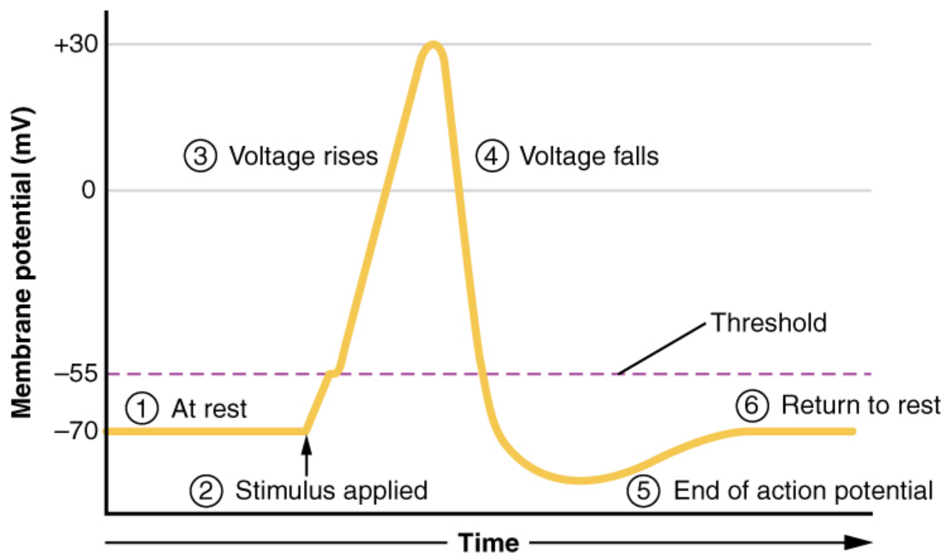
The Neural Code

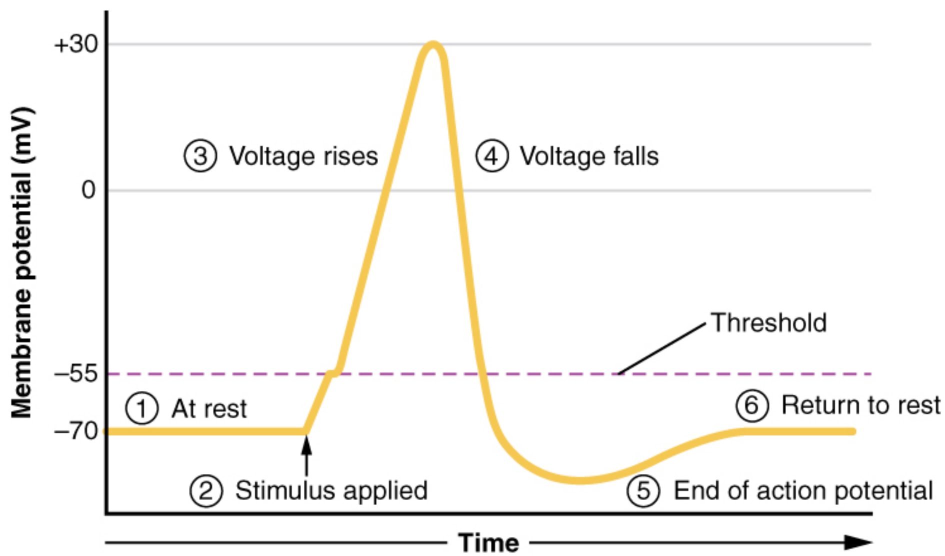
Neurons communicate with action potentials. Understanding what they are communicating requires knowledge of their language: the neural code

Neural Currency



- **Spike (action potential)**: approximately 100 mV rise in voltage, lasting for approximately 1 msec

Neural Currency

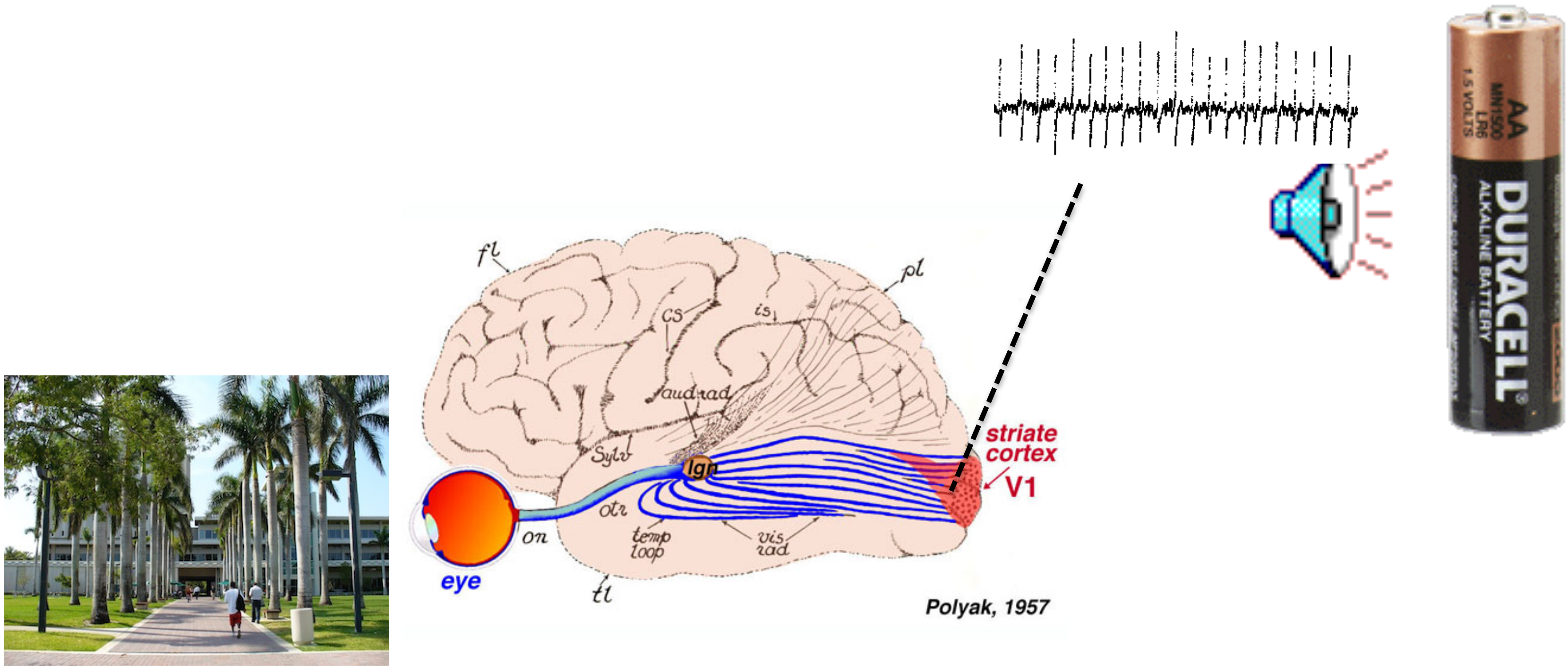


- **Spike (action potential)**: approximately 100 mV rise in voltage, lasting for approximately 1 msec
- Spike is an all or none binary event. To spike or not to spike!

Neural Currency

- **Spike (action potential)**: approximately 100 mV rise in voltage, lasting for approximately 1 msec (spike is an all or none binary event)

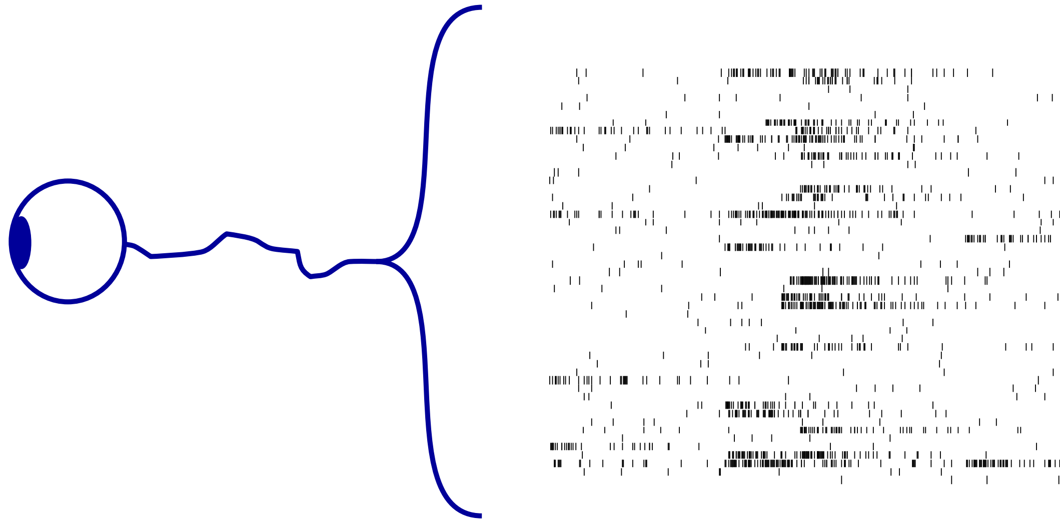
Neural Currency



- Example: Visual neurons spike in response to features or properties of images

What your brain "sees"

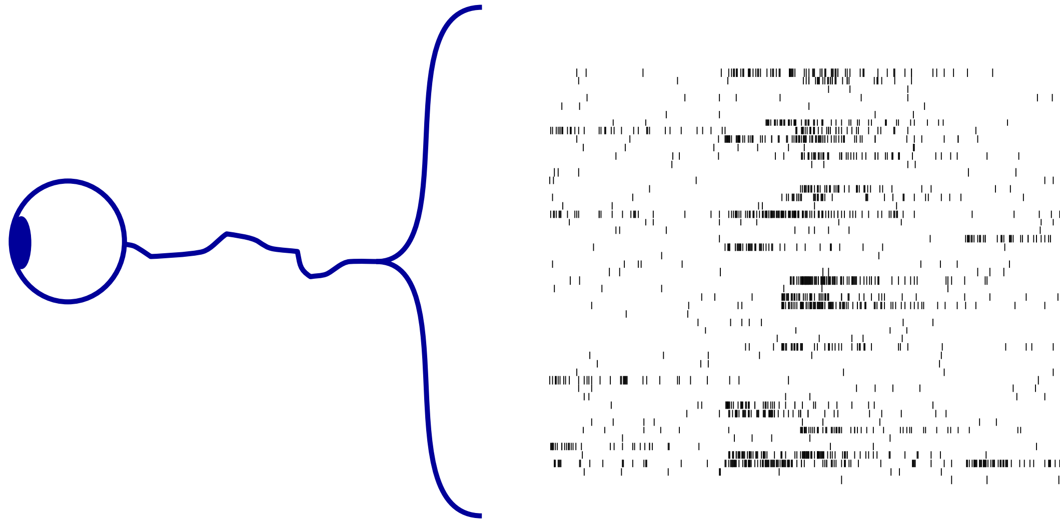
Population of neurons spiking



Adapted from Gatsby Computational Neuroscience course

What your brain "sees"

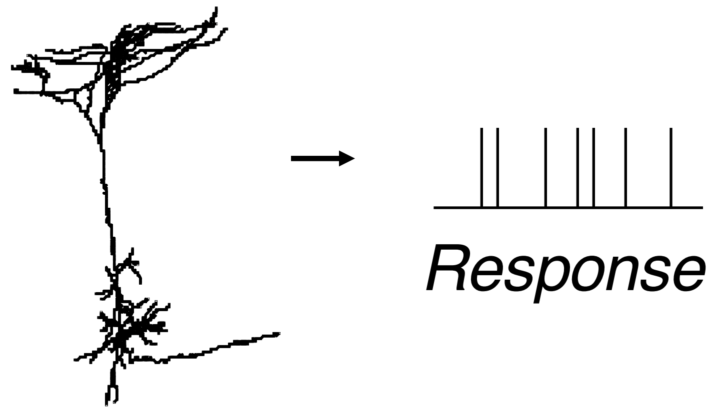
Population of neurons spiking

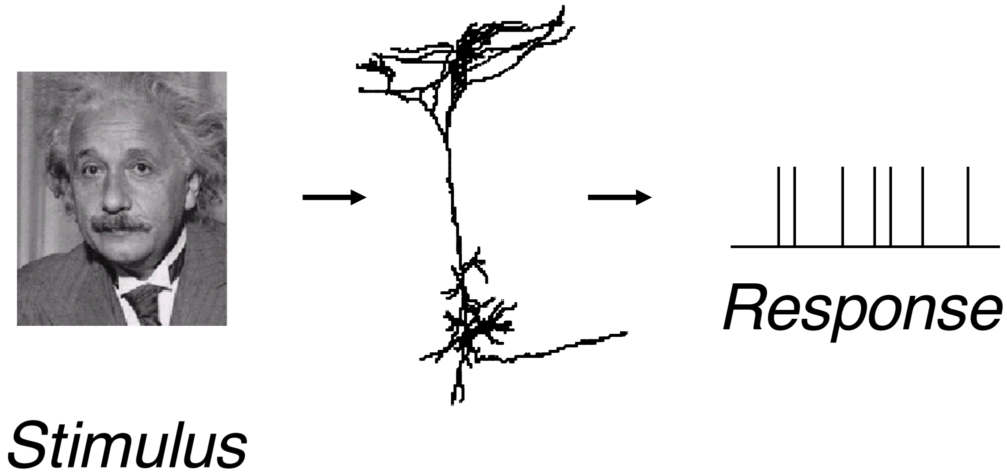


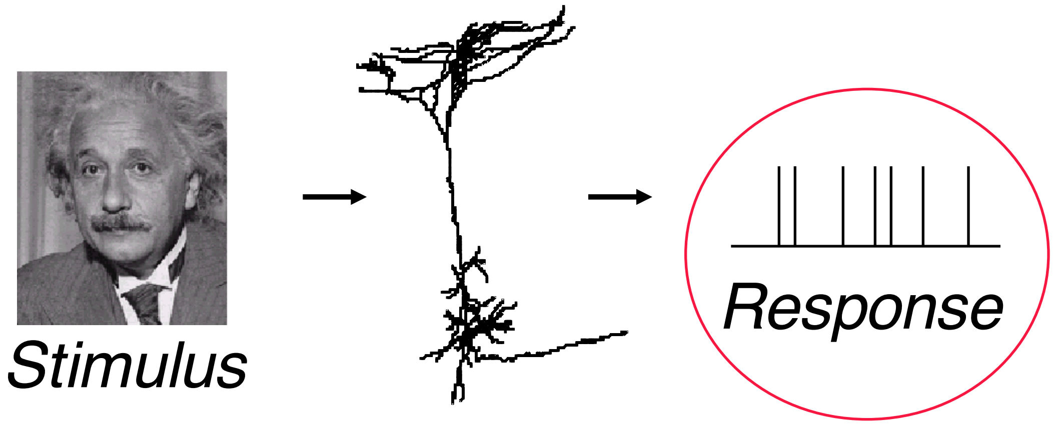
You infer…
Palm trees
UM Campus
Warm weather

