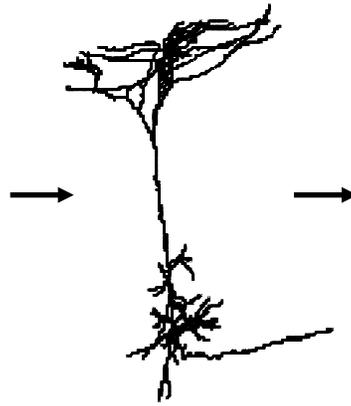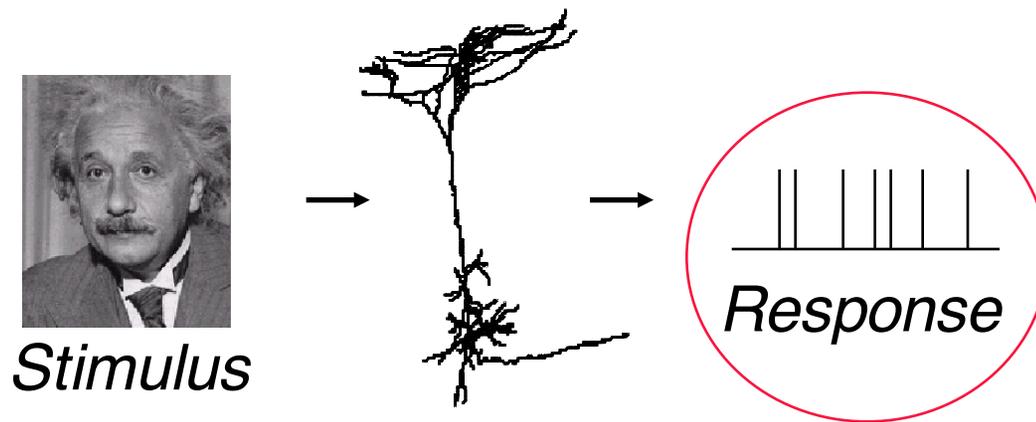
Stimulus

Response

Encoding: Probability(Response | Stimulus)

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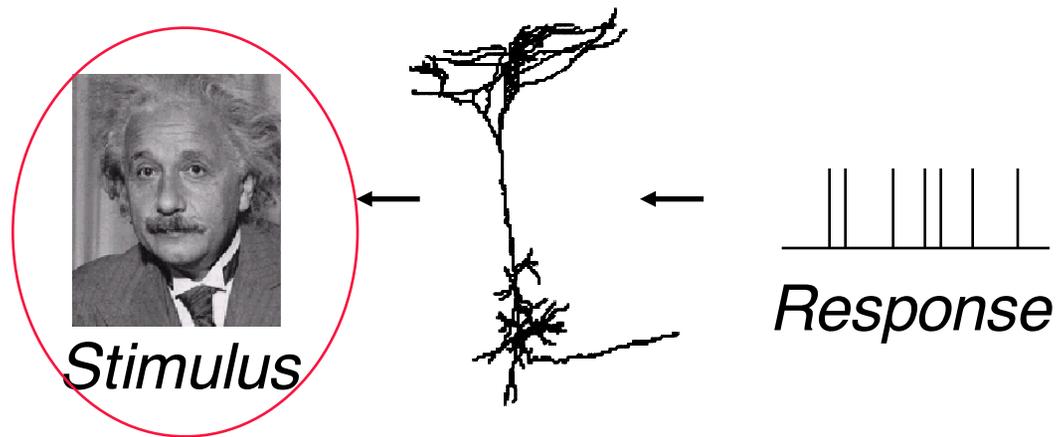
Stimulus

Response

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

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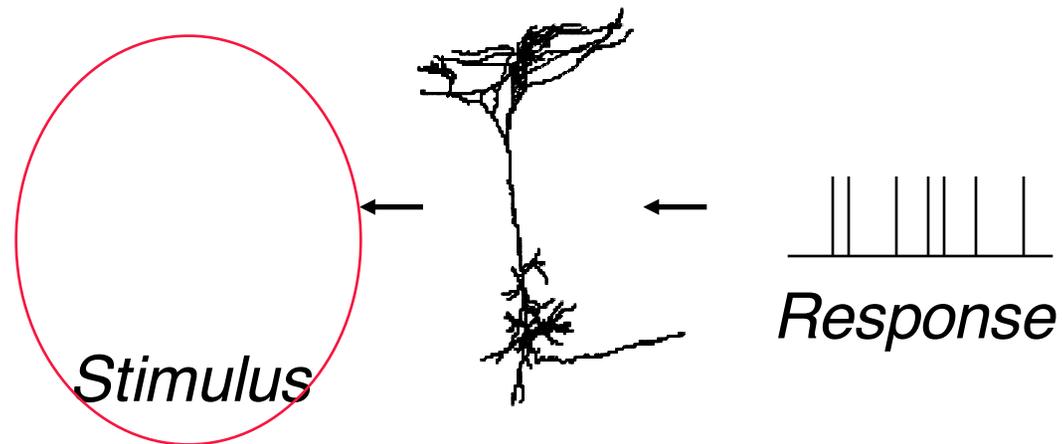
Stimulus   ←   *Response*

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
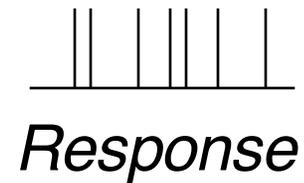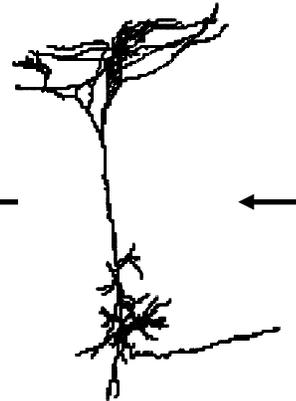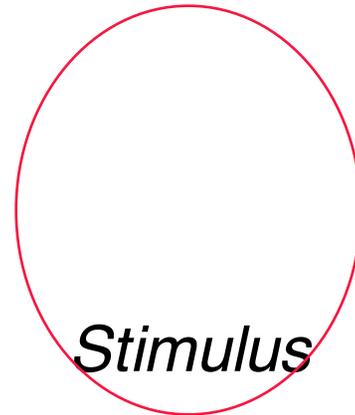
Stimulus

Response

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

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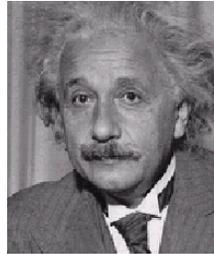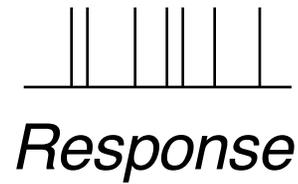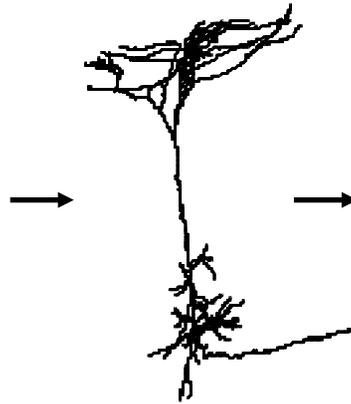
Stimulus

Response

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

Problems in deciphering the neural code?
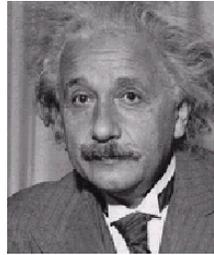
Stimulus
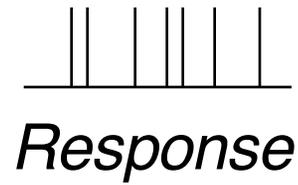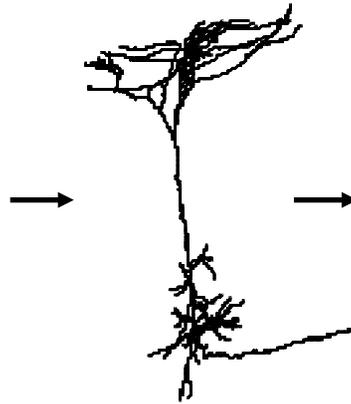
Response

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.

Rate codes

The only important characteristic of a response (spike train) is the number of spikes evoked/the response rate.
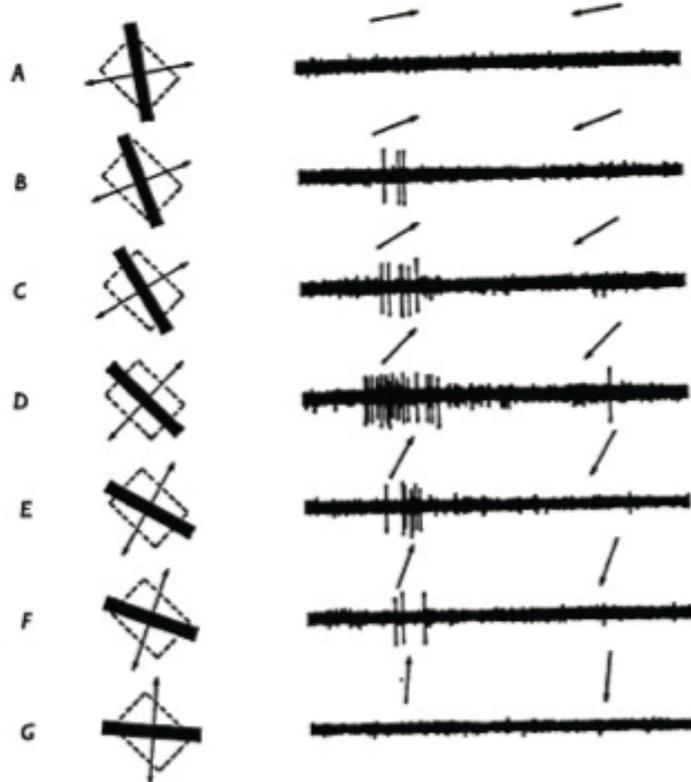
Example 1:   Orientation tuning in primary visual cortex

Rate codes

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

Example 1:   Orientation tuning in primary visual cortex

Wissig and Kohn 2012

Rate codes: example 2

A

90°

0°

B

f (Hz)

s (movement direction in degrees)
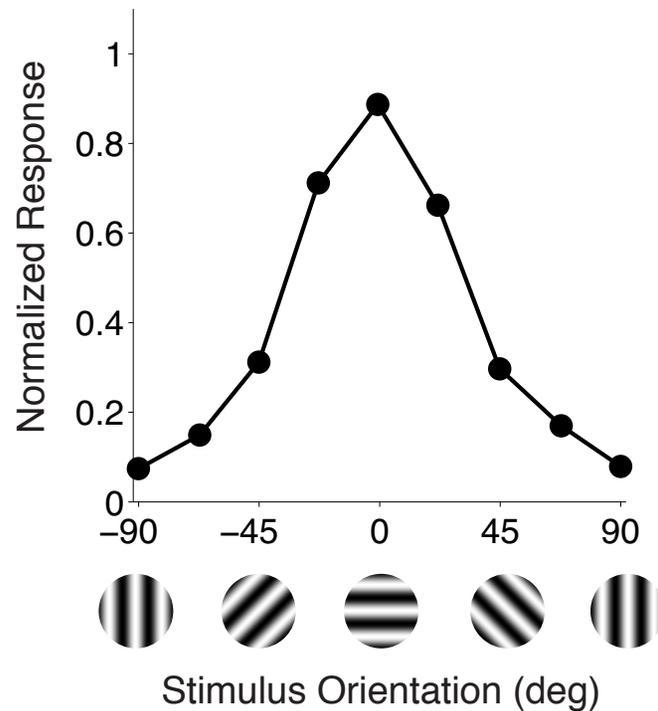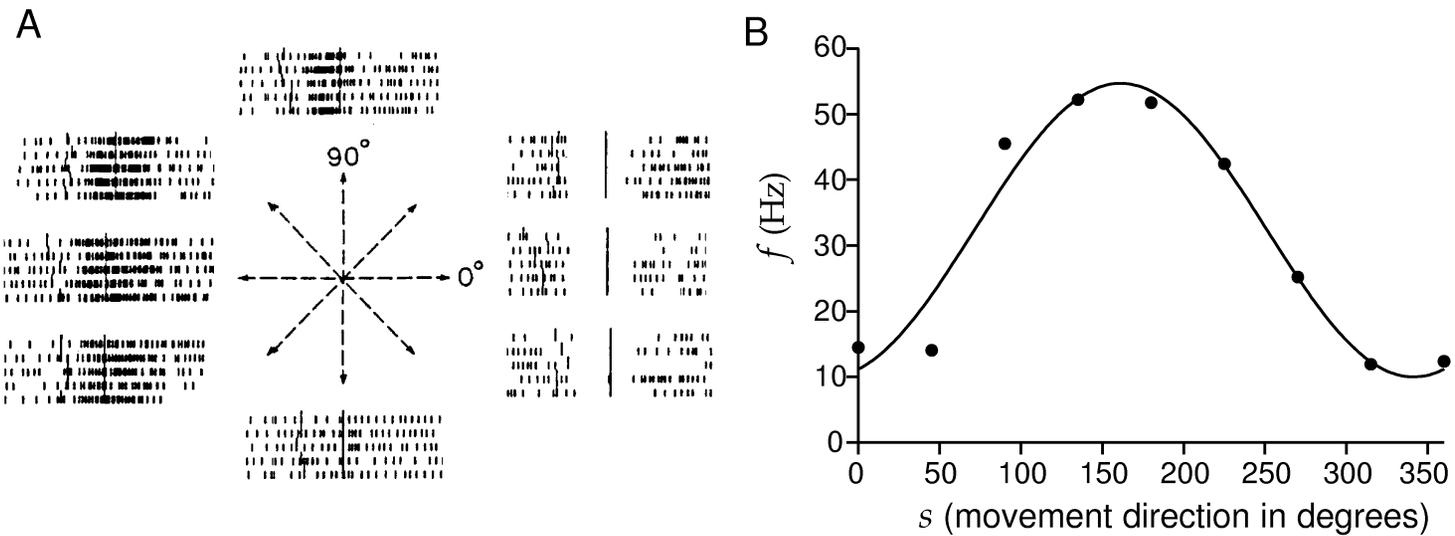
• Dayan and Abbott textbook; adapted from Georgopoulos et al. 1982