Adapted from Gatsby Computational Neuroscience course

Single neuron and spikes

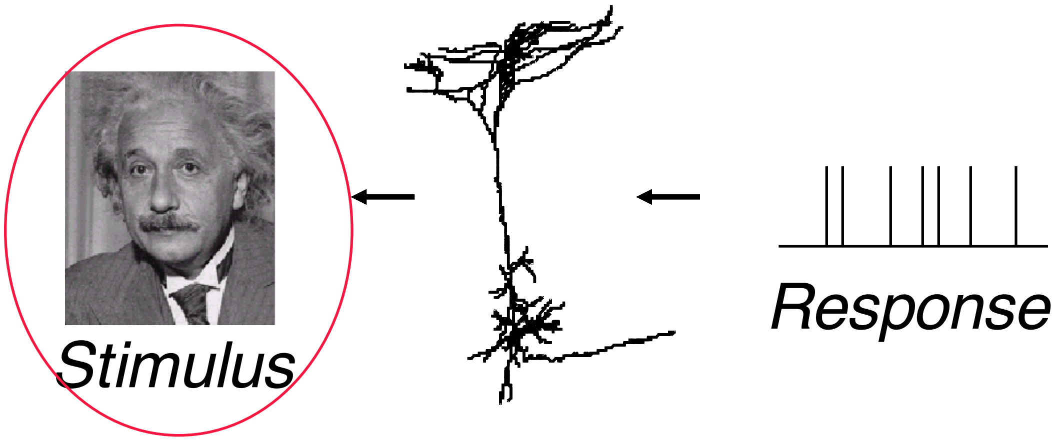



Stimulus
Response



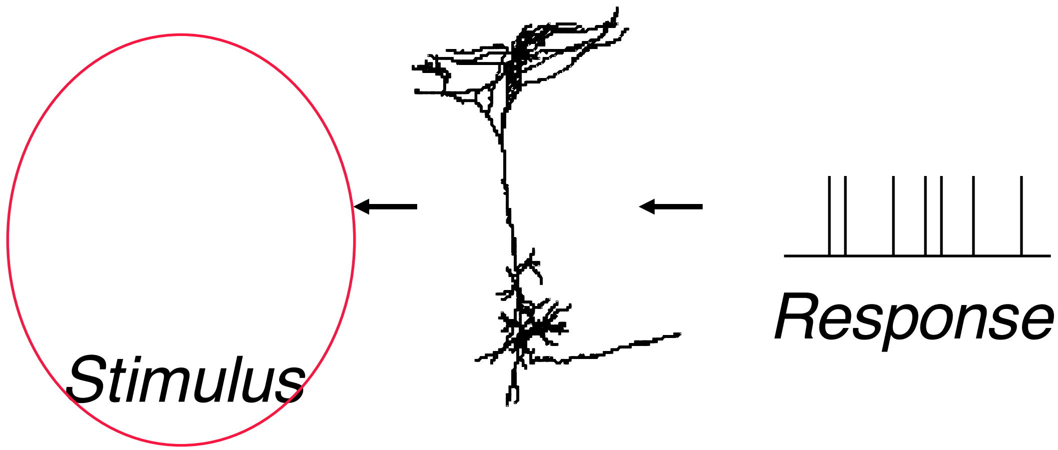
Encoding: Probability(Response | Stimulus)

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



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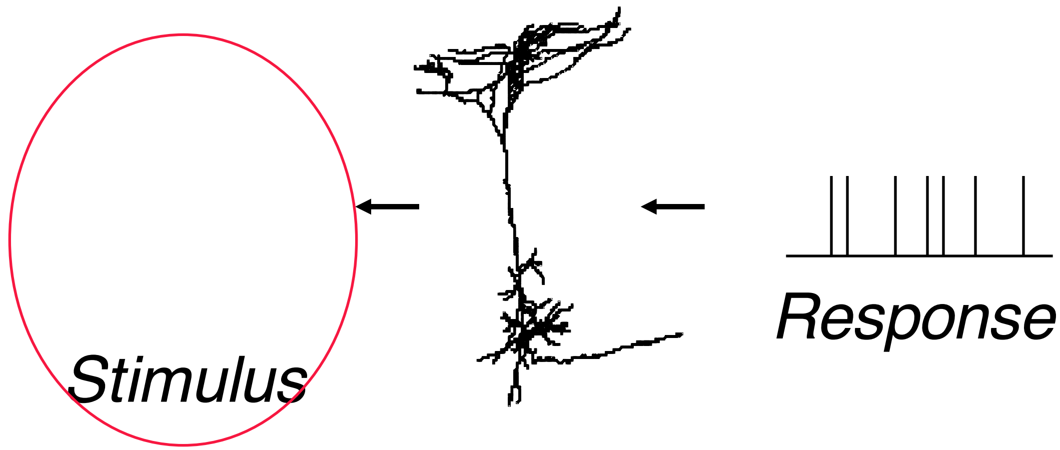
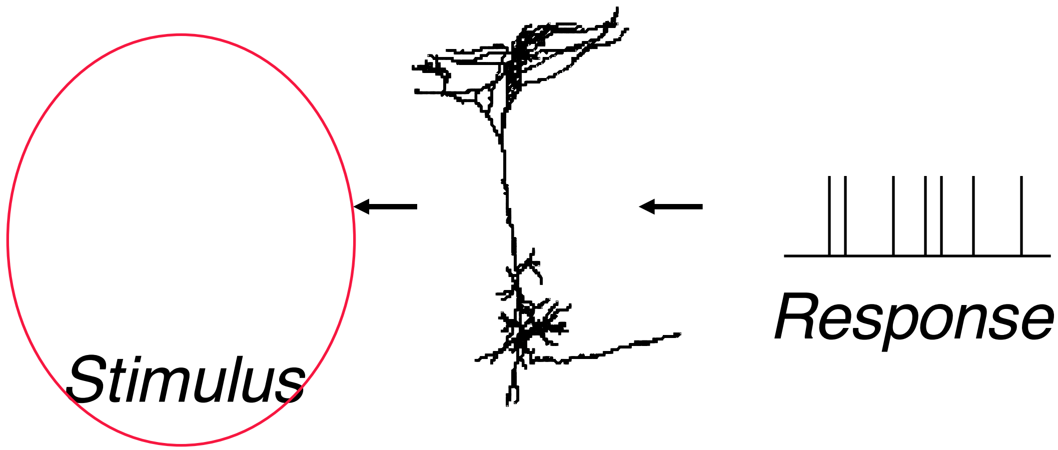


What might we decode
about a stimulus?

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



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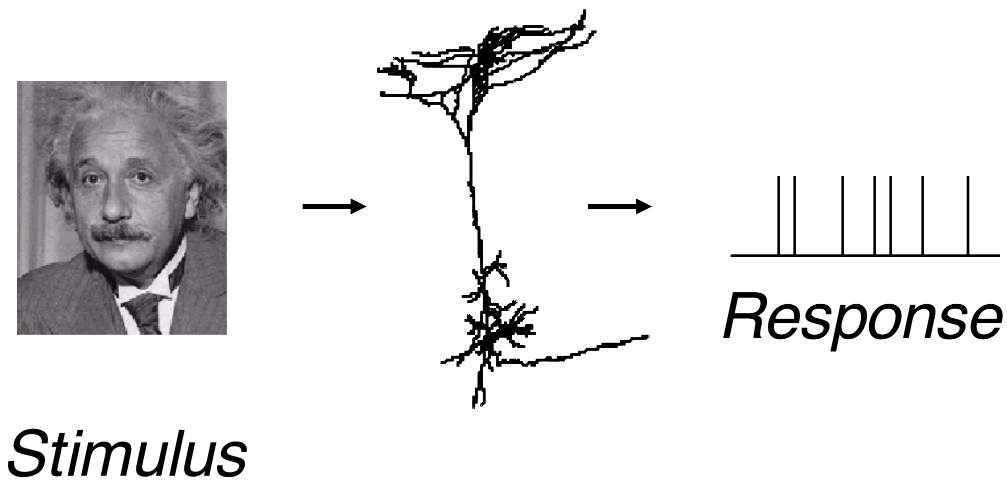
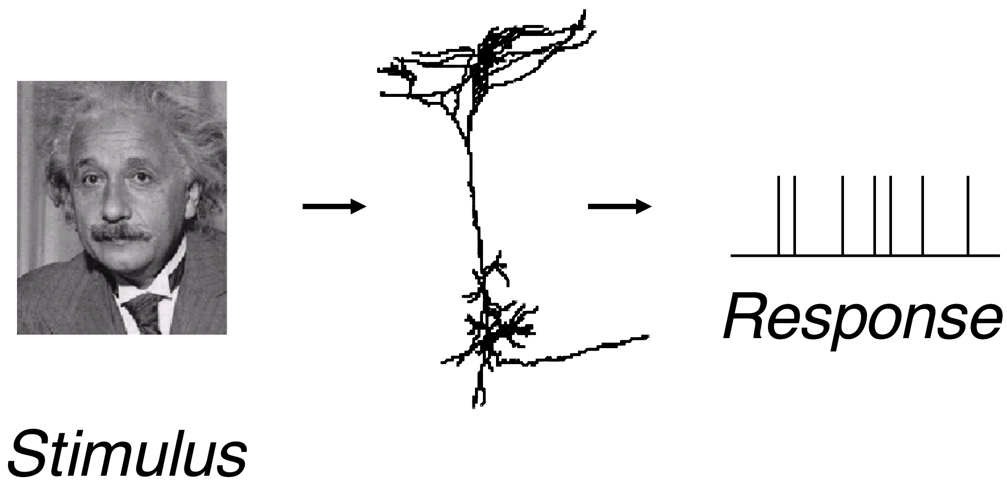


Ideally, for any input we'd like to know the response
And vice versa

Problems in deciphering the neural code?



Stimulus space huge

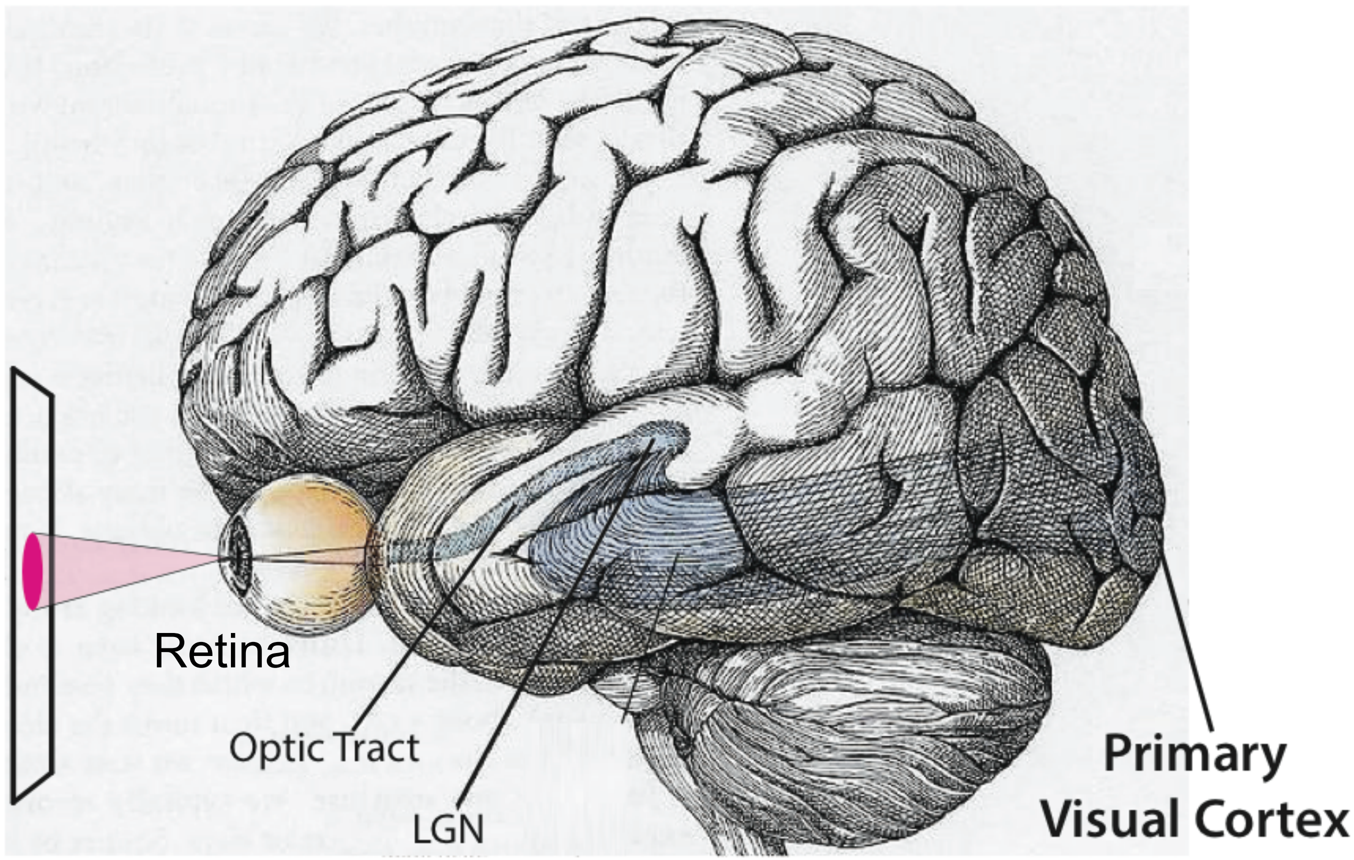
Response space huge

What kind of neural codes?

Rate codes

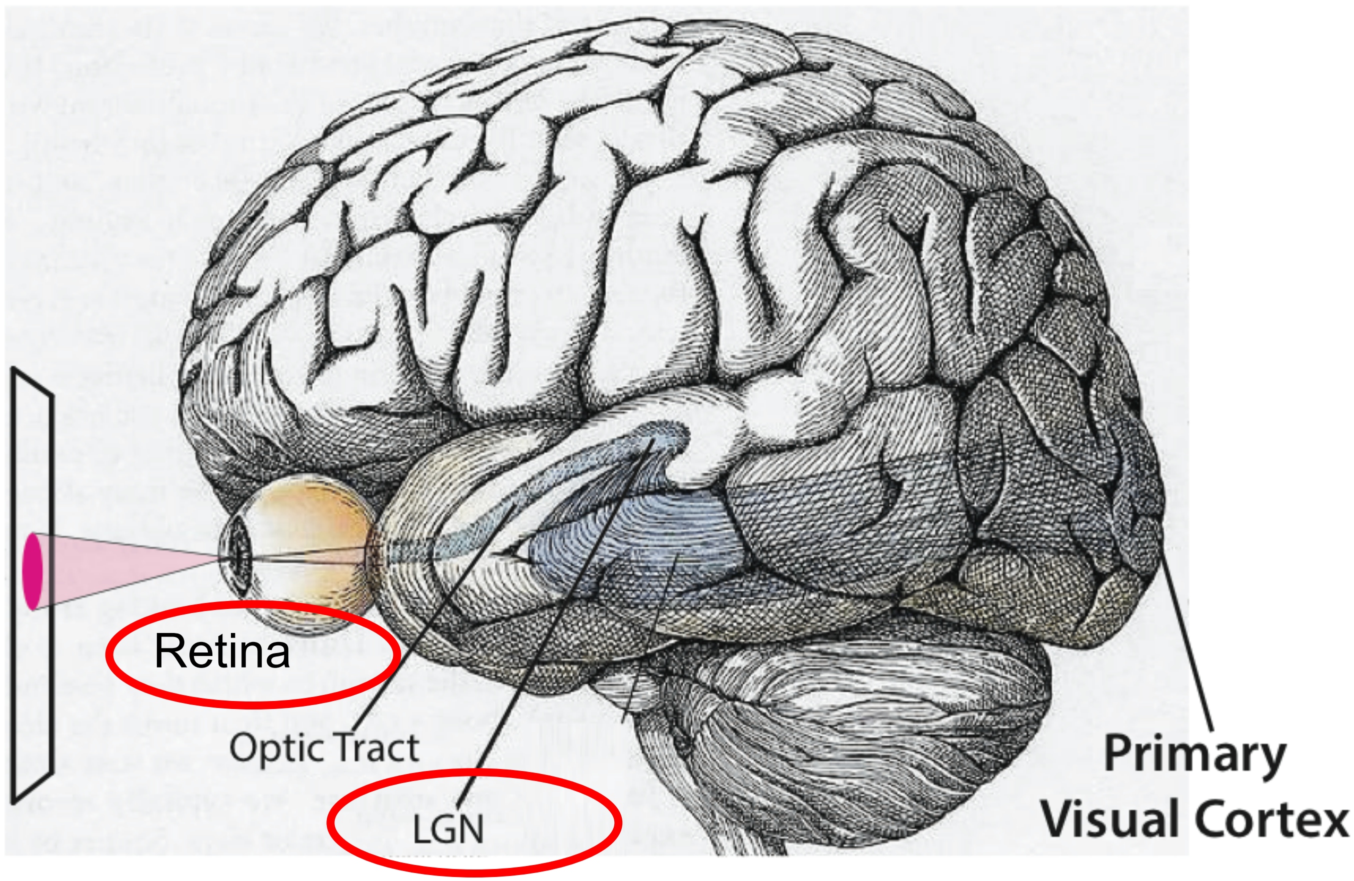
- The only important characteristic of the spike train is the mean firing rate

The Visual System



From Hubel

The Visual System

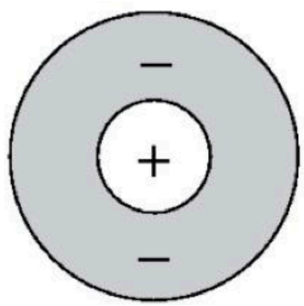


From Hubel

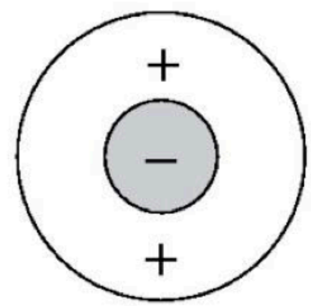
Example: Receptive fields

- Receptive fields in Retina and LGN are similar
- Shown here LGN

Example: Receptive fields retina / LGN

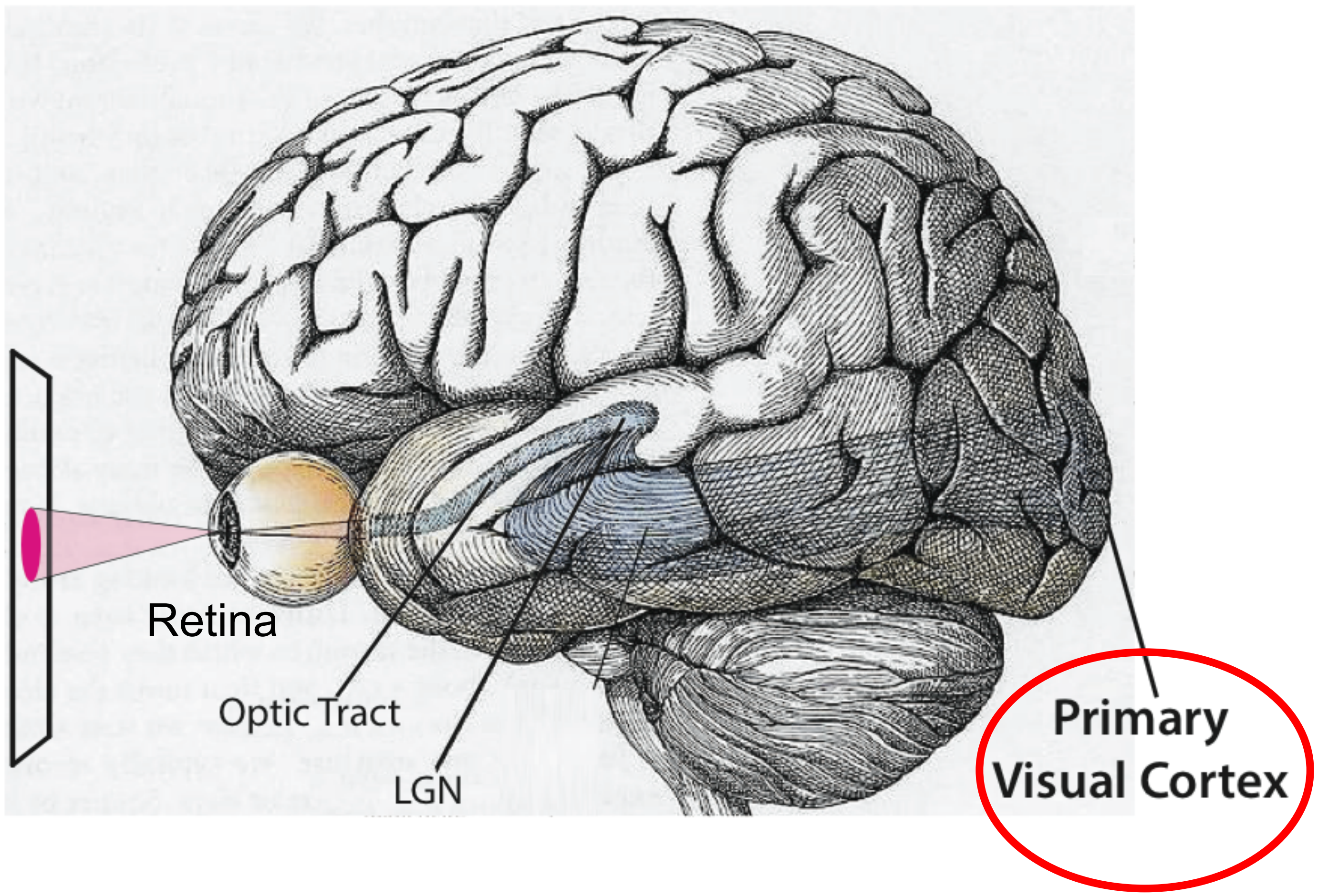


On-Center
Off-Surround
Receptive Field



Off-Center
On-Surround
Receptive Field

The Visual System



From Hubel

Neural processing

Primary visual cortex

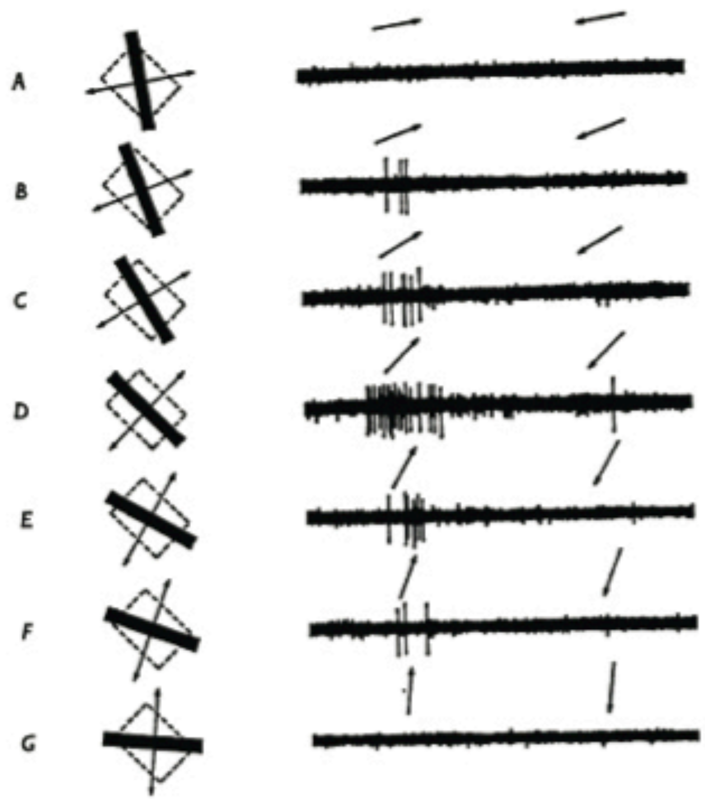
Hubel and Wiesel, 1959

Example: Receptive fields

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*



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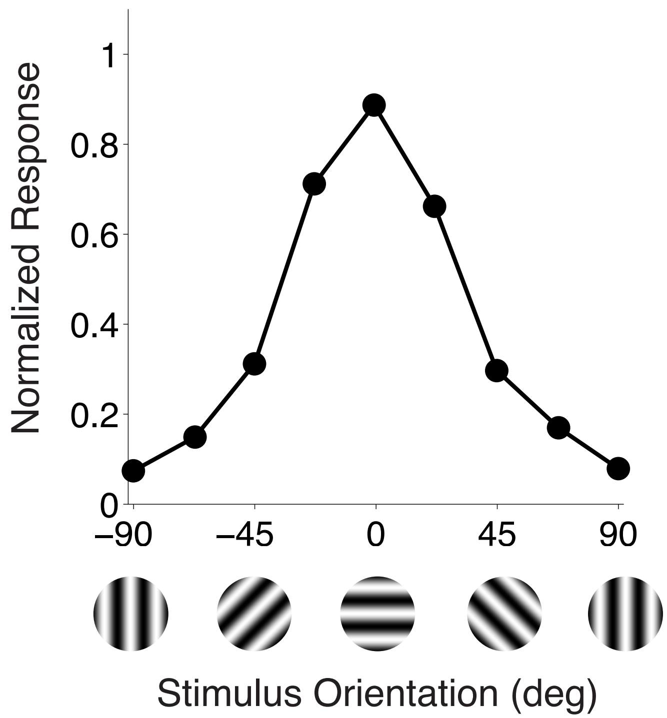


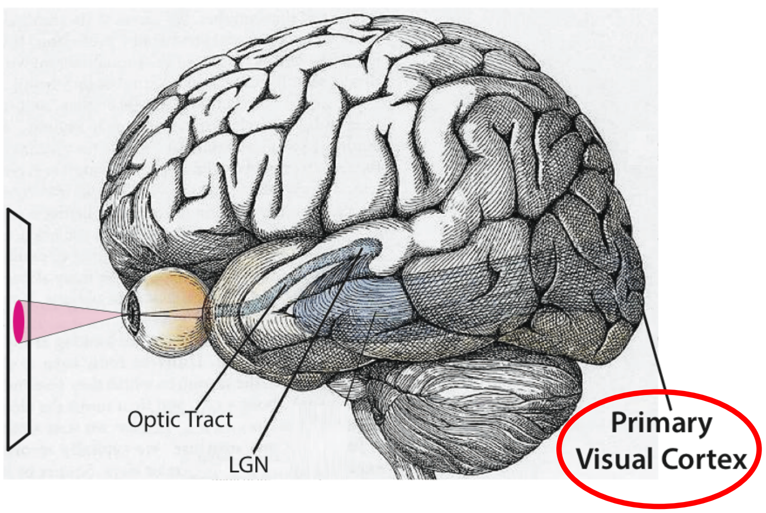
Wissig and Kohn 2012

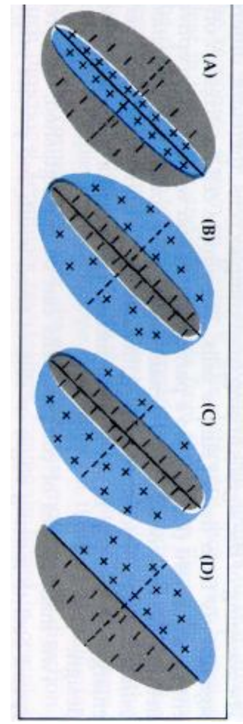
Receptive fields

Classical definition: A region of the visual field that must be Stimulated directly in order to obtain a response from a neuron.