Rate codes: example 3
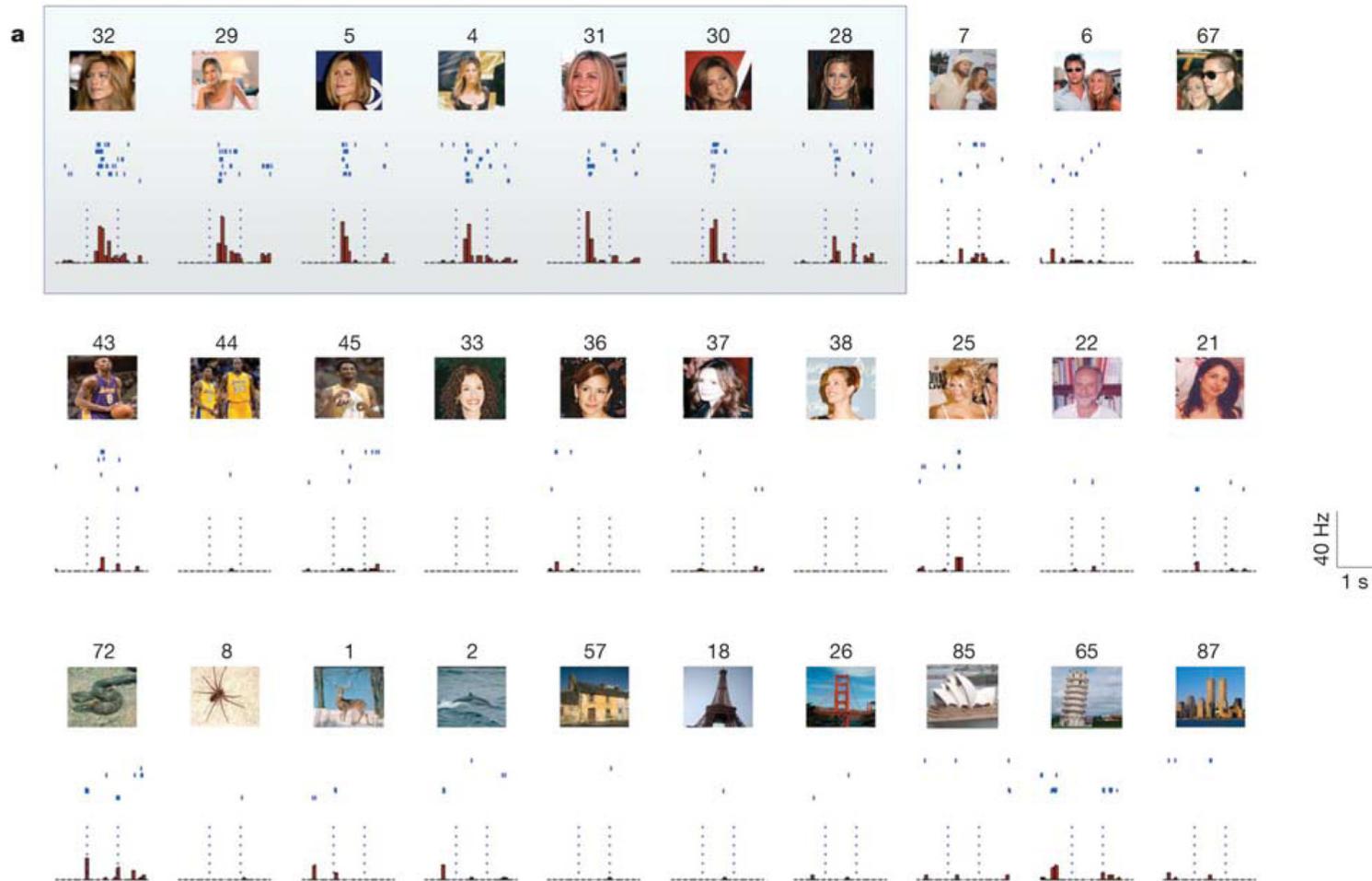
• Quiroga et al. 2005 (Nature)

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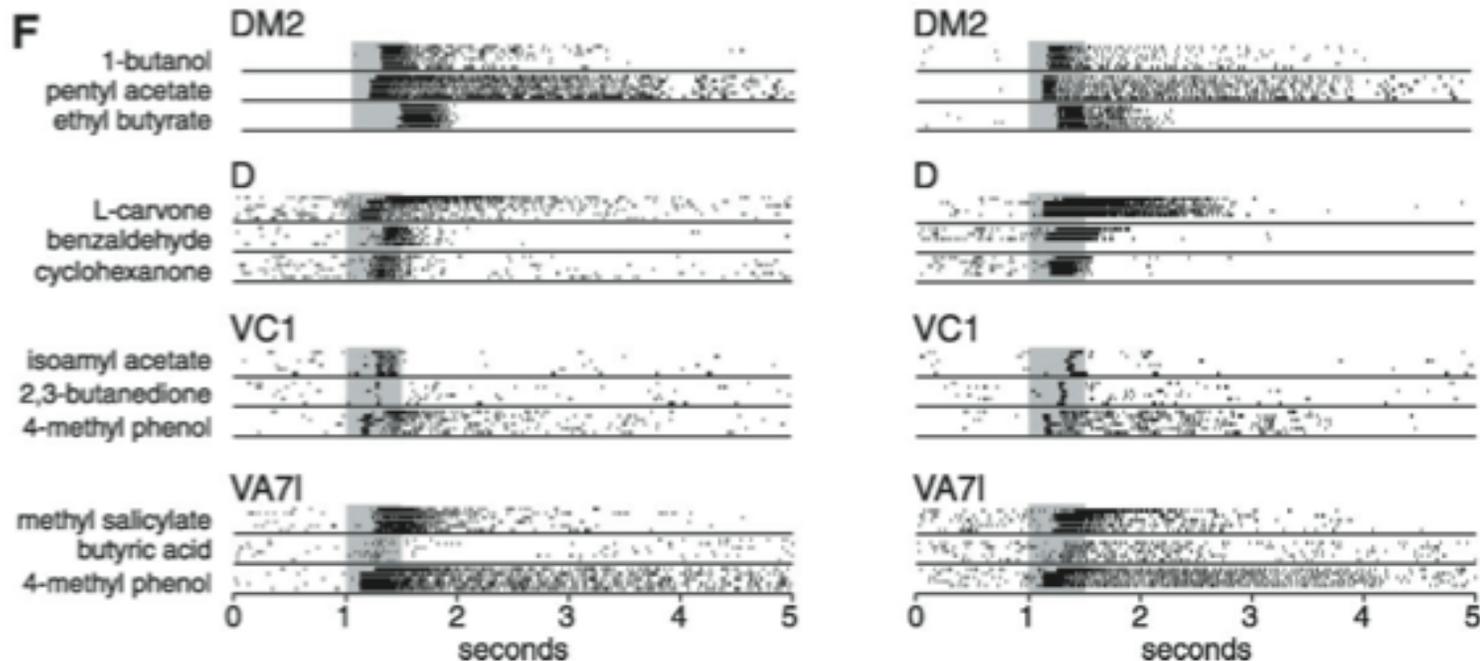
Neurons in the fly within a glomerulus: "Responses across flies were similar not just in intensity but also in temporal pattern, implying that odors elicit stereotyped dynamics in the antennal lobe network"; Wilson et al. 2004

• Stimuli that change quickly typically generate rapidly changing firing rates regardless of coding strategy
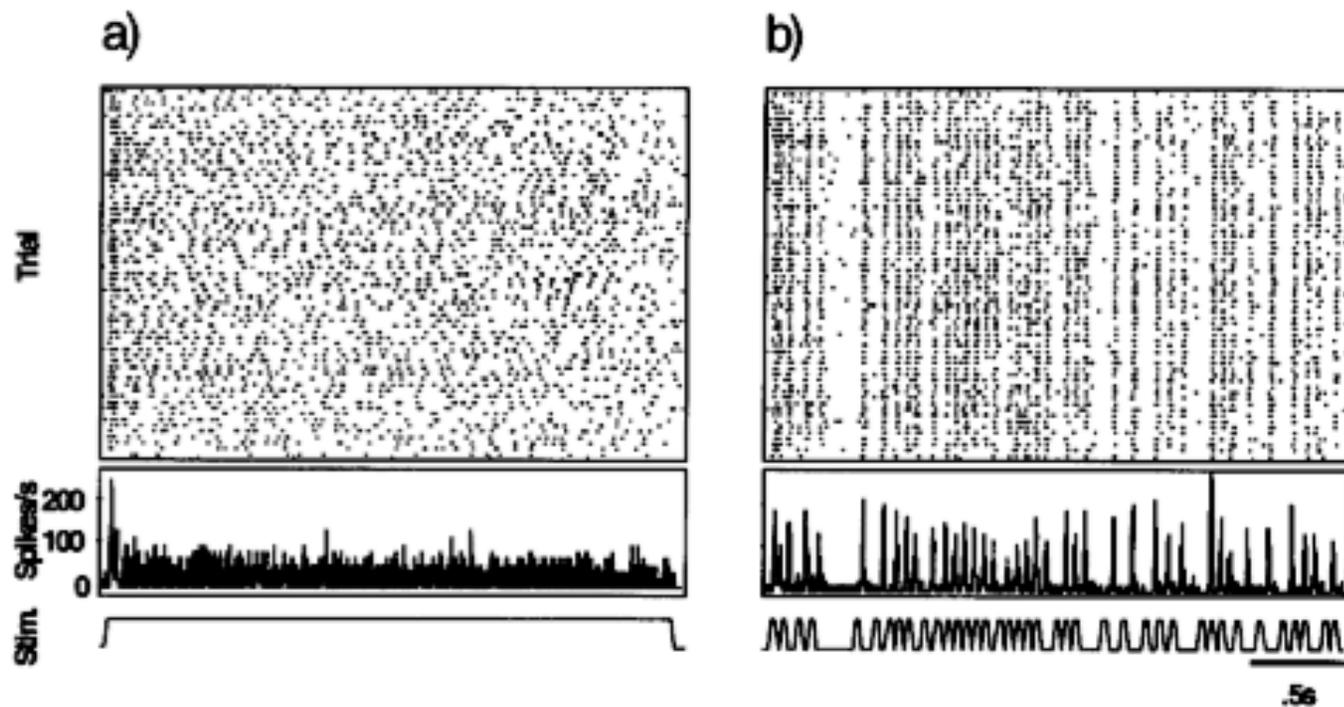
MT neurons, deCharms and Zador (after Buracas et al., 1998)

Importance of timing

Zebra finch song learning
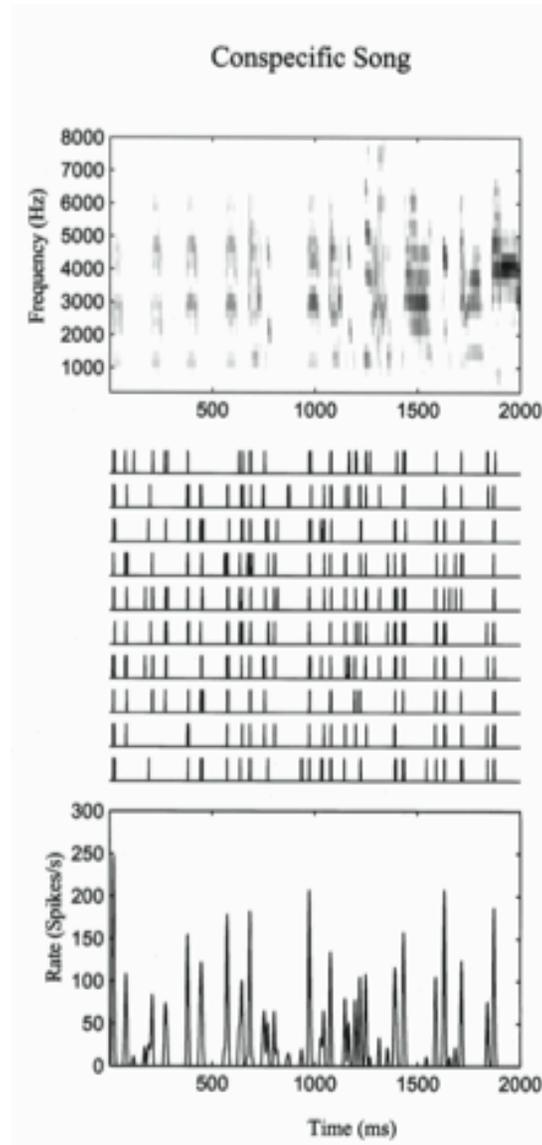
Conspecific Song

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"
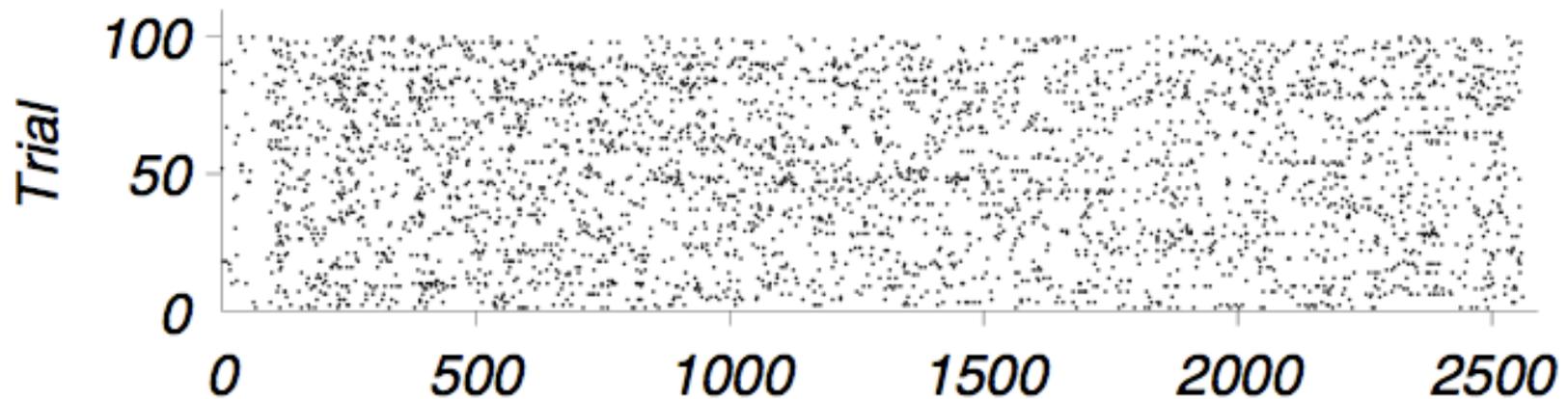
Same stimulus presented many times…