Modern / Computer Science / engineering: filter that captures those attributes of the stimulus that generate responses.
Often assumed linear.

Example: Receptive fields V1



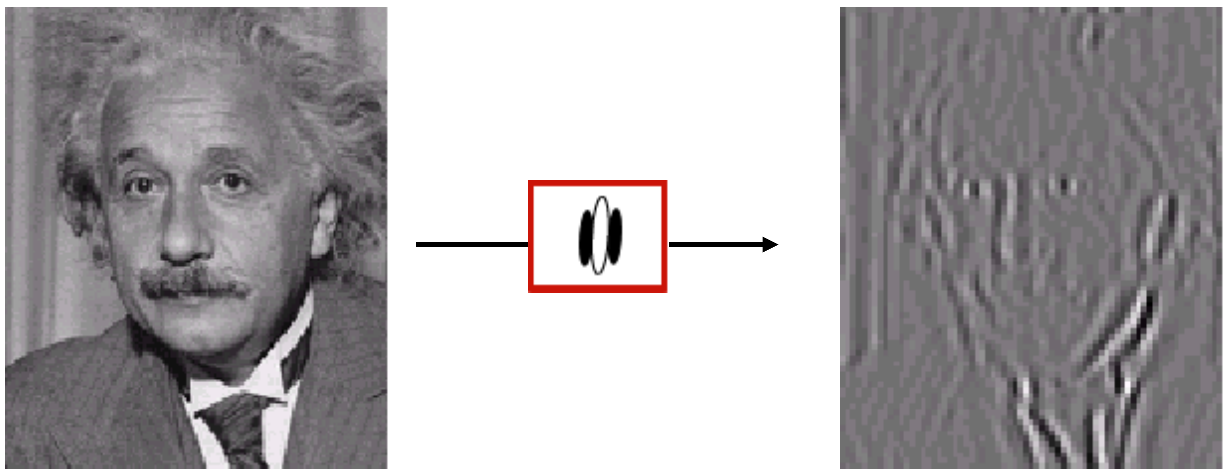


(From Nicholls et al., 1992)

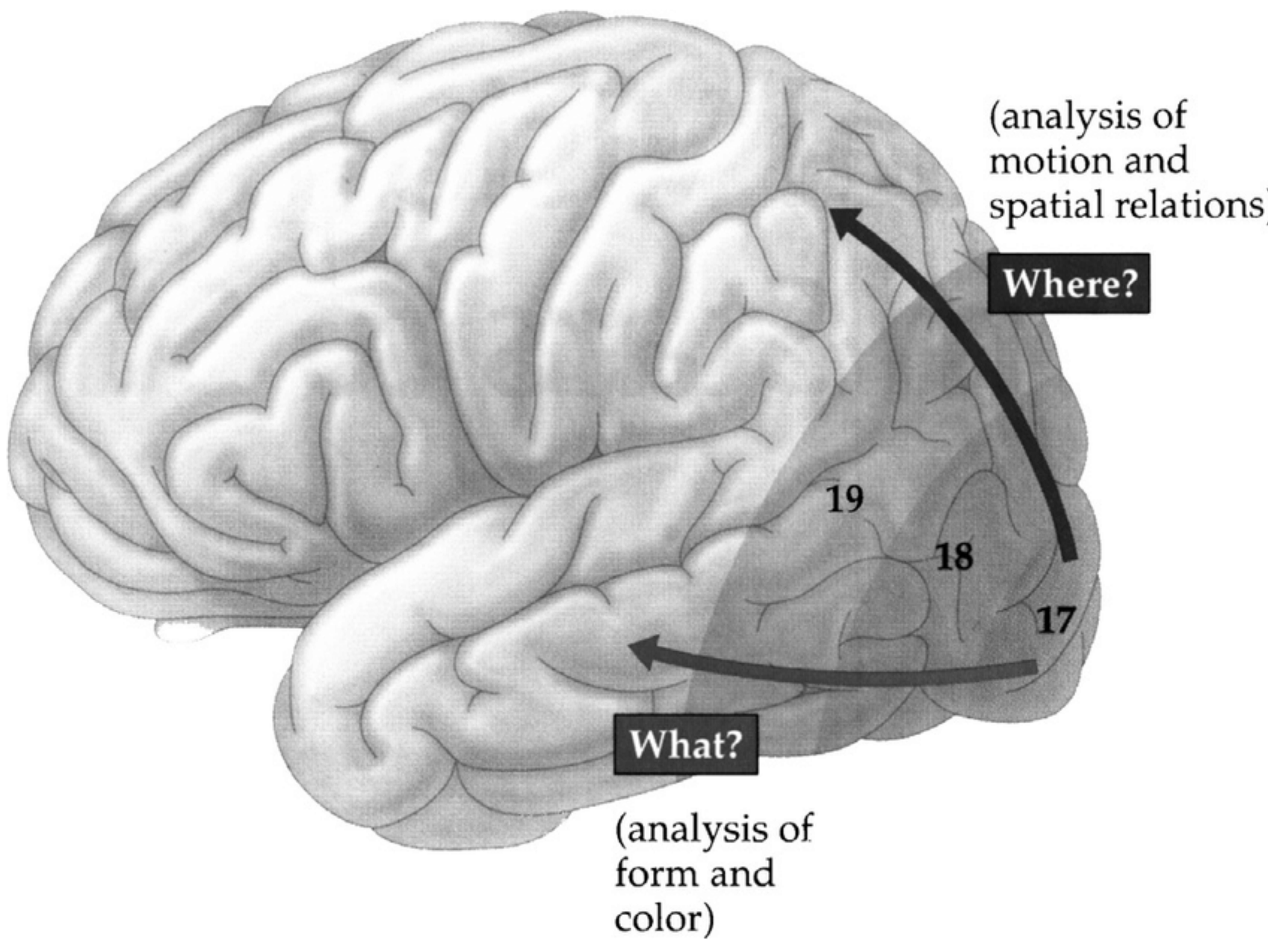
Examples of receptive fields in primary visual cortex (V1)

Computer science / engineering

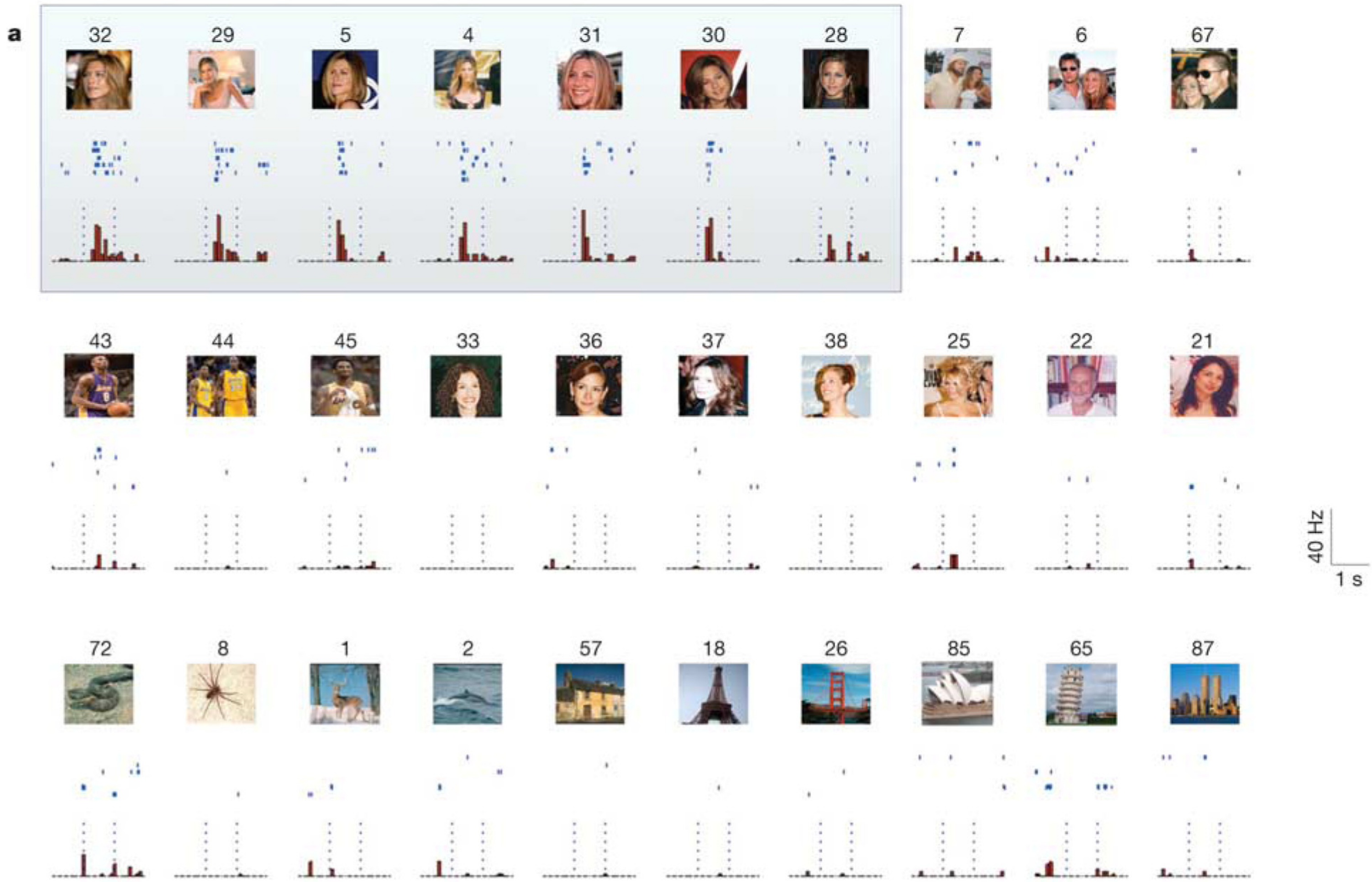
Visual receptive field or filter!



The Visual System

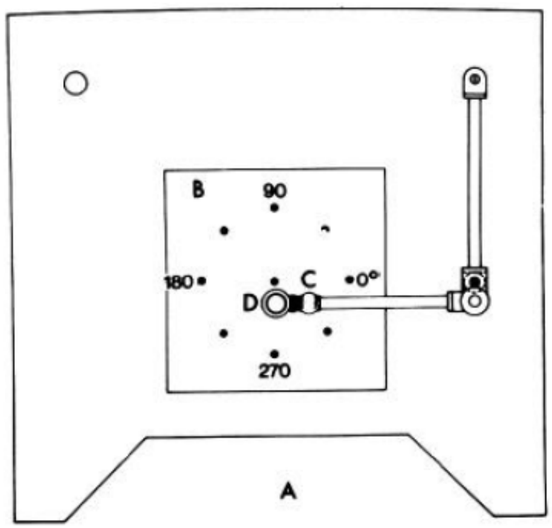


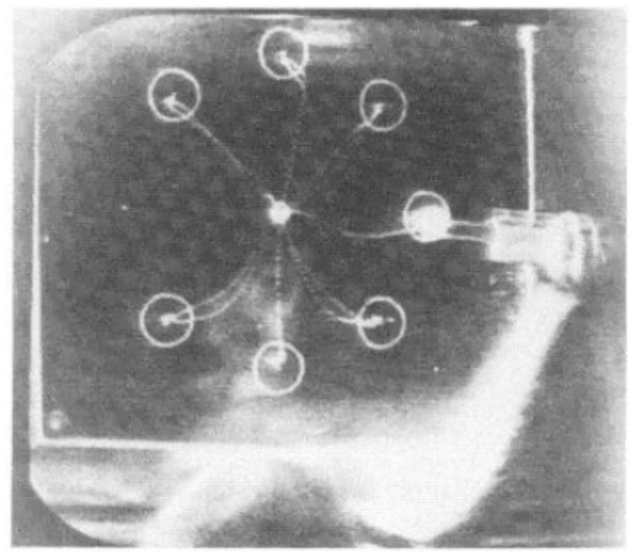
Rate codes: example 2



- Quiroga et al. 2005 (Nature)

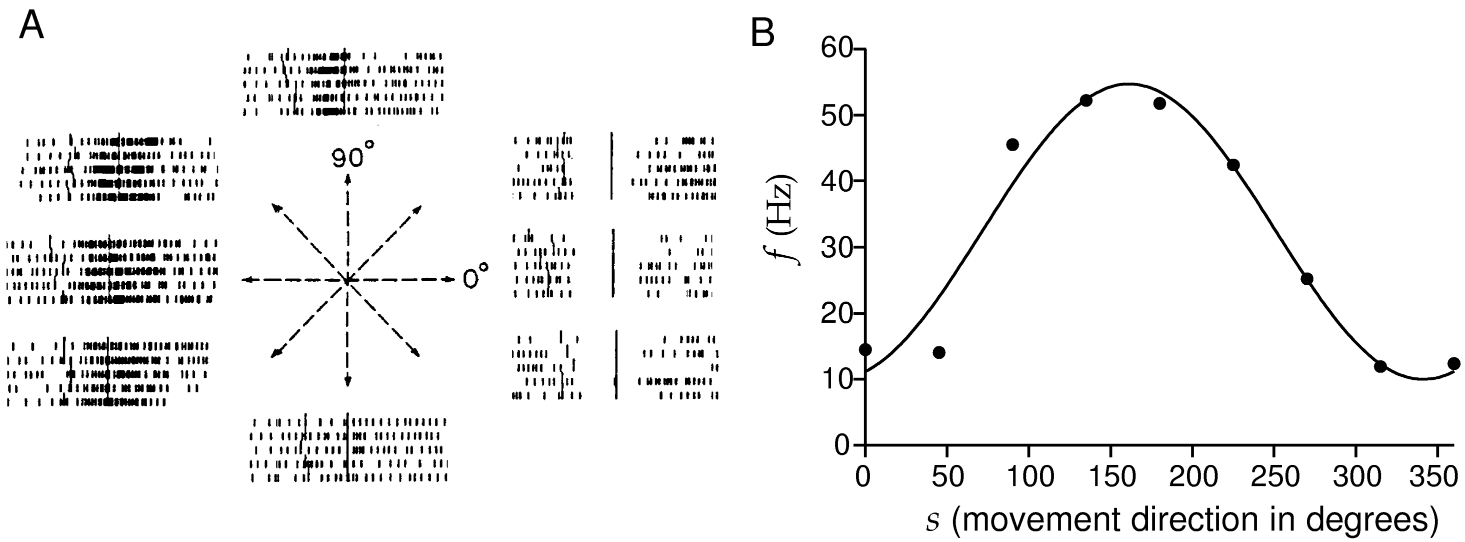
Rate codes: example 3: Motor cortex





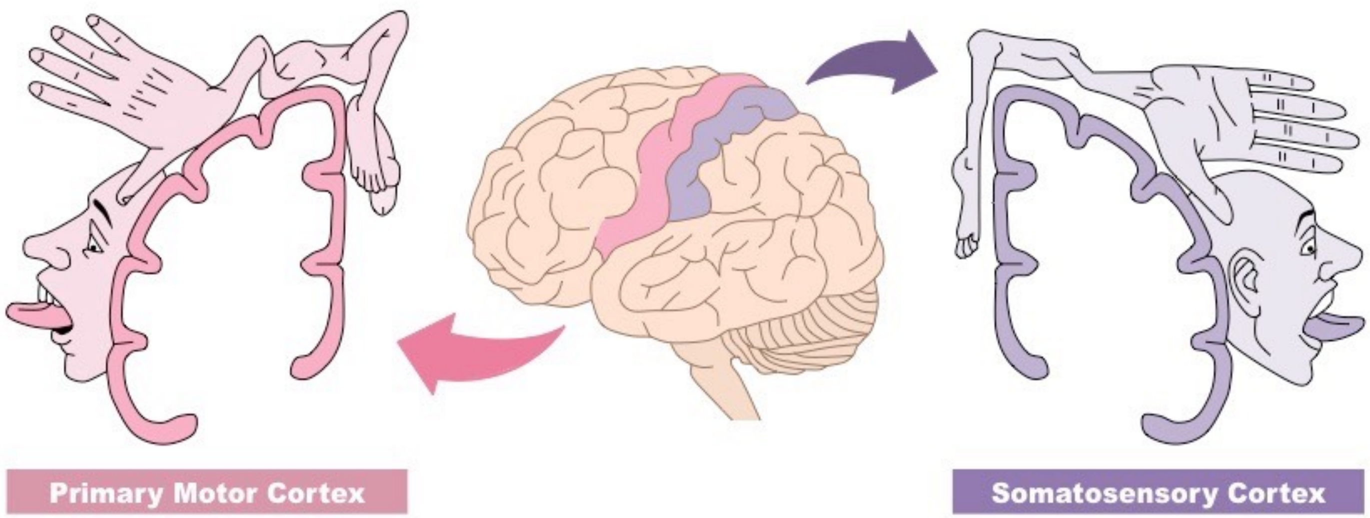
• adapted from Georgopoulos et al. 1982

Rate codes: example 3: Motor cortex



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

Motor and Somatosensory Cortex



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Rate codes

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

- What other codes?

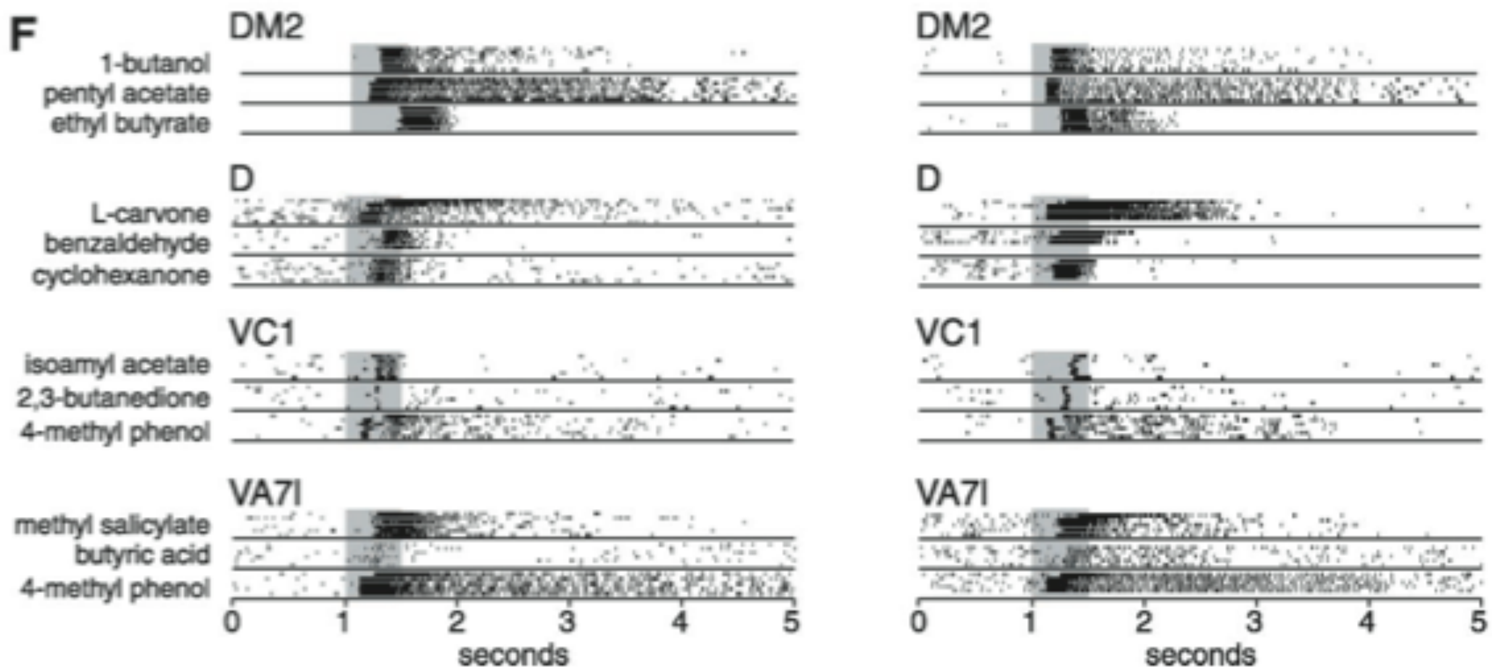
Rate codes

- 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

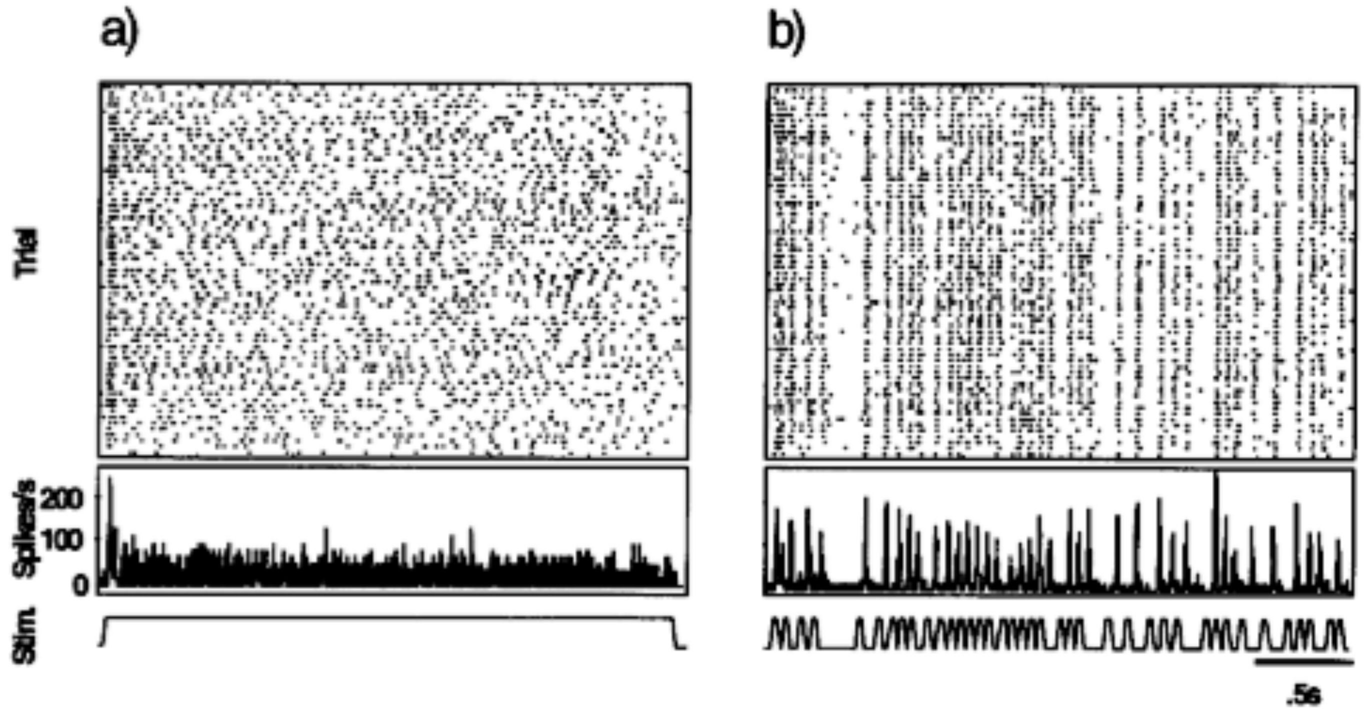
Temporal codes

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

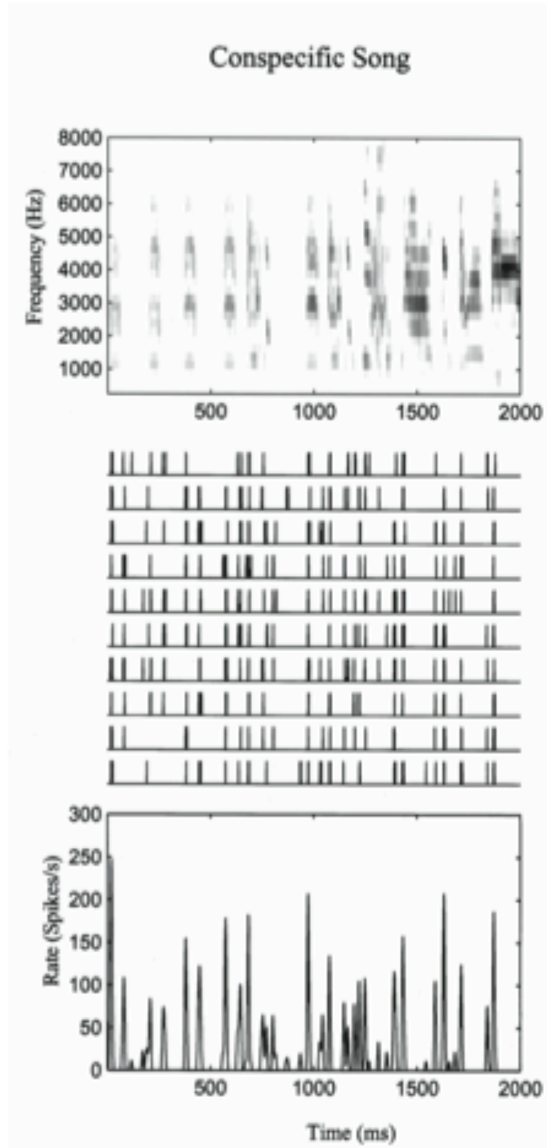
• Stimuli that change quickly typically generate rapidly changing firing rates regardless of coding strategy



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

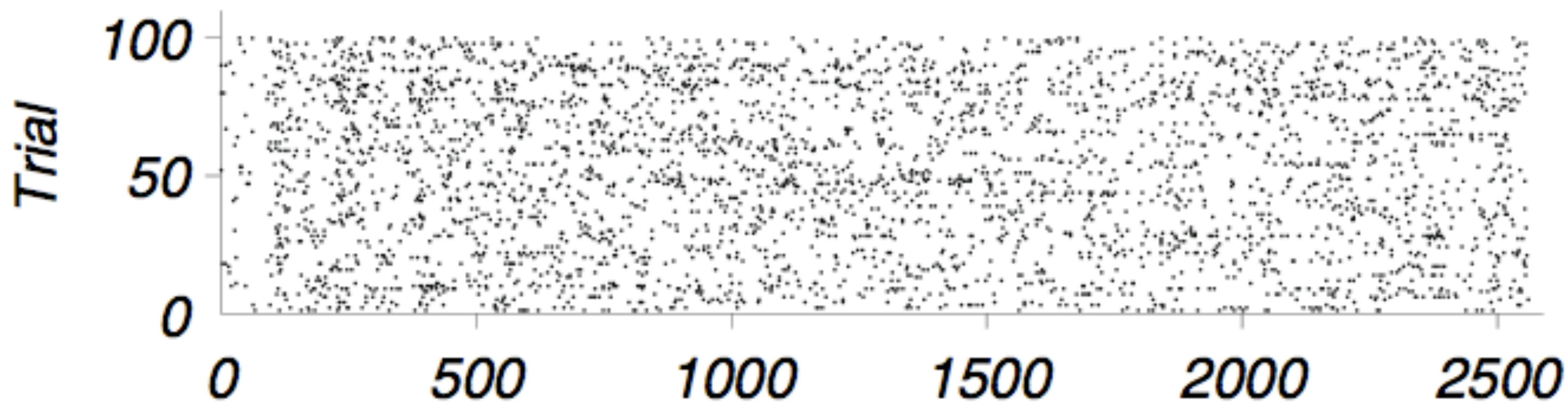
- Stimuli that change quickly typically generate rapidly changing firing rates regardless of coding strategy