Problems for both rate and temporal codes
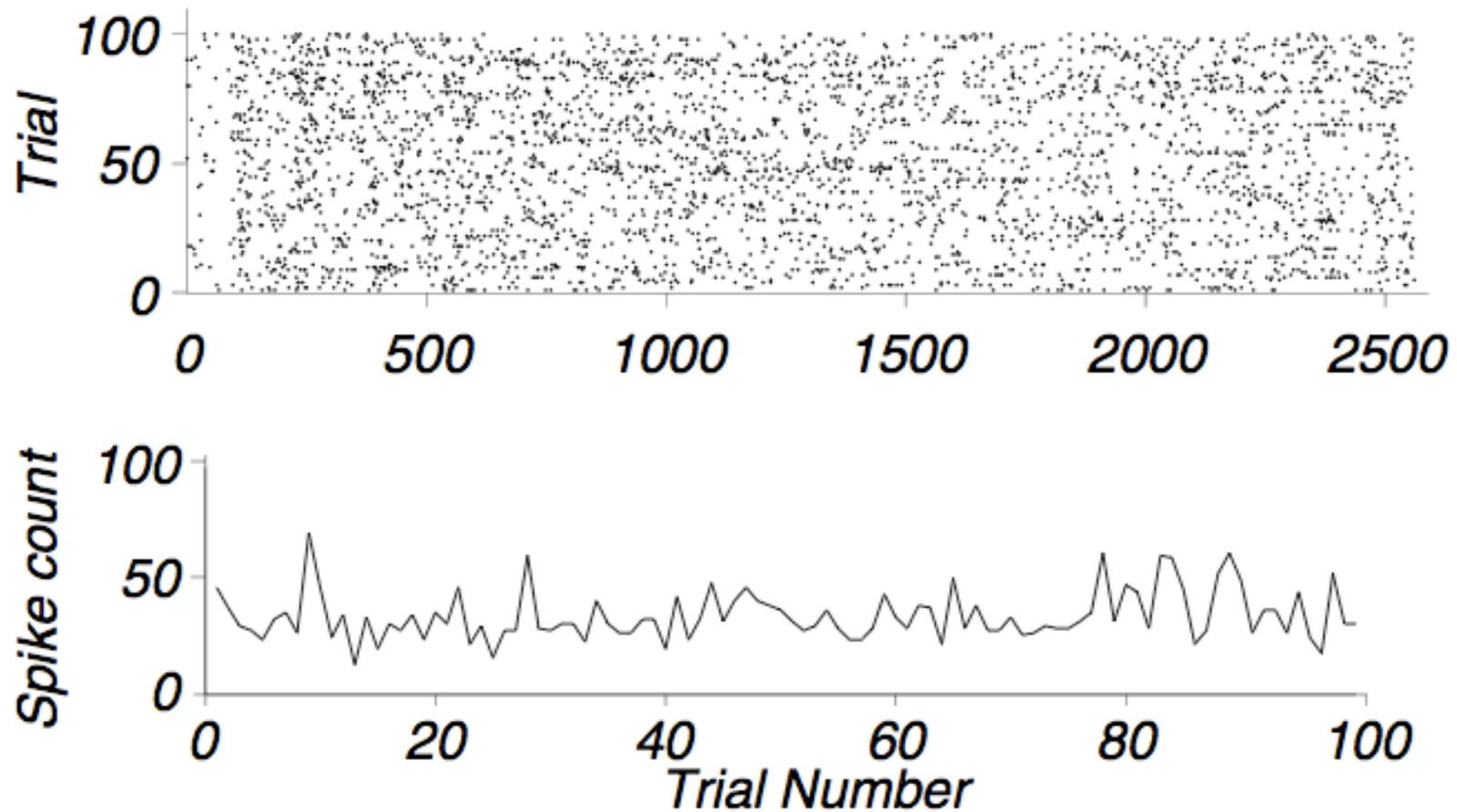
Neuronal responses are "noisy"

Noise in temporal codes
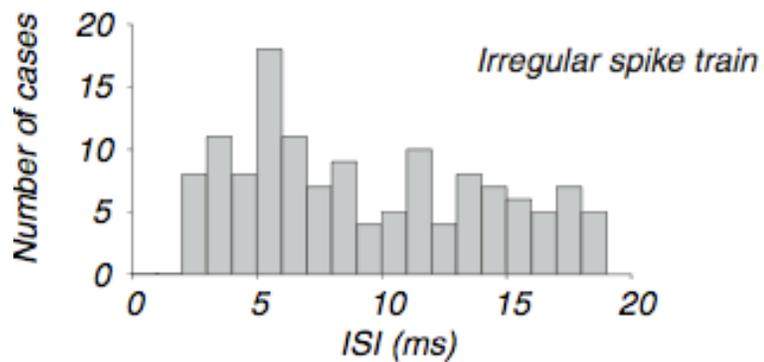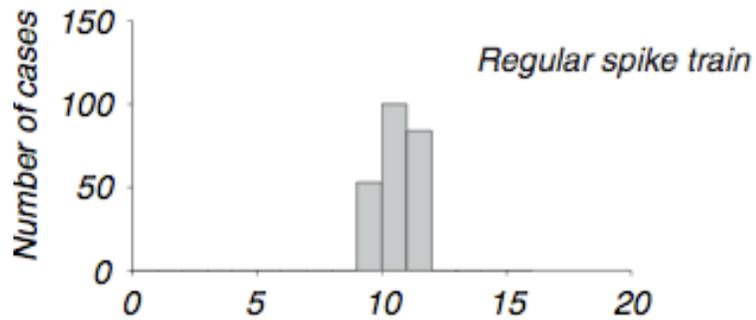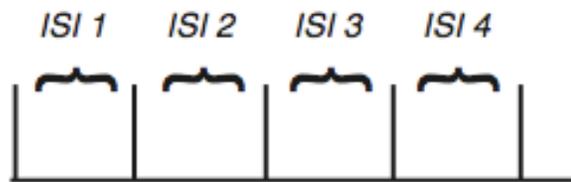
Difficult to measure:

Measure of spike train regularity

ISI 1   ISI 2   ISI 3   ISI 4

Regular spike train

Irregular spike train

ISI (ms)

Noise in temporal codes

Difficult to measure:

Measure of spike train regularity

ISI 1   ISI 2   ISI 3   ISI 4
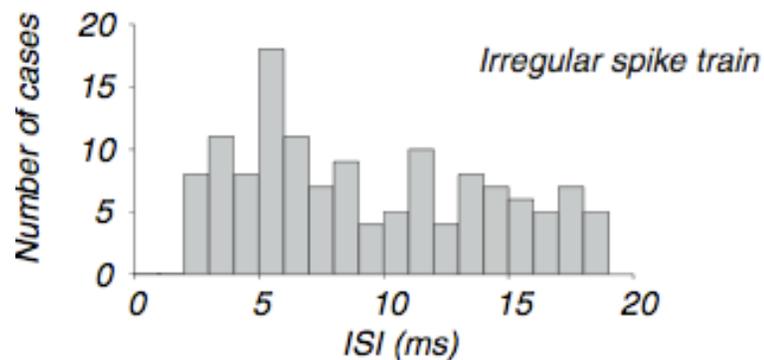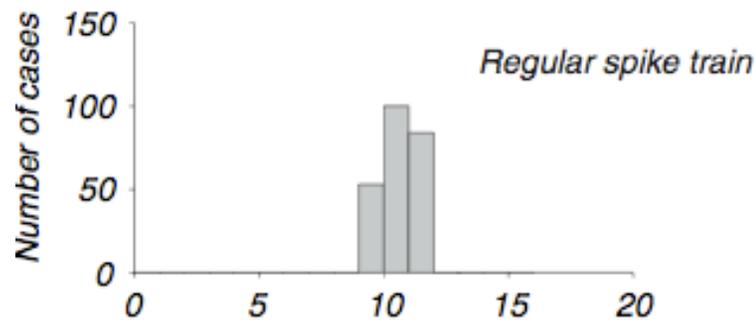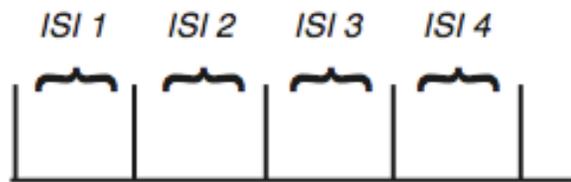
Measure of pattern repeatability: Cost-based metric for transforming one spike train to another
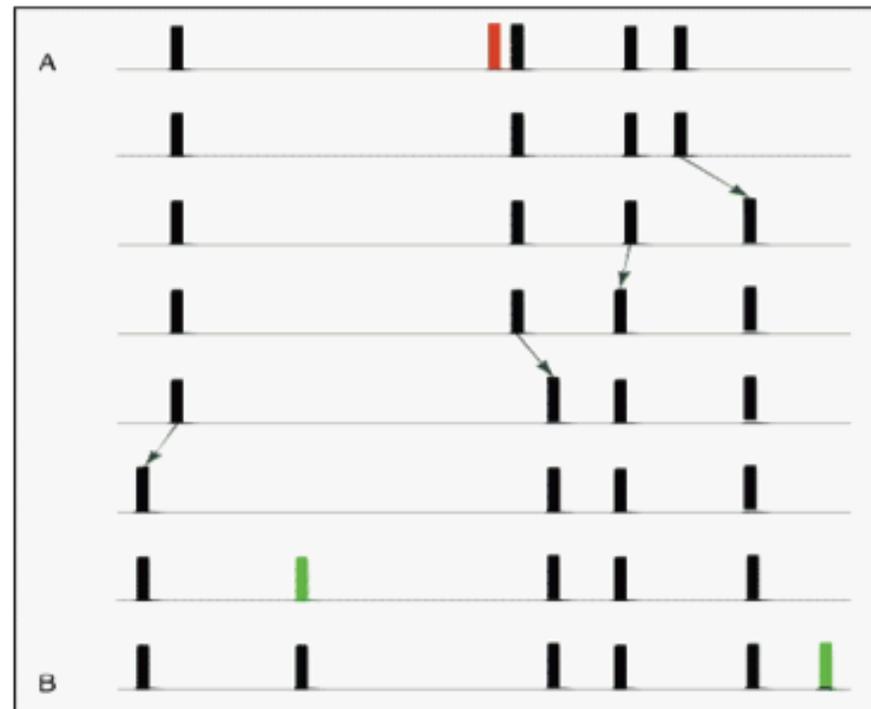
Victor JD (2005) Curr Opin Neurobiol. 15: 585-92.

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)
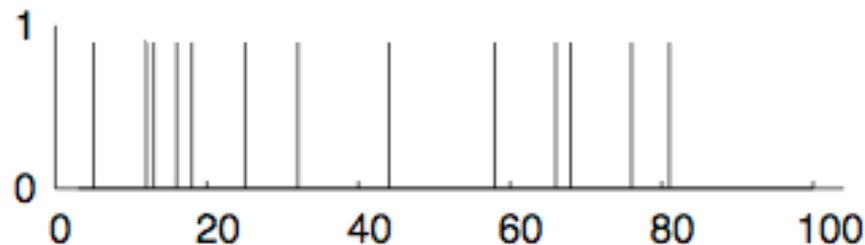
Poisson spike trains
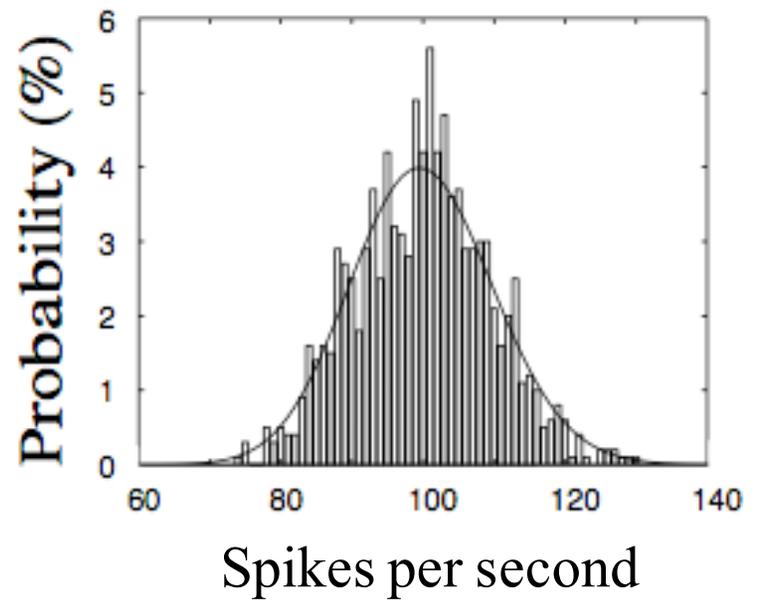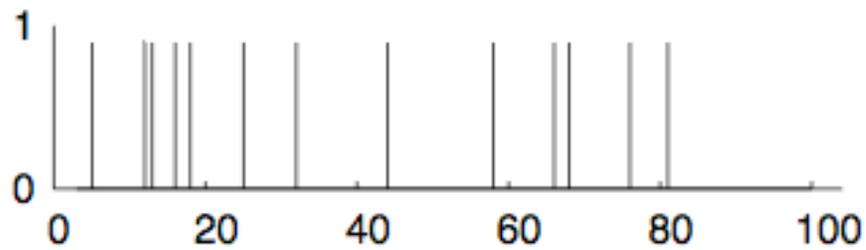
Fano factor: var(count)/mean(count) = 1

Poisson spike trains
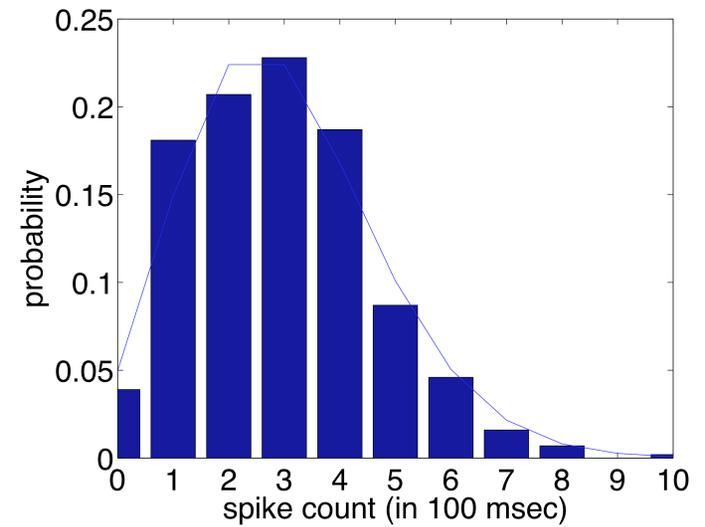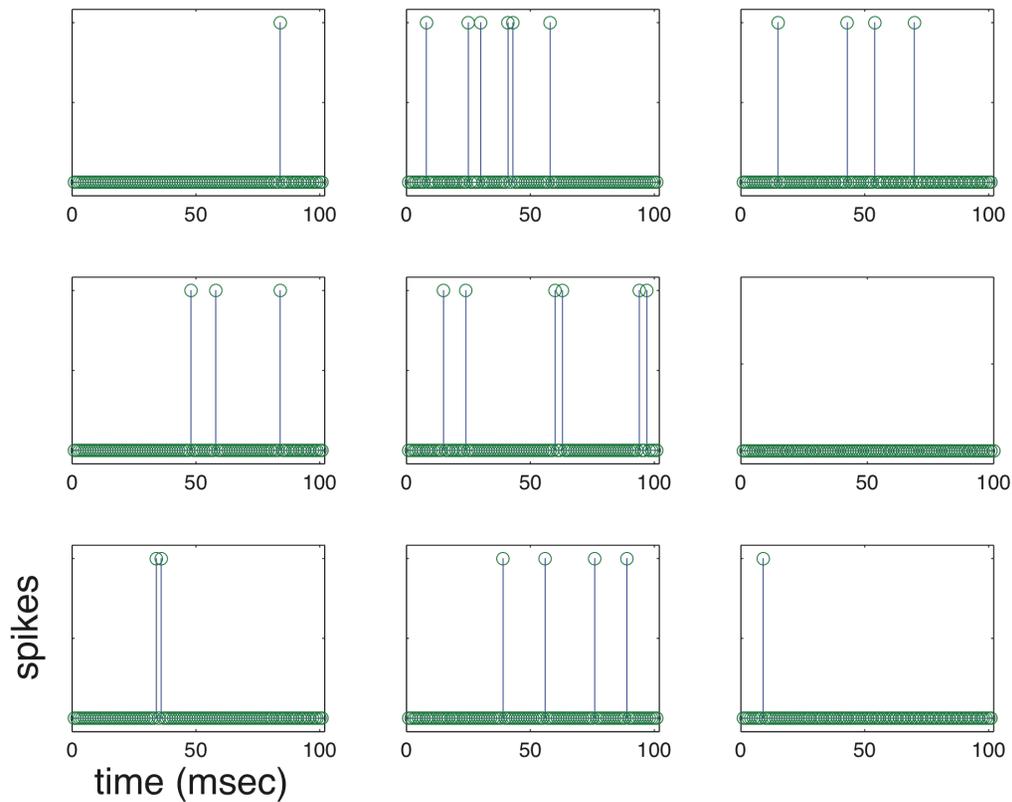
Fano factor: var(count)/mean(count) = 1

Poisson spike trains
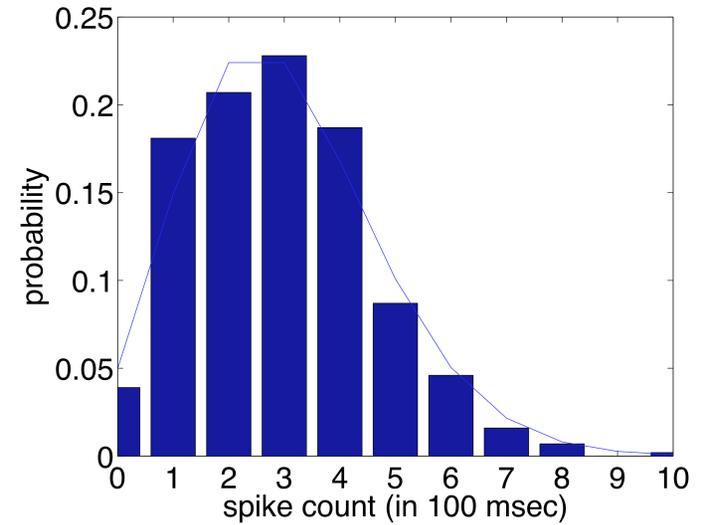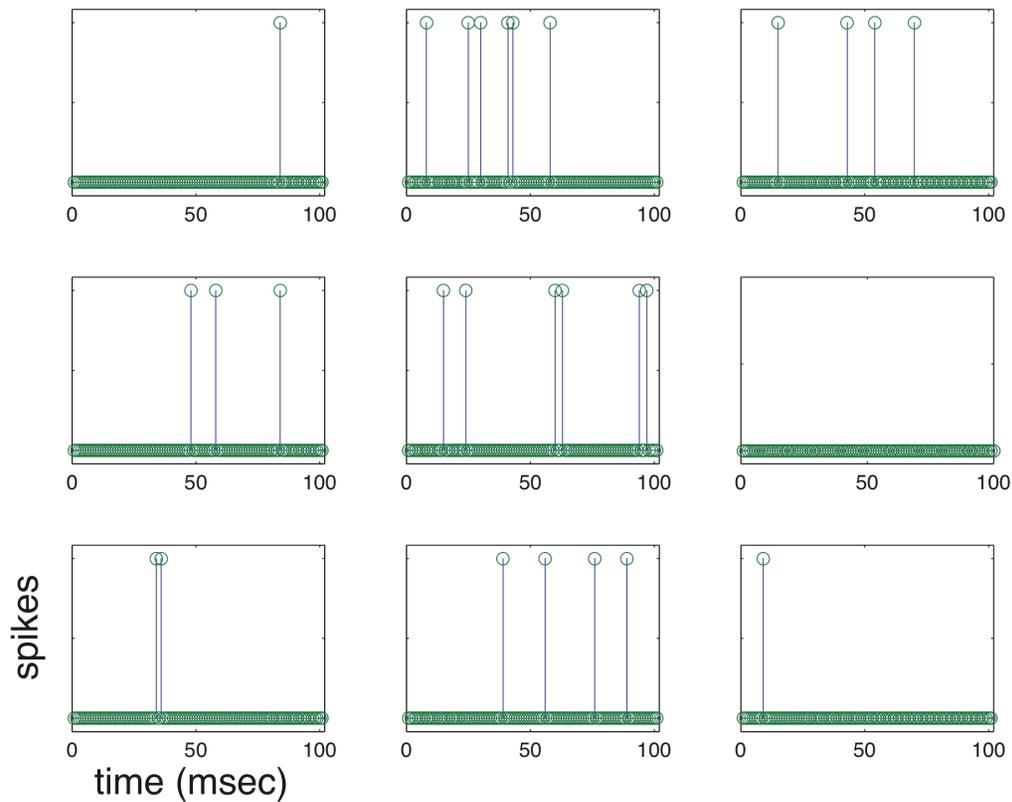
We'll generate Poisson spikes
in the computer lab...

Less variability than Poisson

RGC cells

Poisson model
(independent spikes)

IF model
(spike history matters)
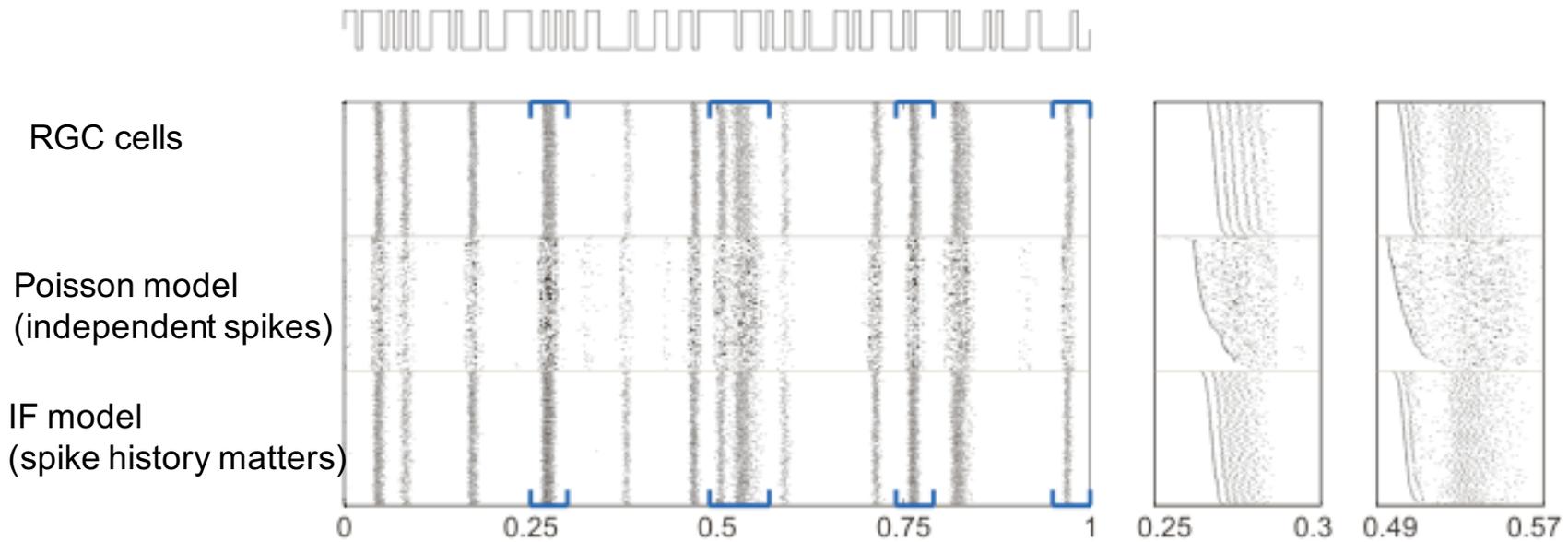
Retinal Ganglion Cells, Pillow et al., 2006

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
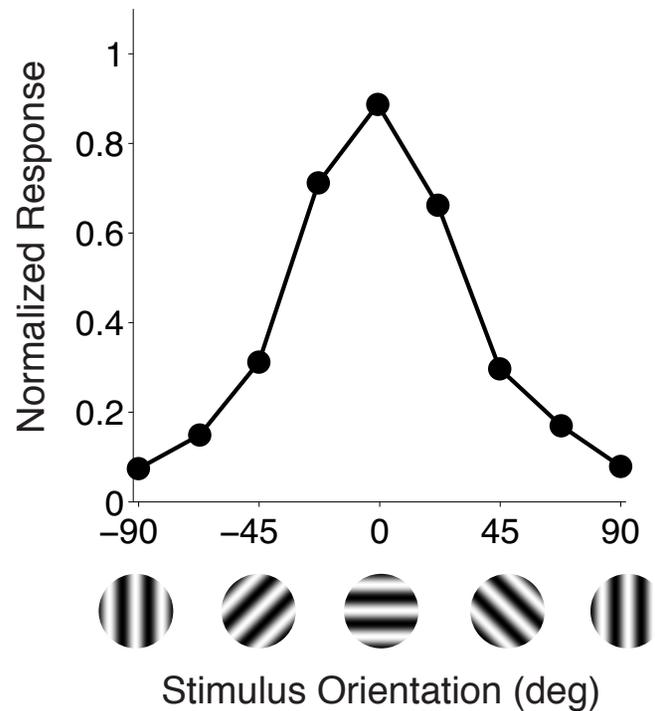
We've already seen…

- 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)
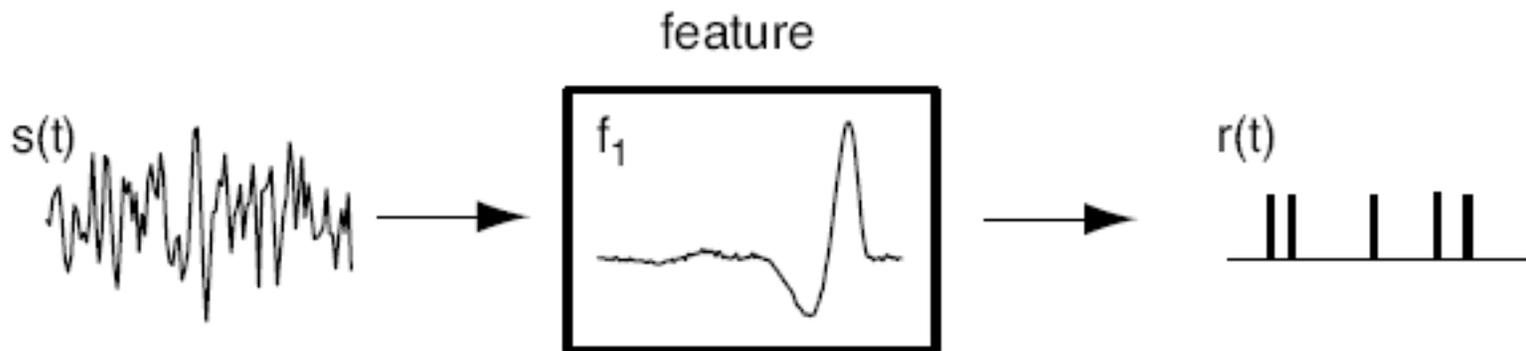
Basic coding model: temporal

- This can also be seen as a descriptive model!
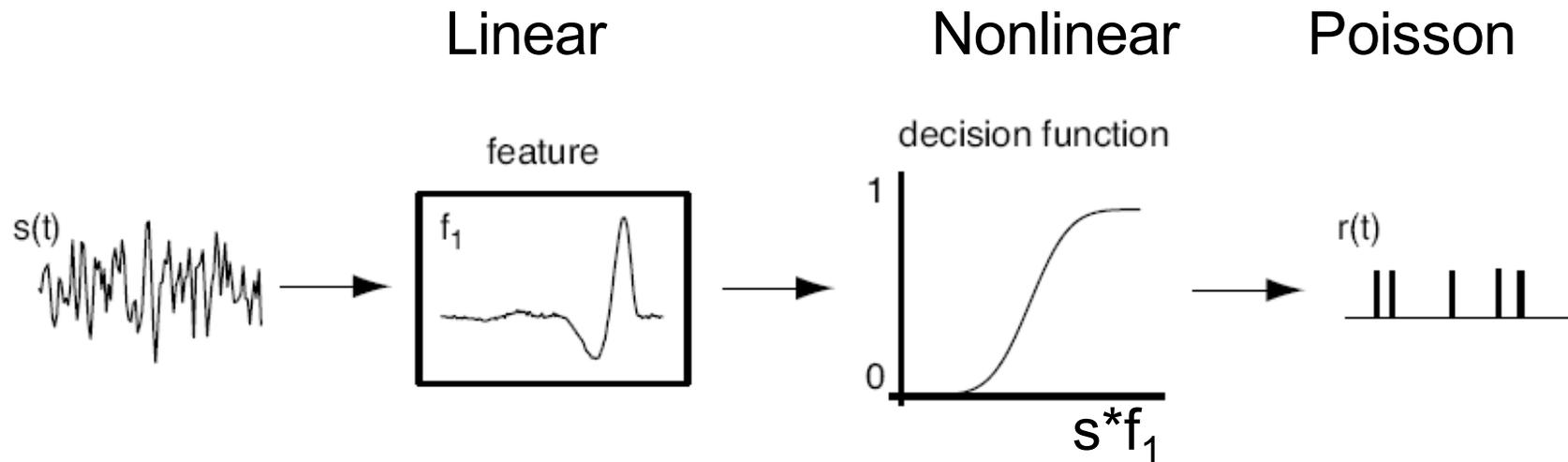
Basic coding model: temporal

Linear   Nonlinear   Poisson

- This can also be seen as a descriptive model!