- 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

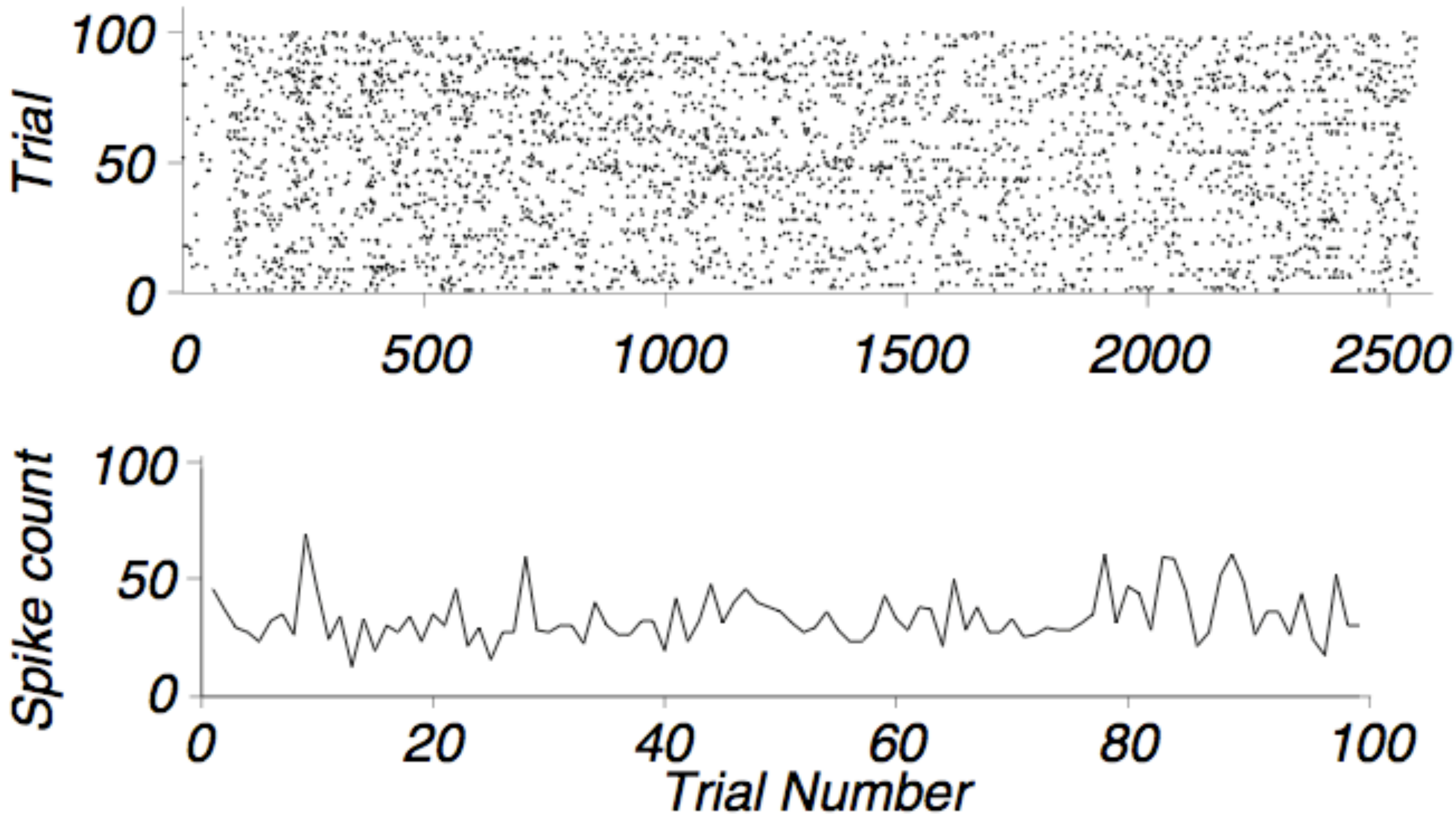
Neuronal responses are "noisy"



Spike trains for same stimulus presented many times…

Problems for both rate and temporal codes

Neuronal responses are "noisy"

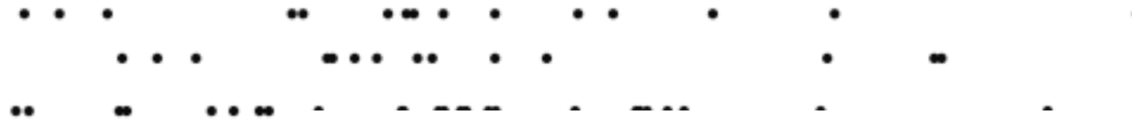


Noise in temporal codes

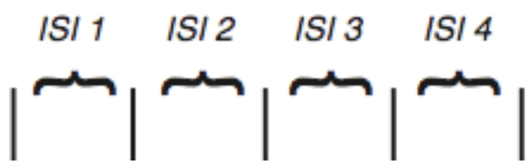
Difficult to measure:

Noise in temporal codes

Difficult to measure:



Measure of spike train regularity

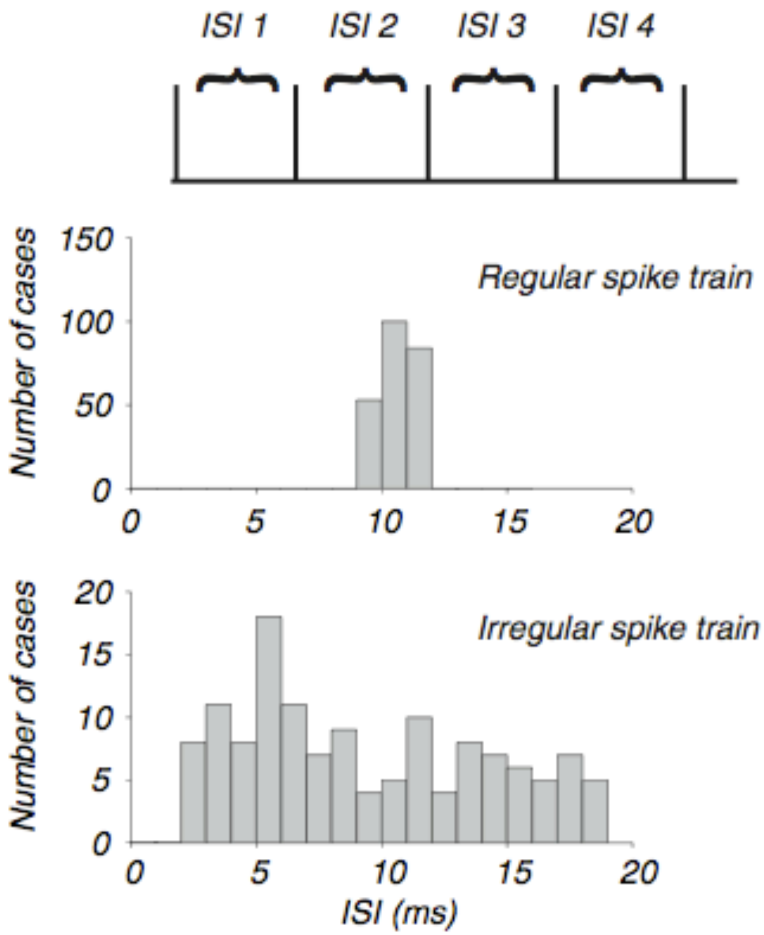


Victor JD (2005) Curr Opin Neurobiol 15: 585-92

Noise in temporal codes

Difficult to measure:

Measure of spike train regularity



Interval between spikes always around 10 milliseconds

Interval between spikes variable

Noise in temporal codes

Difficult to measure:

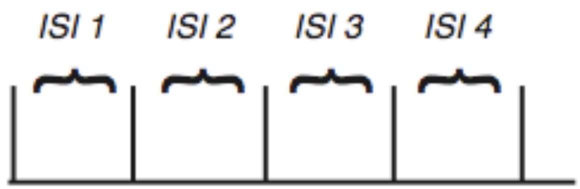
Measure of pattern repeatability: Cost-based metric for transforming one spike train to another

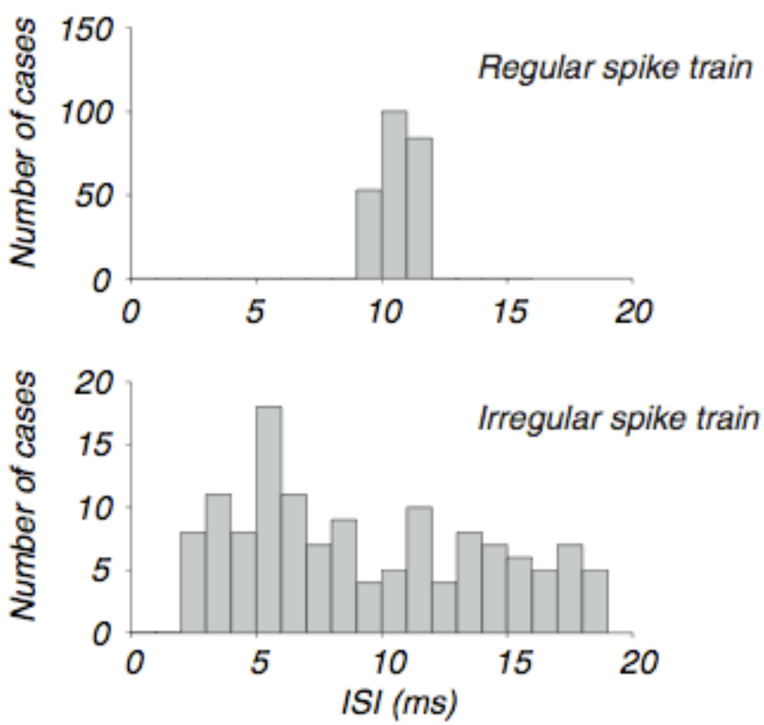
Victor JD (2005) Curr Opin Neurobiol. 15: 585-92.

Noise in temporal codes

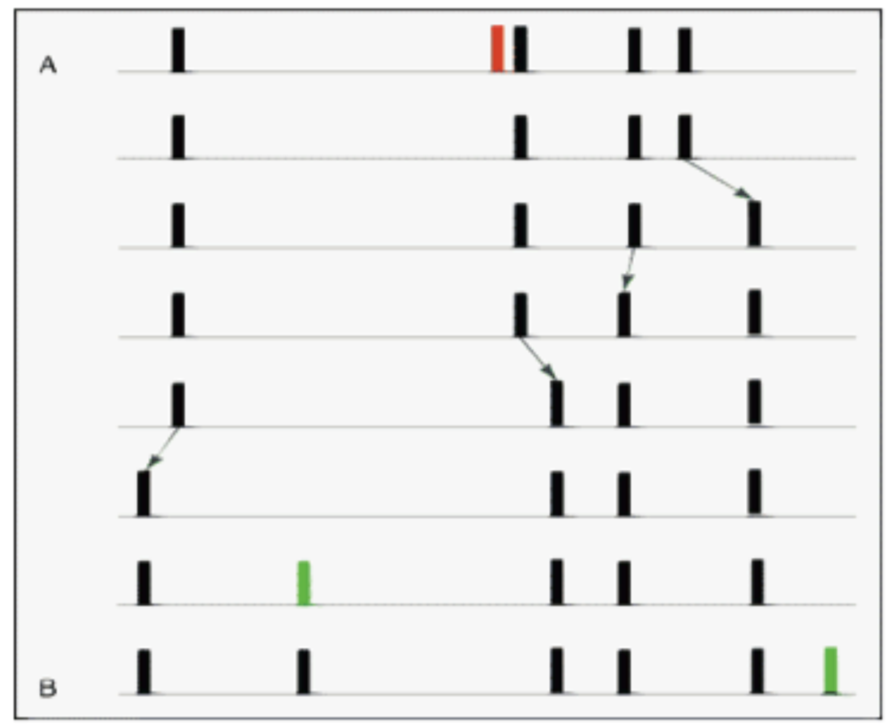
Difficult to measure:

Measure of spike train regularity





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



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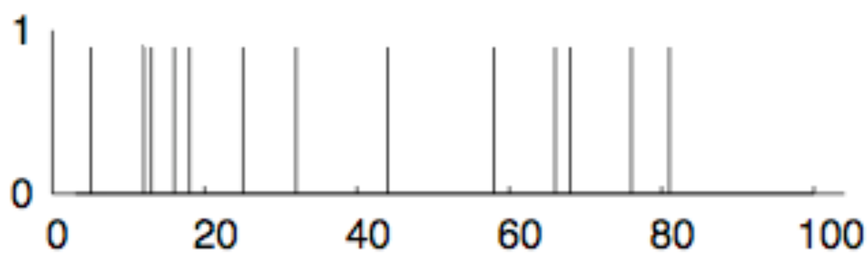
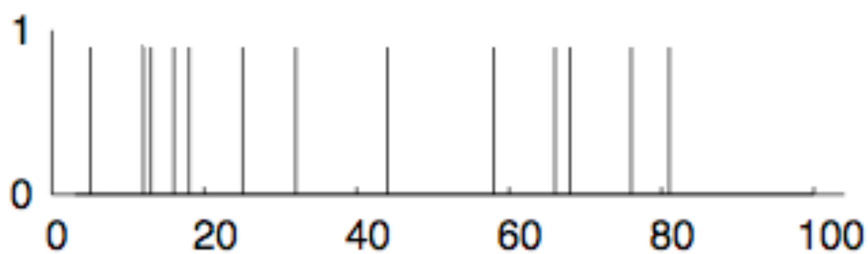
Poisson spike trains