Basic coding model: temporal

Linear Nonlinear Poisson
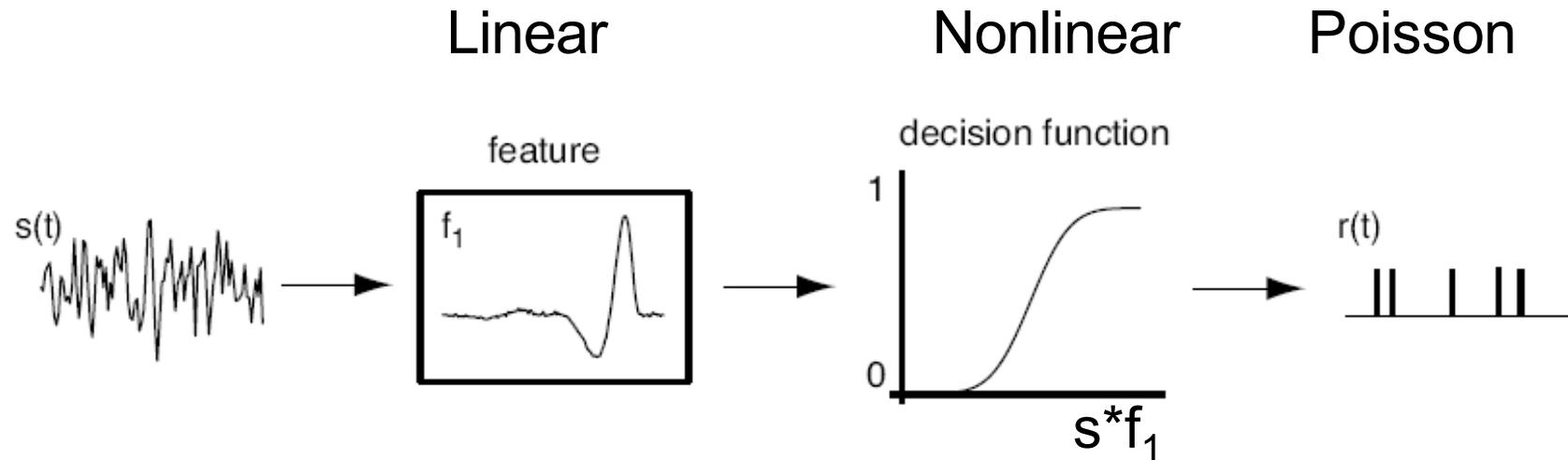
In an experiment:
- We know the input stimuli
- And we measure the corresponding spike trains

Basic coding model: temporal
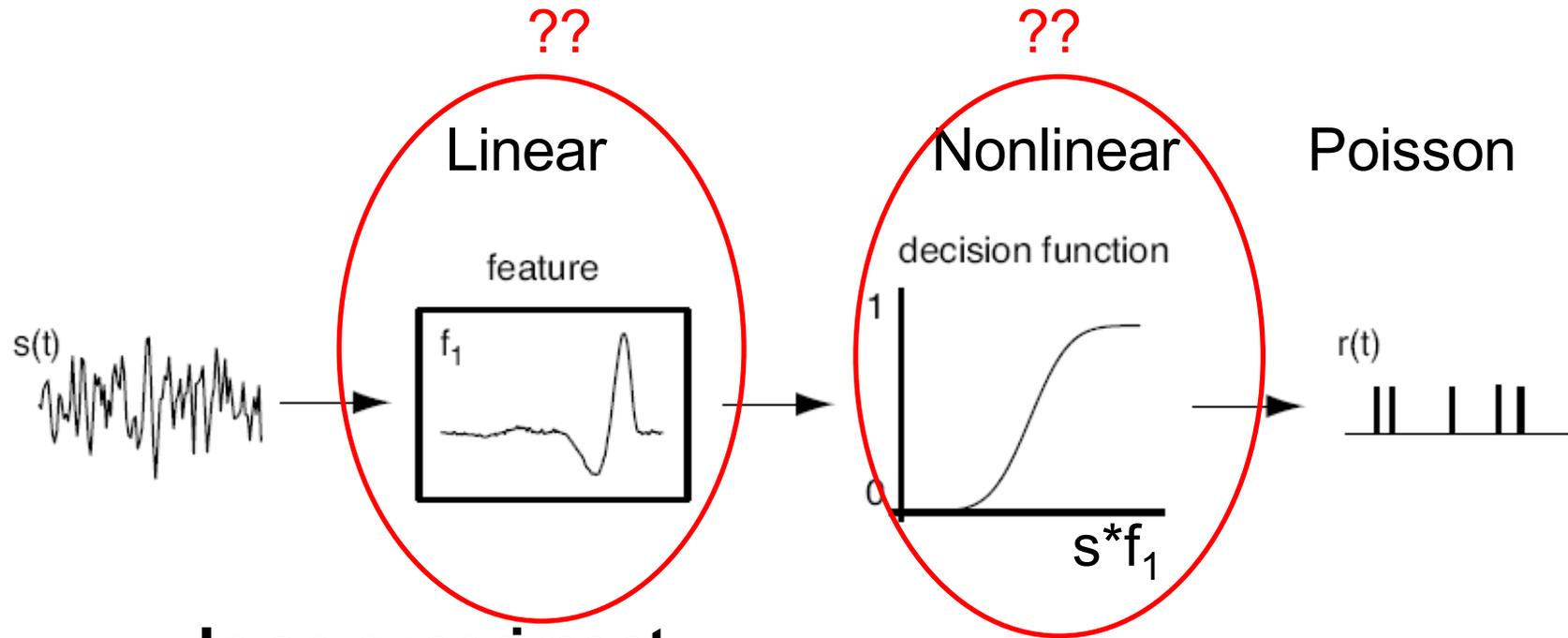
In an experiment:
- We know the input stimuli
- And we measure the corresponding spike trains
- We don't know the Linear or Nolinear boxes!

Basic coding model: temporal
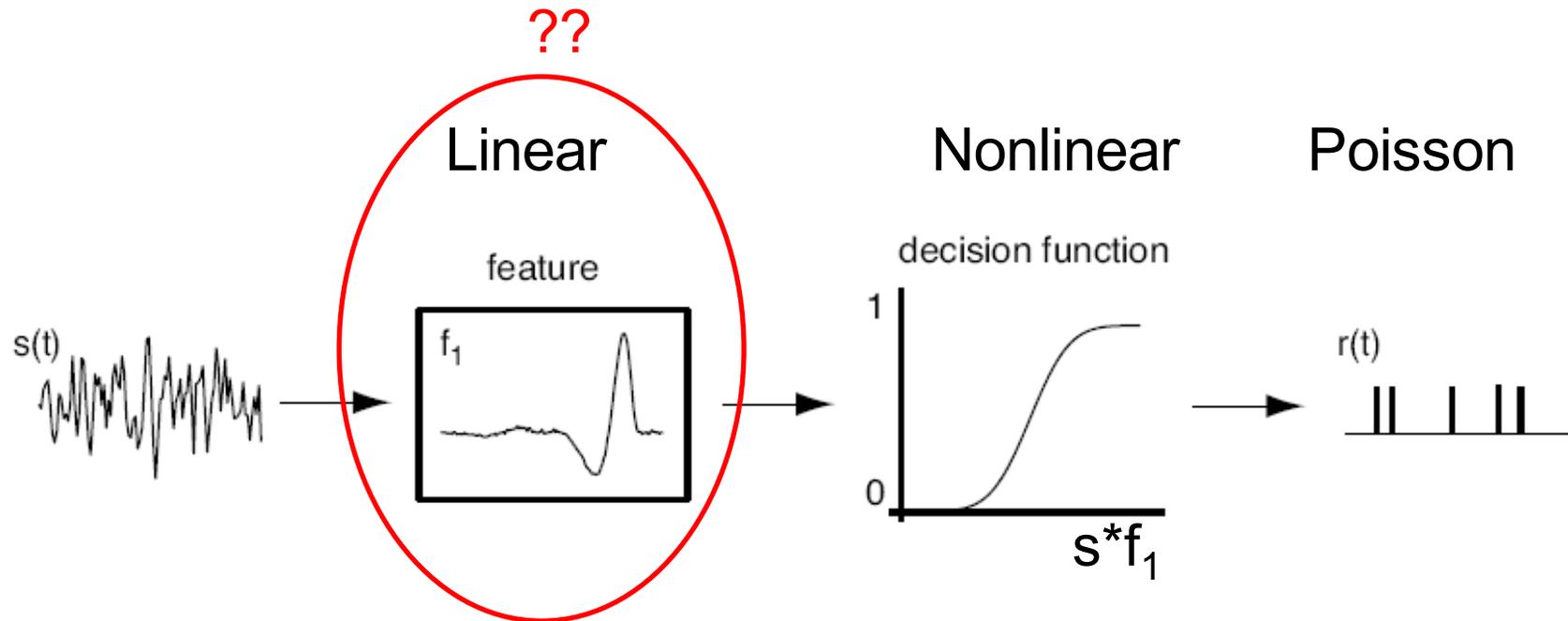
In an experiment:
- We know the input stimuli
- And we measure the corresponding spike trains
- We don't know the Linear or Nolinear boxes!
- Here we will show how to find the Linear

Basic coding model: temporal
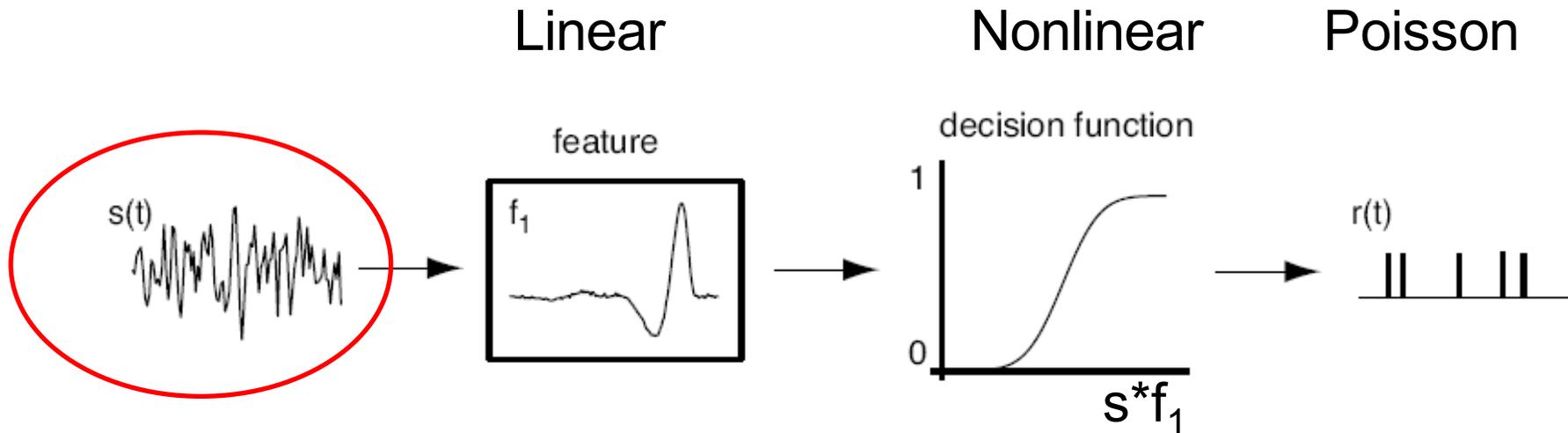
Linear   Nonlinear   Poisson

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
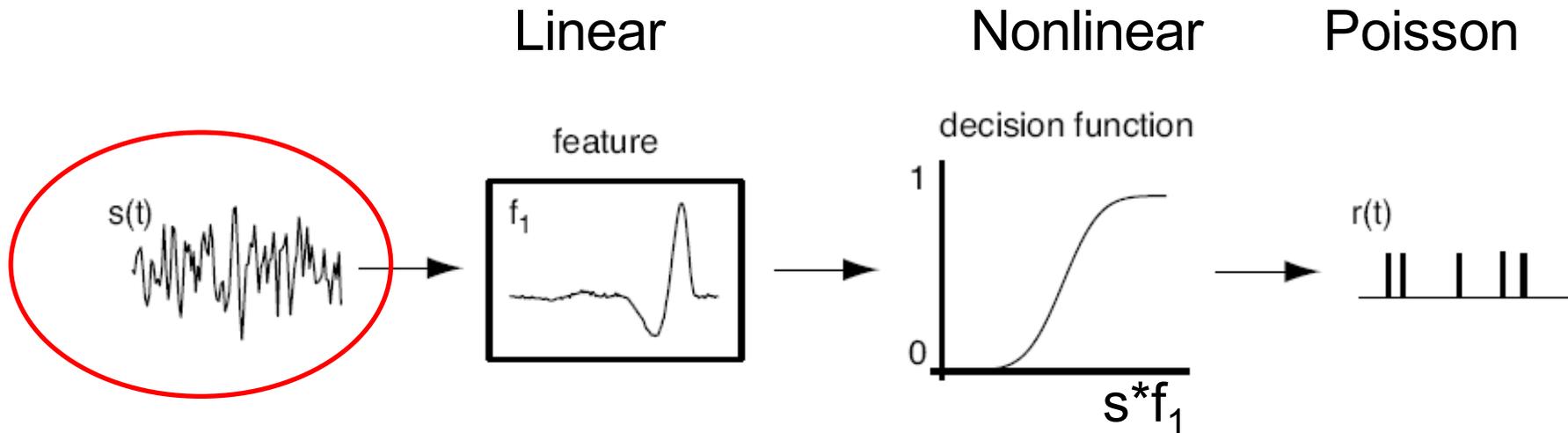
Linear   Nonlinear   Poisson

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)
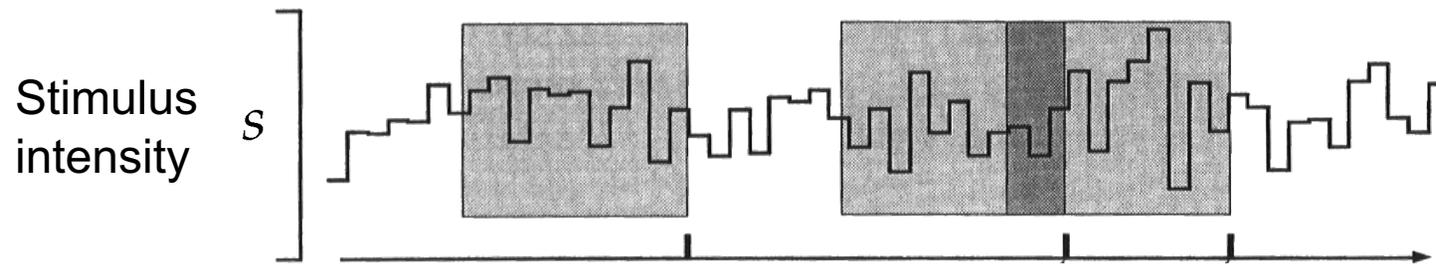
Stimulus
intensity $\quad s$

From Dayan and Abbott textbook; 2001

Spike-triggered Average (STA)

Stimulus intensity s

time

+

+

+

From Dayan and Abbott textbook; 2001

Spike-triggered Average (STA)

Stimulus intensity s

time

τ

spike-triggered average

= estimated linear filter
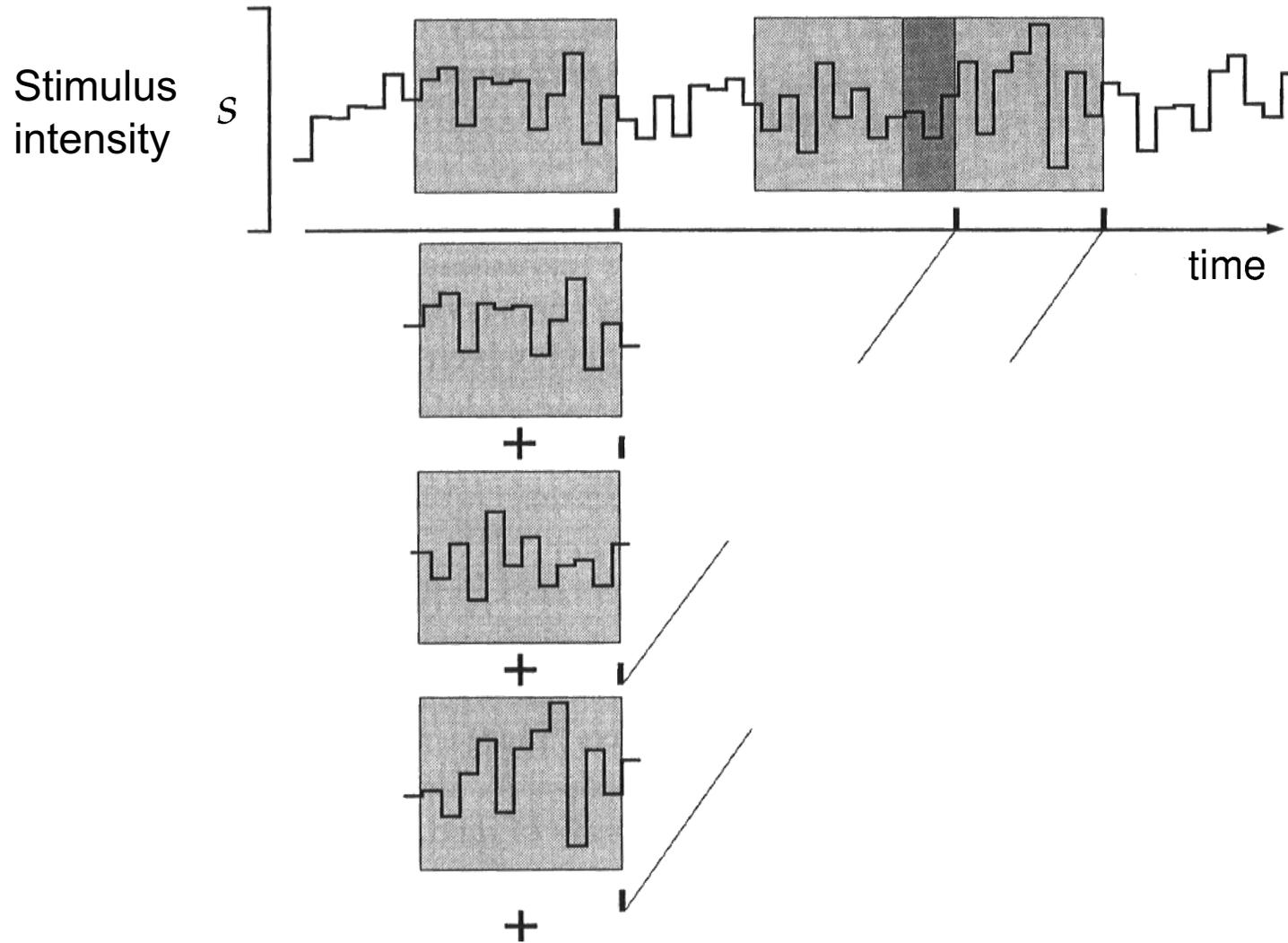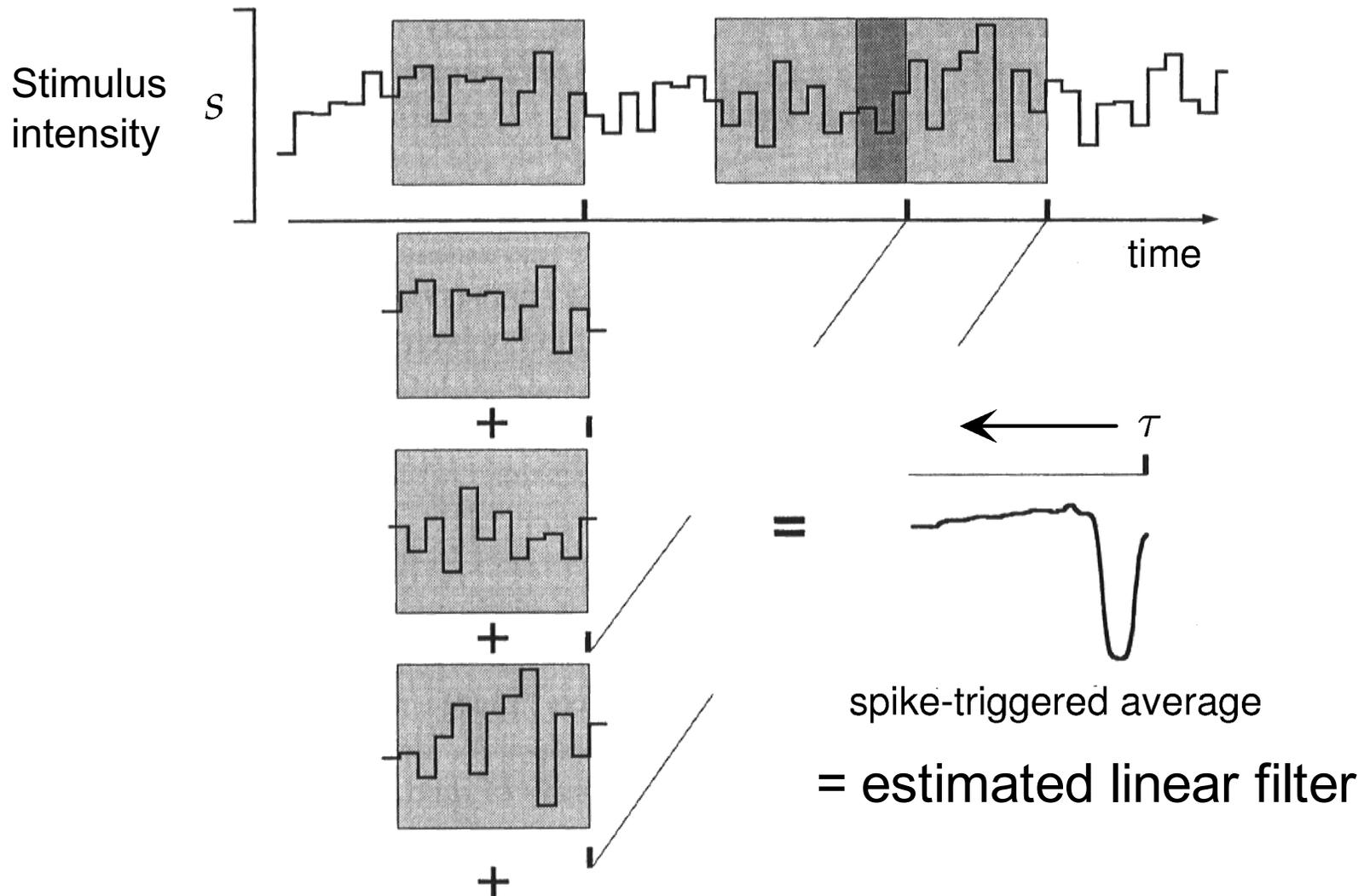
From Dayan and Abbott textbook; 2001

Primary Visual Cortex Receptive Fields

Optic Tract

LGN
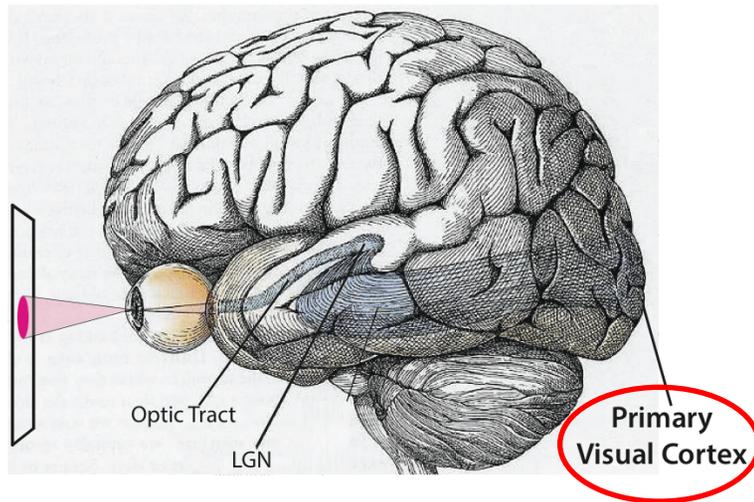
Primary
Visual Cortex
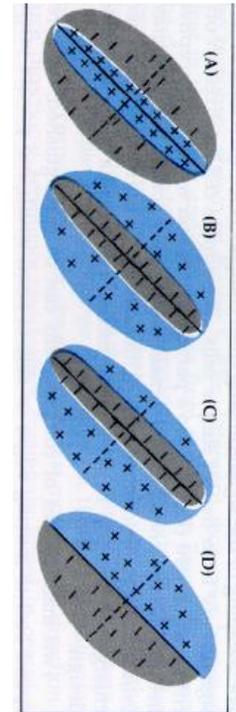
Examples of
receptive
fields in
primary
visual cortex
(V1)

R. Rao, 528 Lecture 1

(From Nicholls et al., 1992)

16

Spike-triggered average (STA)
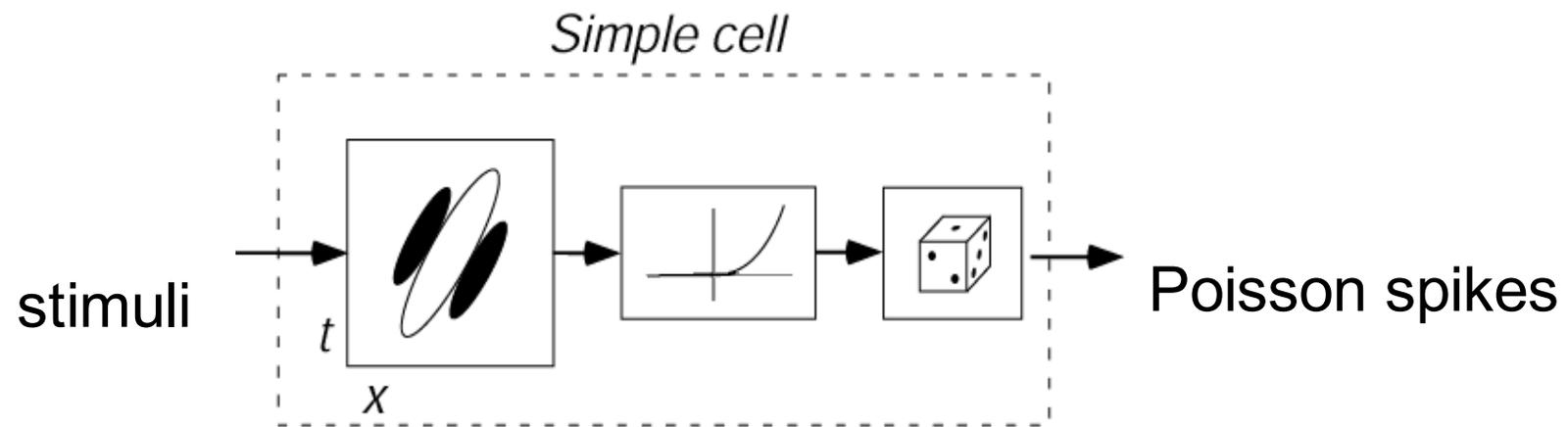
Linear, Nonlinear, Poisson encoding model