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

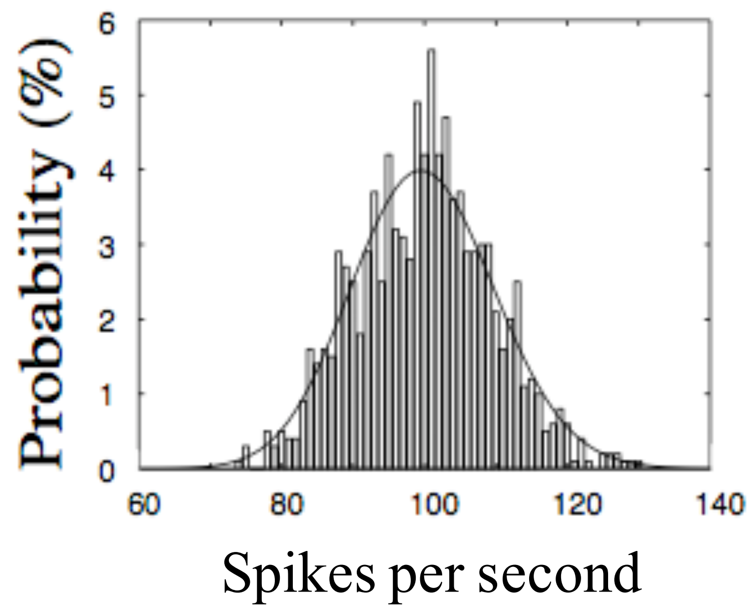
Process is defined ***by a single parameter—firing rate****. The probability of a spike in any time interval is a random event (and independent of previous spikes)*



Poisson spike trains

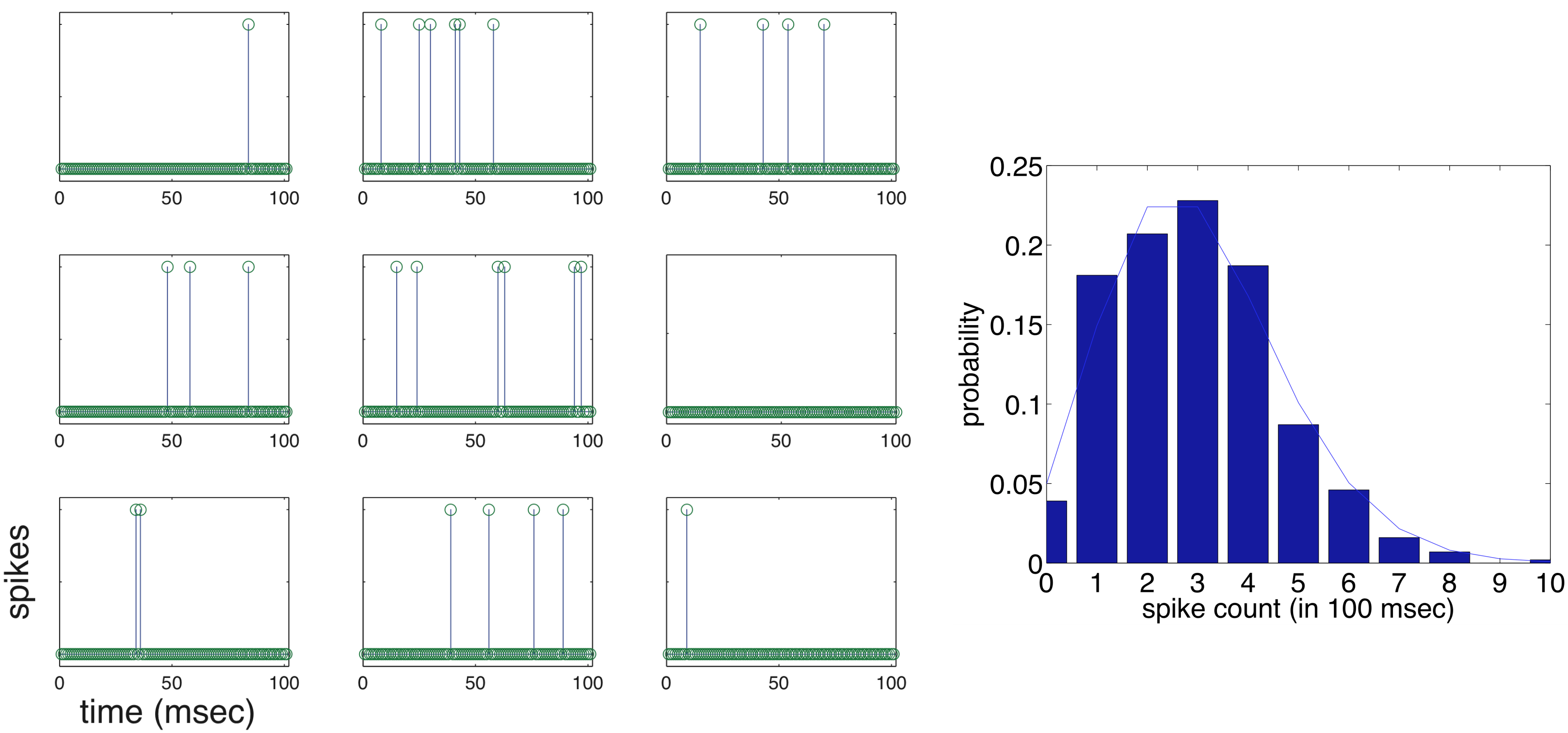


100 milliseconds



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

Poisson spike trains



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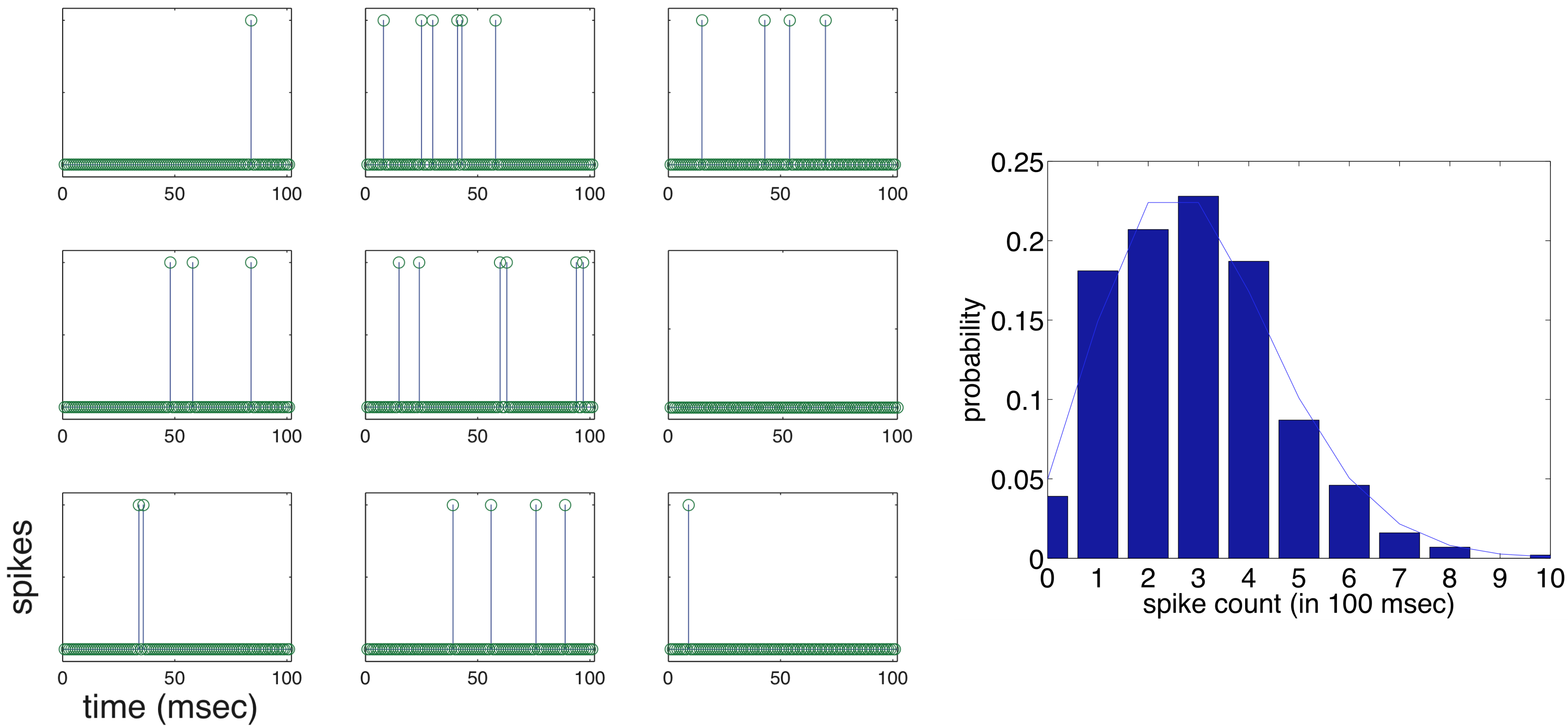
Poisson spike trains



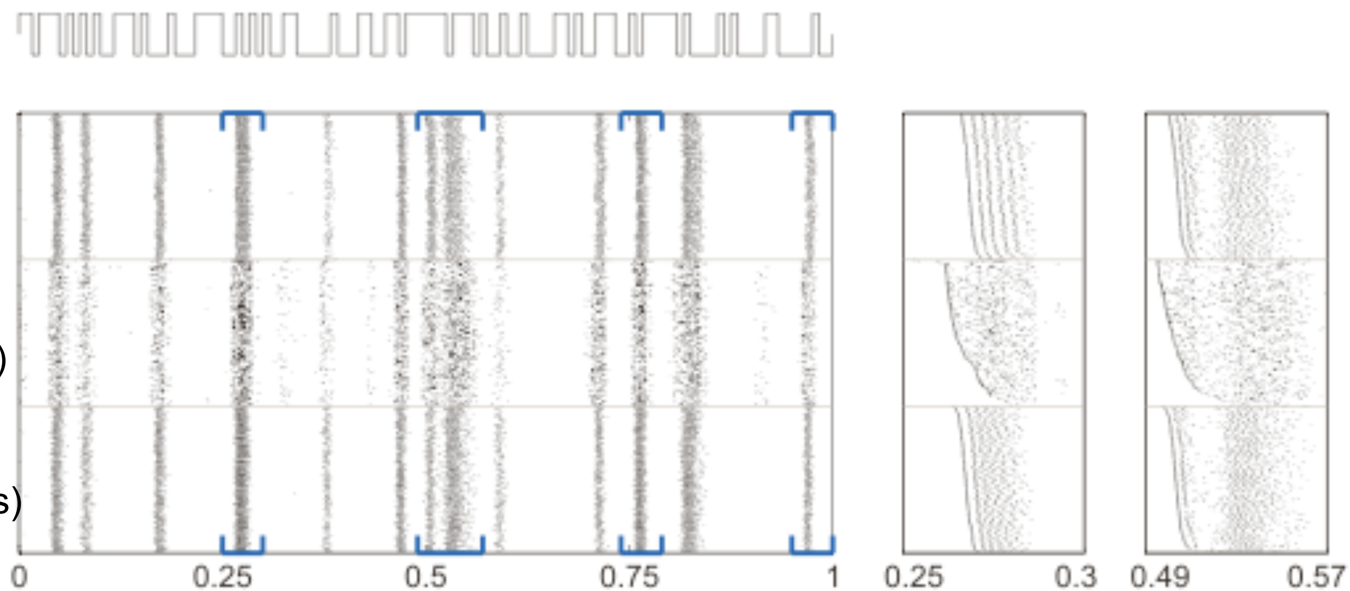
We'll generate Poisson spikes
in the computer lab…

Less variability than Poisson

RGC cells

Poisson model
(independent spikes)

IF model
(spike history matters)



Retinal Ganglion Cells, Pillow et al., 2006

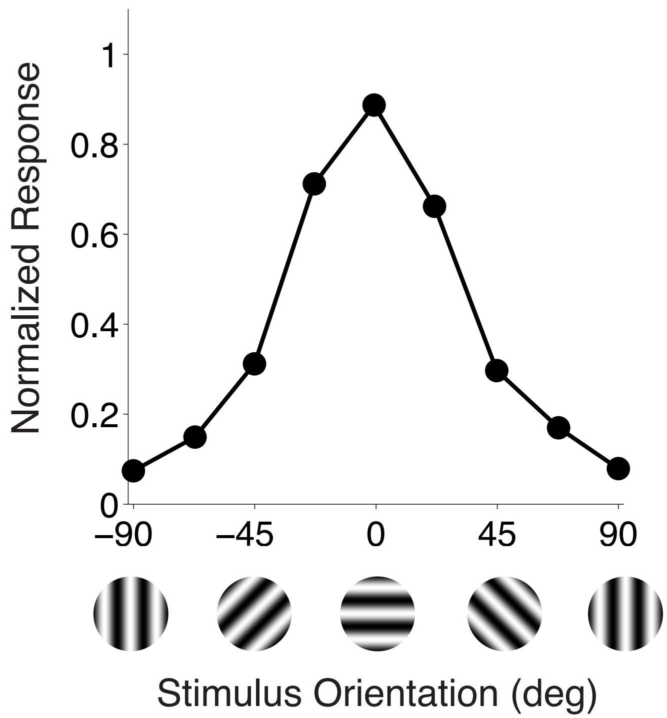
Summary so far…

- 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??