Spike-triggered average (STA)
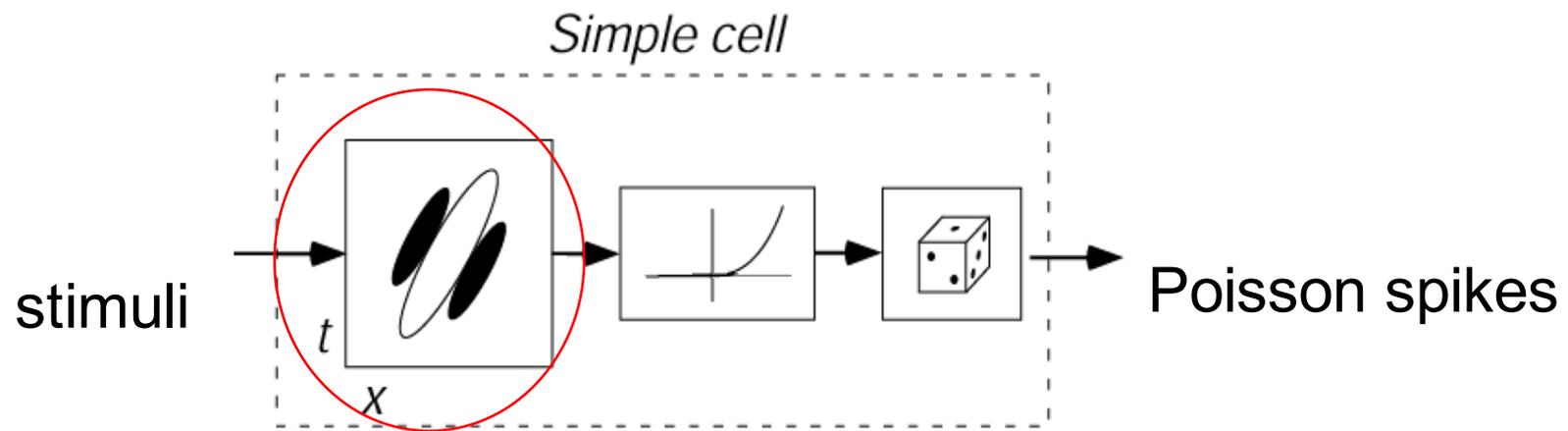
Linear, Nonlinear, Poisson (LNP) encoding model

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

Spike-triggered Average (STA): example
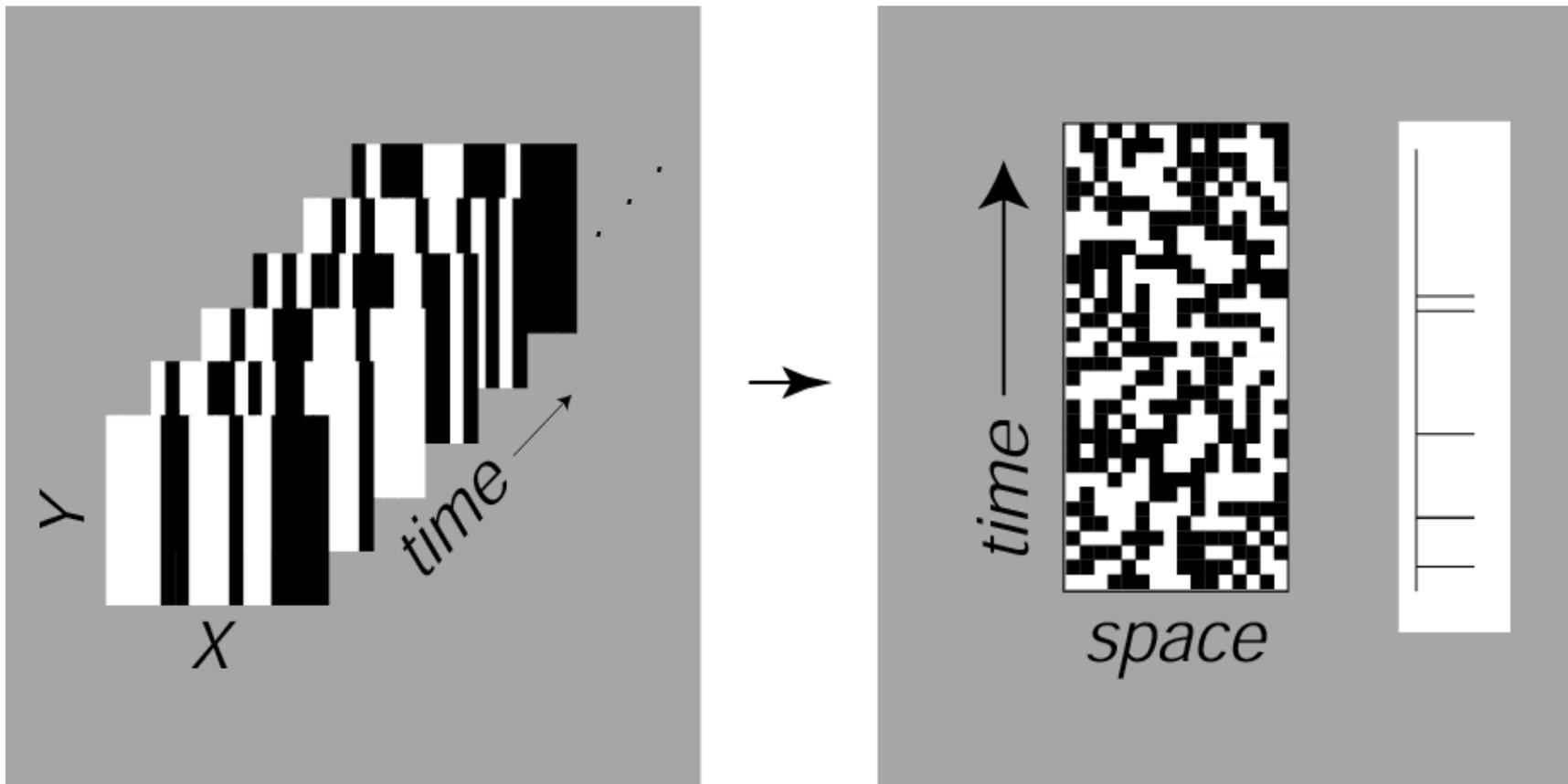
From Nicole Rust

Spike-triggered Average (STA): example

Spike-triggered Average (STA): example

From Nicole Rust

Spike-triggered Average (STA) : example

STA

Average of spike-triggered stimuli

time

x
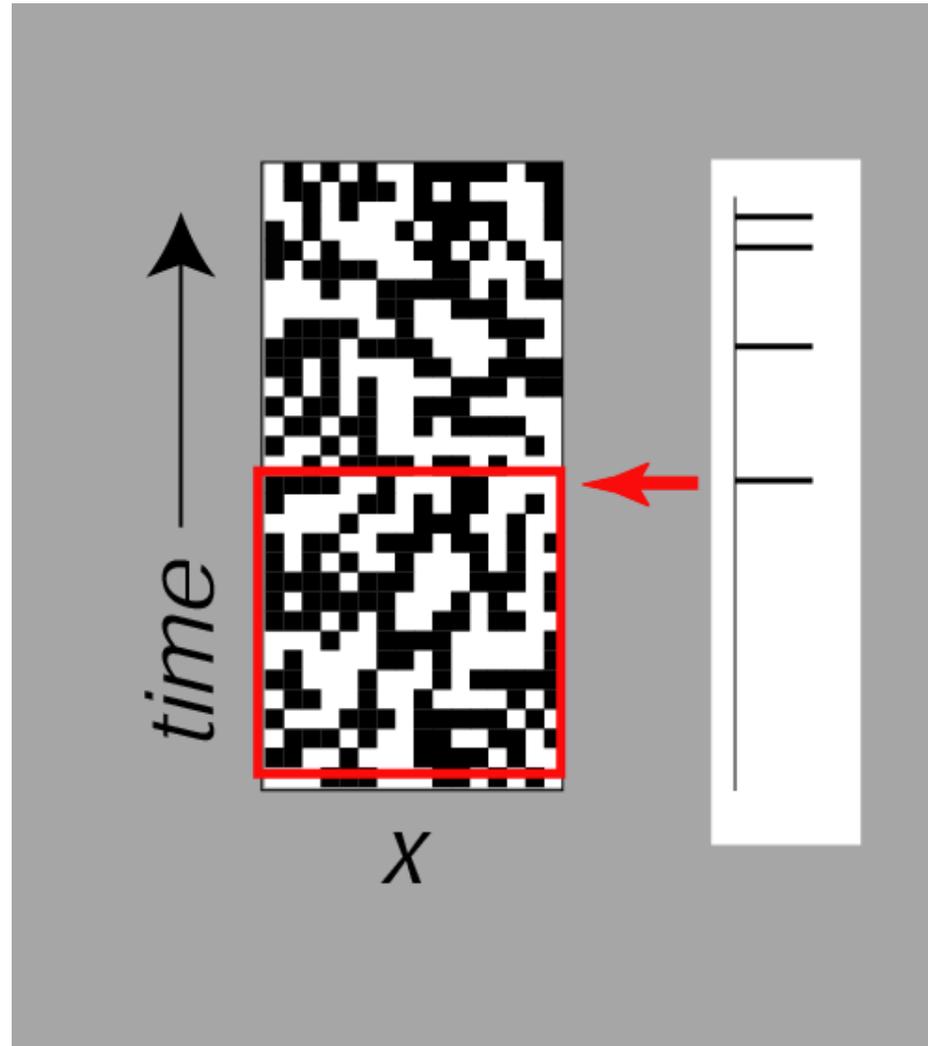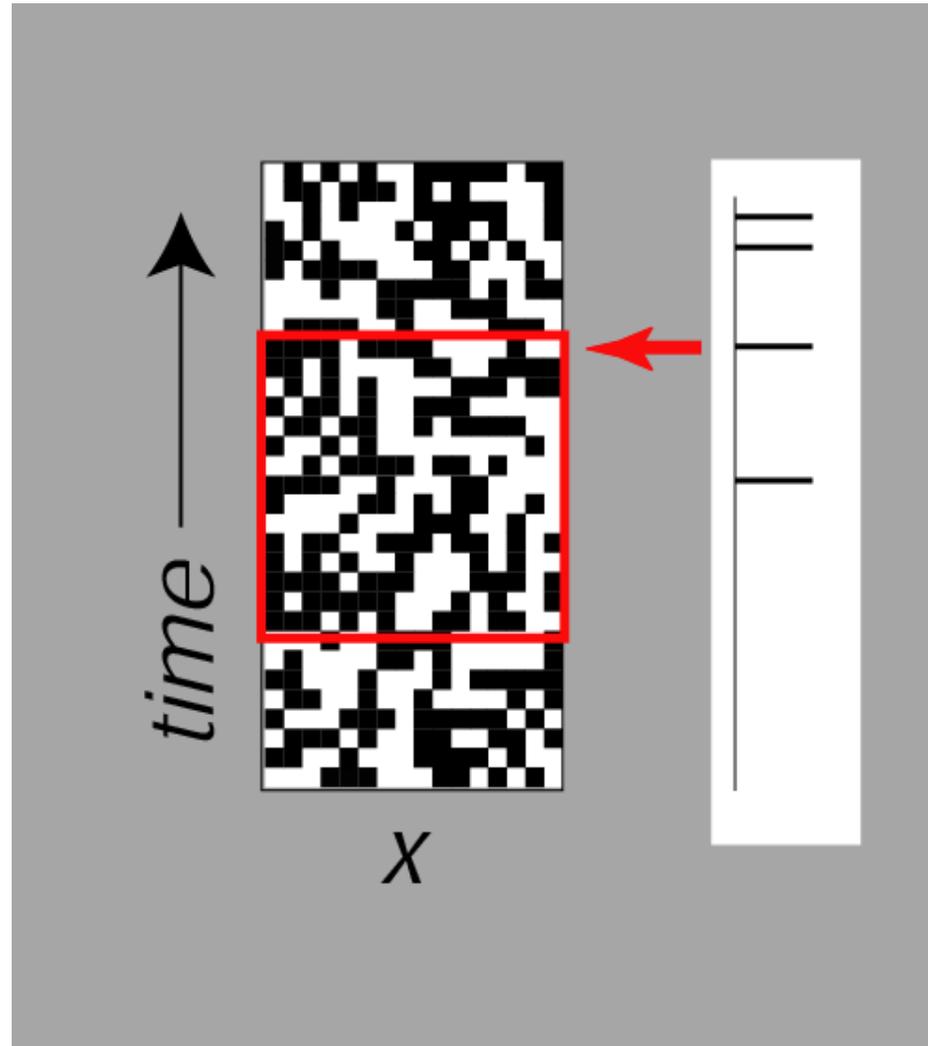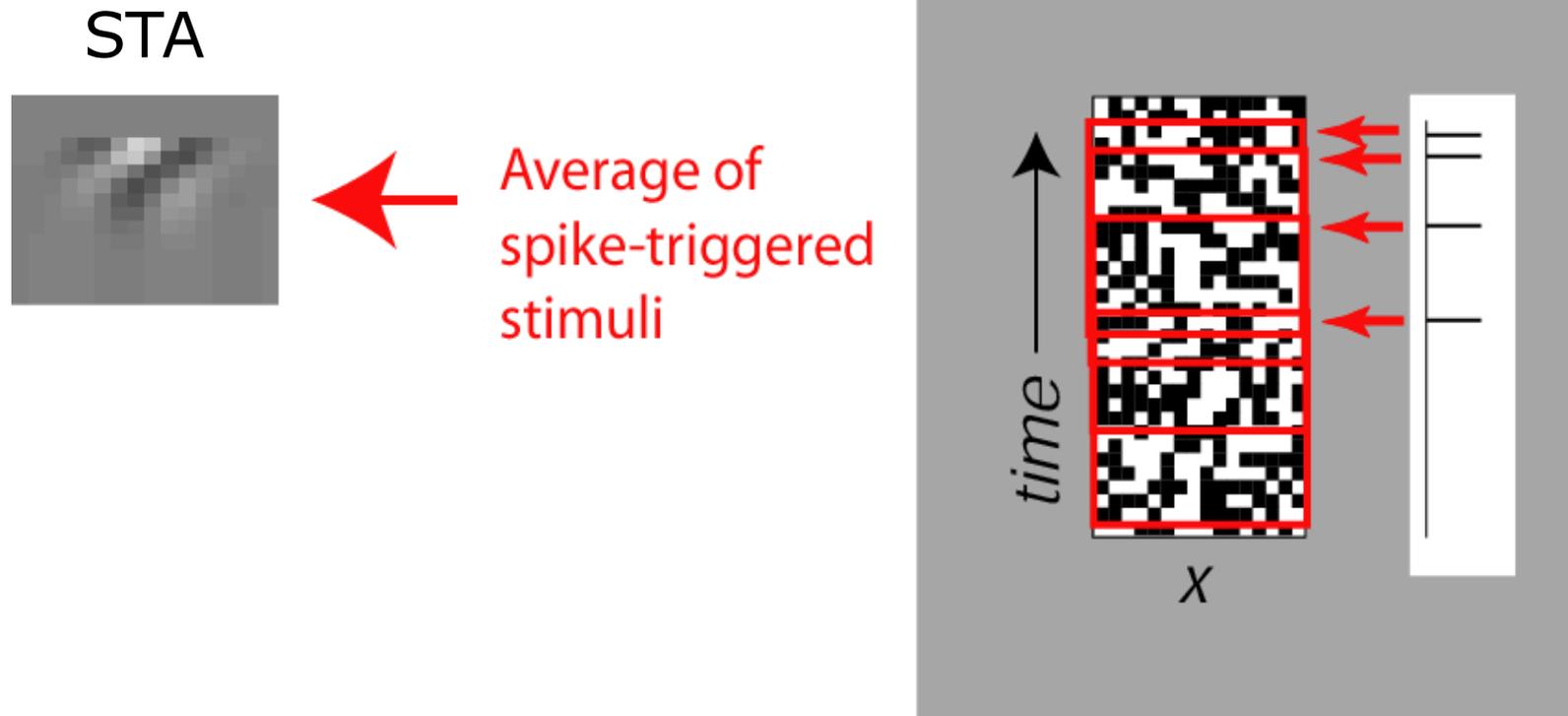
From Nicole Rust

Spike-triggered average (STA)
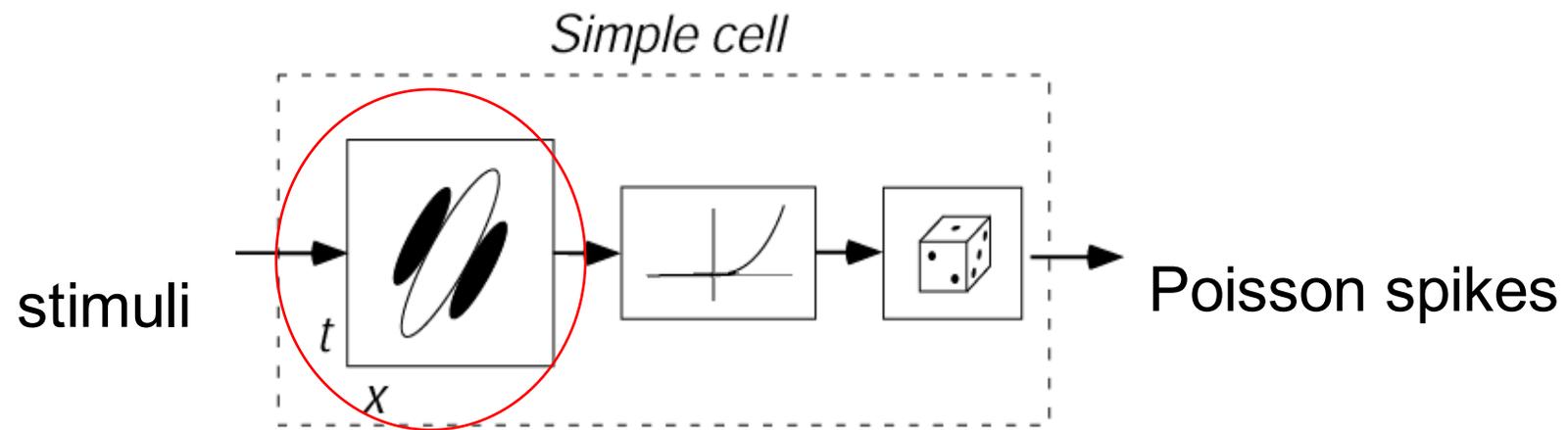
Linear, Nonlinear, Poisson (LNP) encoding model

Will estimate of Linear always work??

Spike-triggered average (STA)

Simple cell

stimuli
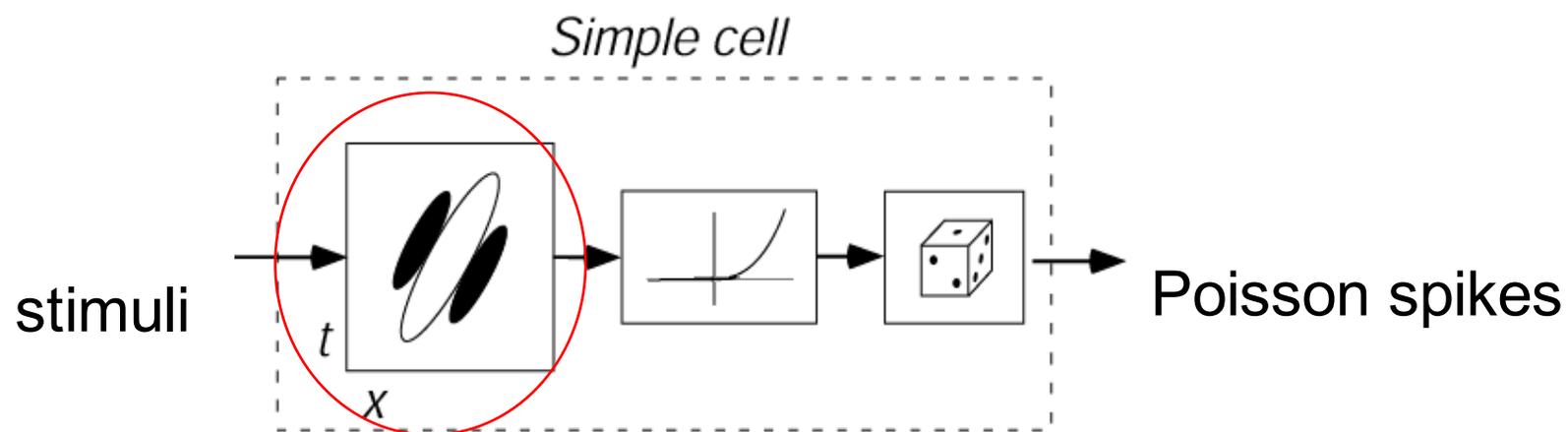
Poisson spikes

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)

Simple cell

stimuli
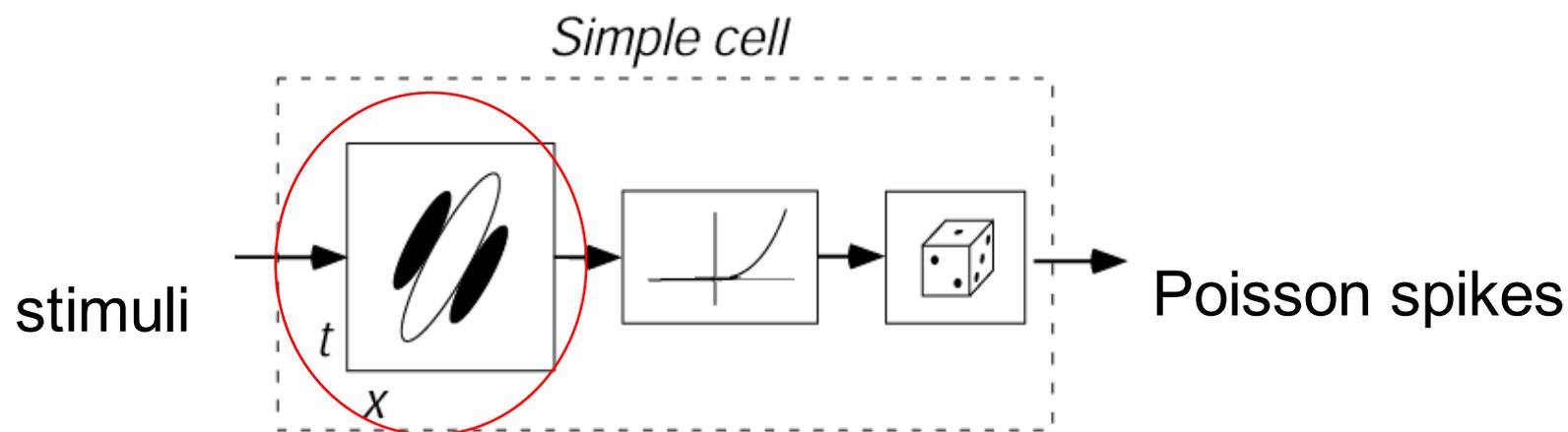
Poisson spikes

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"

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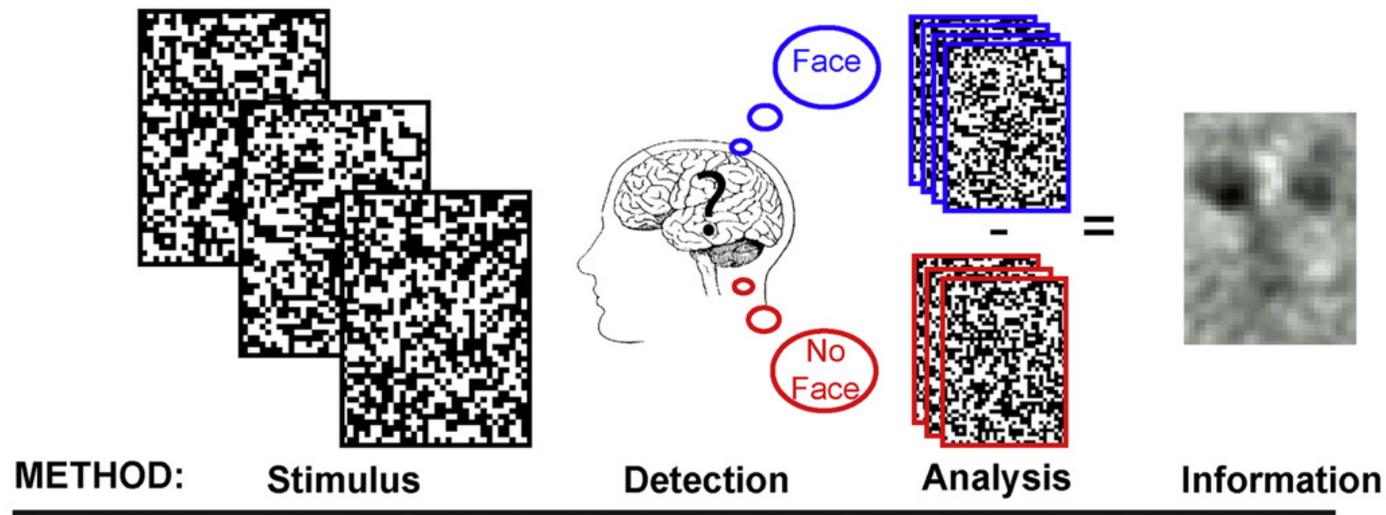
Smith et al. Current Biology 2012:
Subjects told that half the noise stimuli contain
faces, although there are no faces…

In Psychology: termed "Classification Images"

ERP Face Present vs. Absent

S1, S2, S3, S4, S5

Time windows: [-100 0] [0 100] [100 200] [200 300] [300 400] [400 500] [500 600] [600 700]

Behaviour

1μV / -1μV

——— Frontal sensors
——— OT sensors
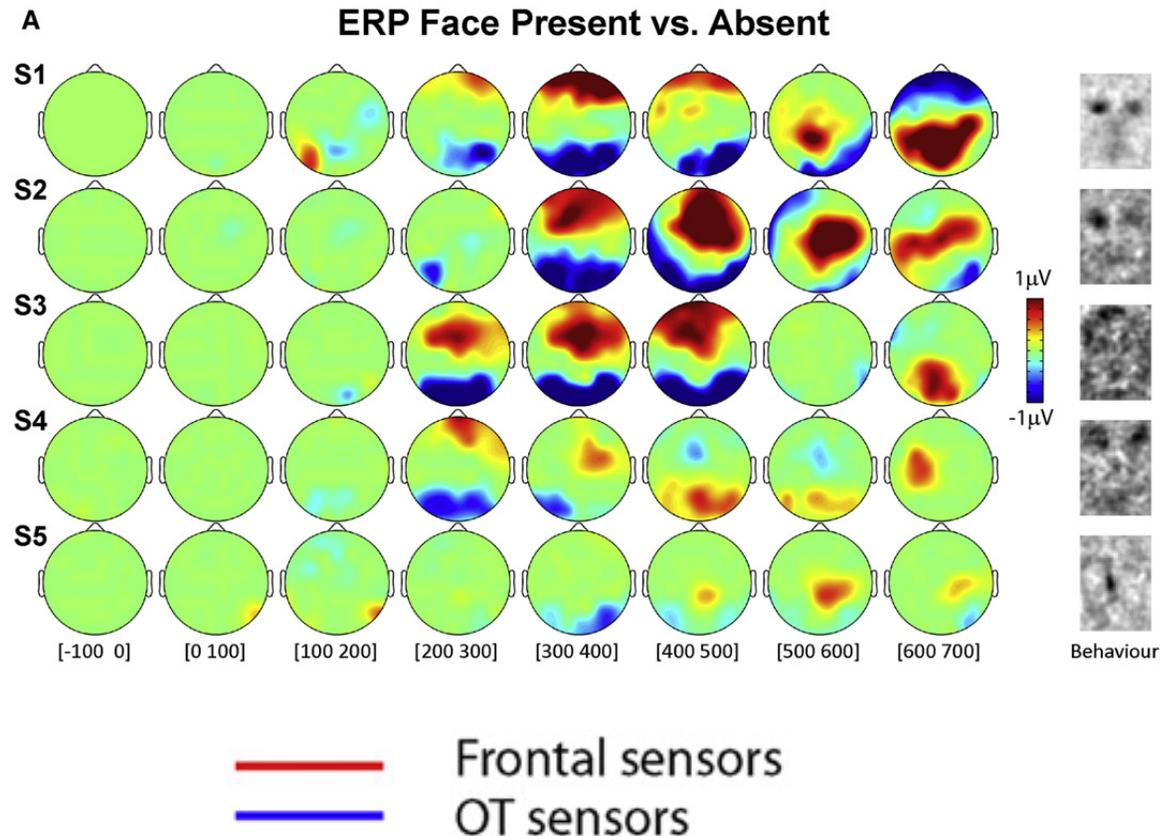
"direct association between increasing faceness content of the stimuli and enhanced positivity in the single-trial EEG amplitudes over frontal sensors— i.e., the more face-like noise stimuli drove larger neural responses … and a significant association between increased negative responses over occipitotemporal sensors and the faceness of the noise."

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