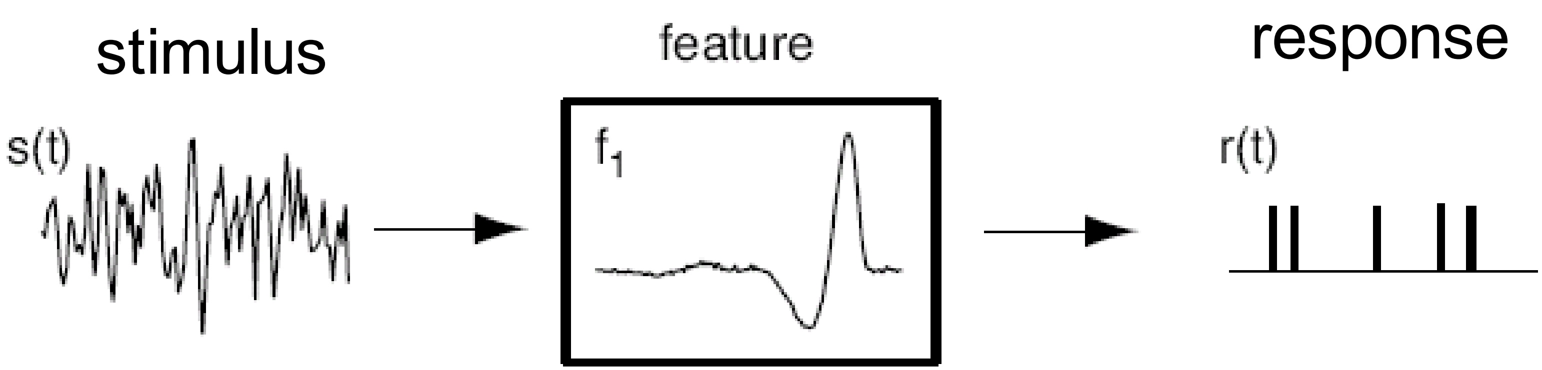
Characterizing response properties of neurons

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

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

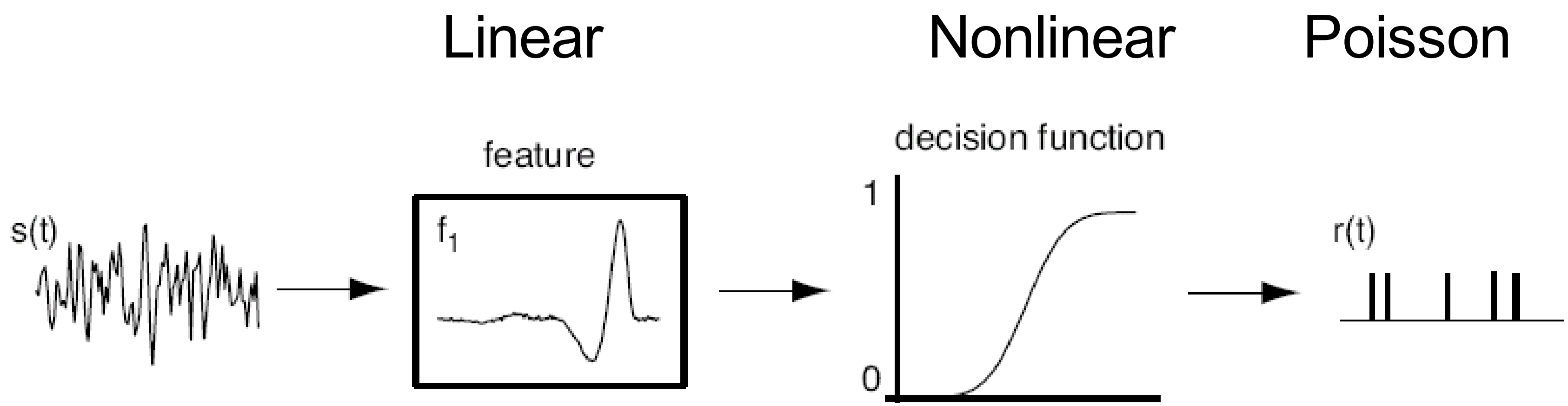
- Here we'll use a simple approach known as spike-triggered average (or reverse correlation)

Basic coding model: temporal



- This can also be seen as a descriptive model!

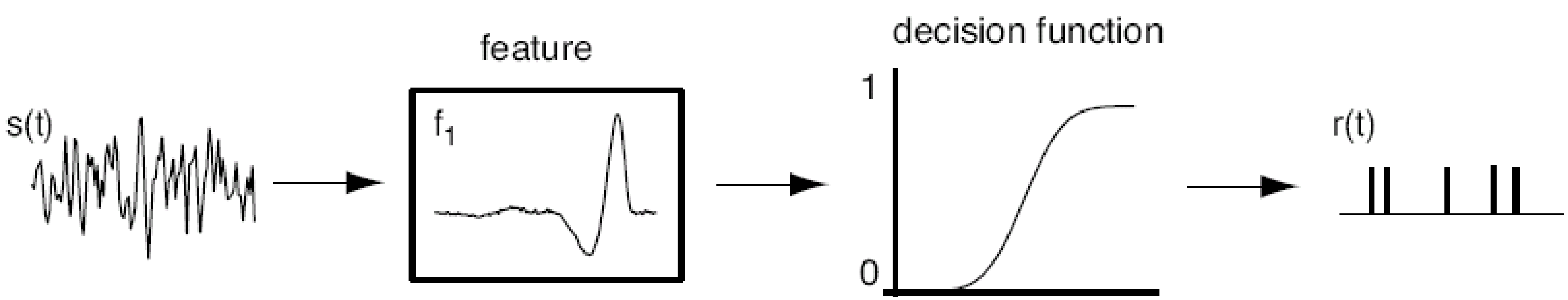
Basic coding model: temporal



- This can also be seen as a descriptive model!

Basic coding model: temporal

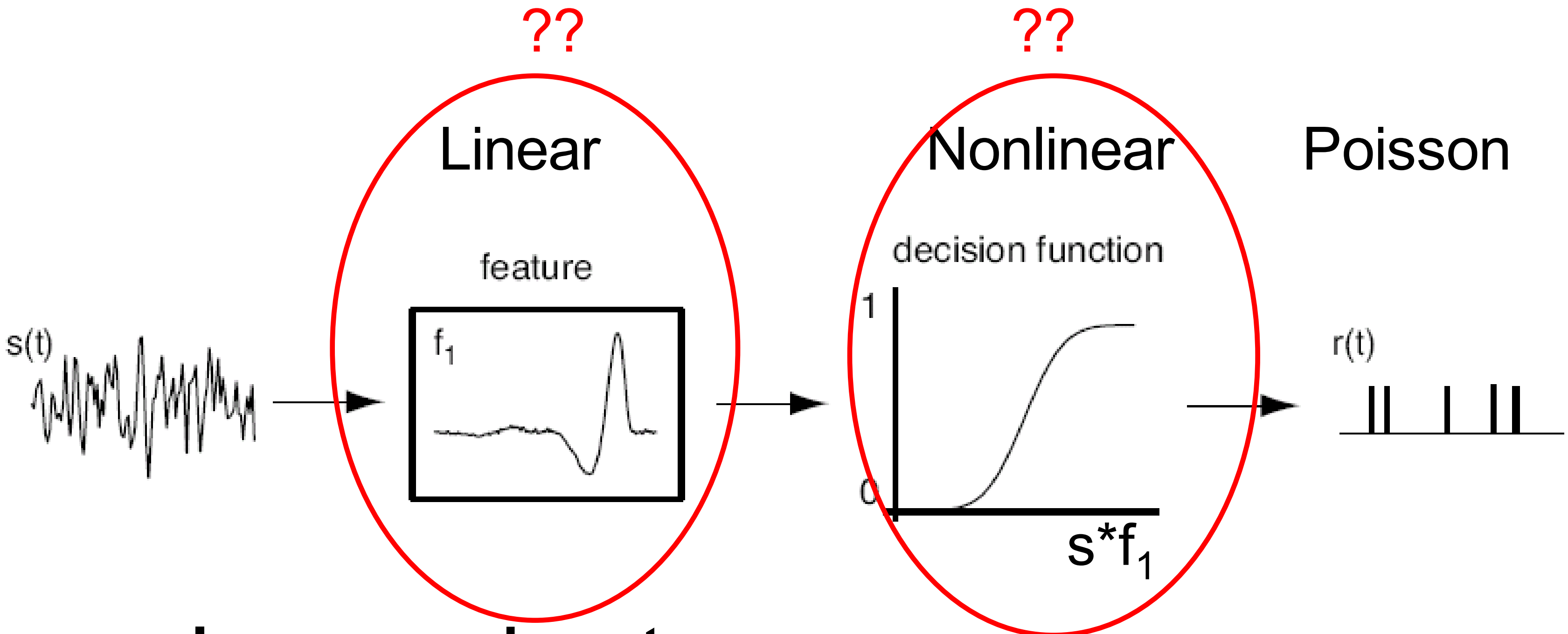
Linear Nonlinear Poisson



In an experiment:

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

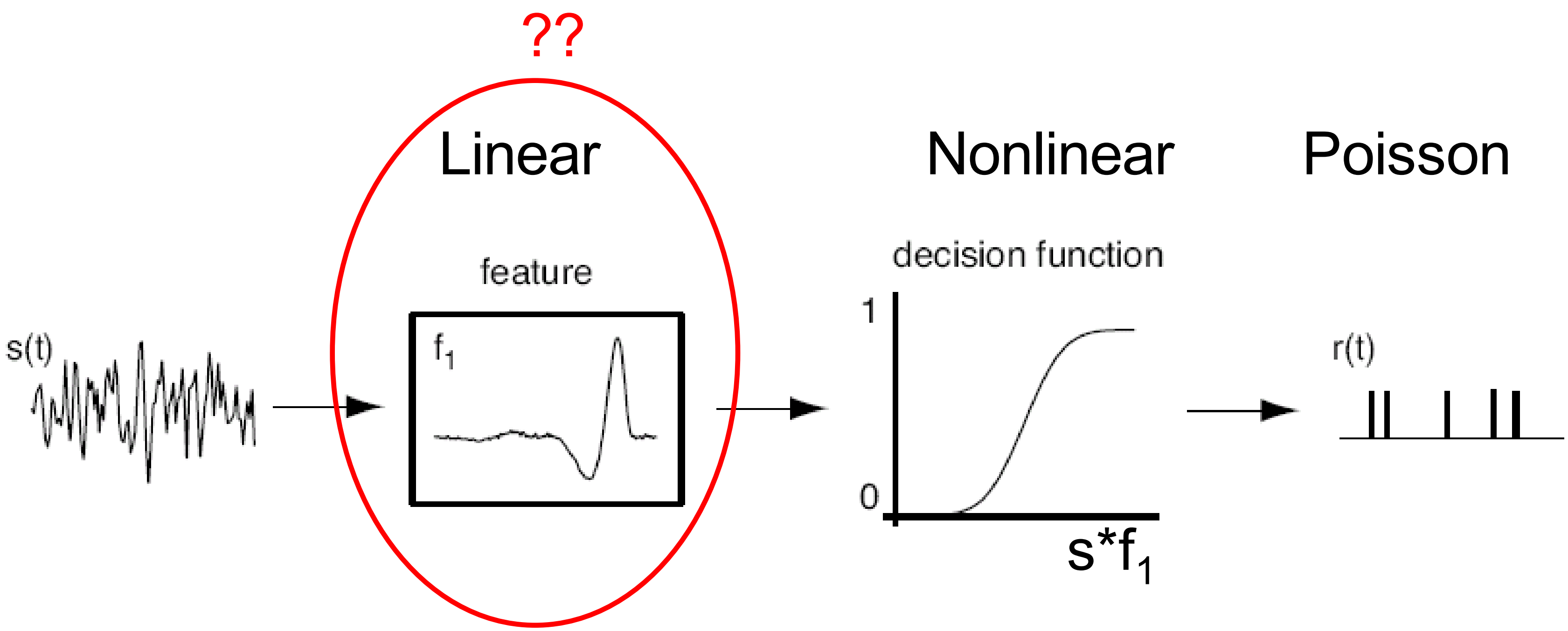
Basic coding model: temporal



In an experiment:

- We know the input stimuli
- And we measure the corresponding spike trains
- We don’t know the Linear or Nonlinear boxes!

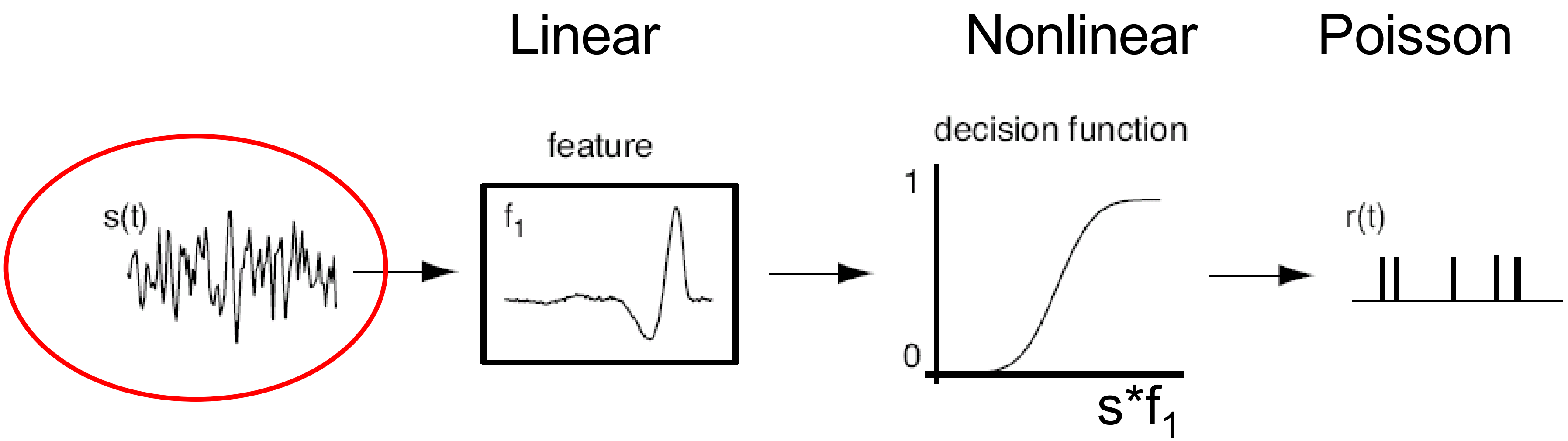
Basic coding model: temporal



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

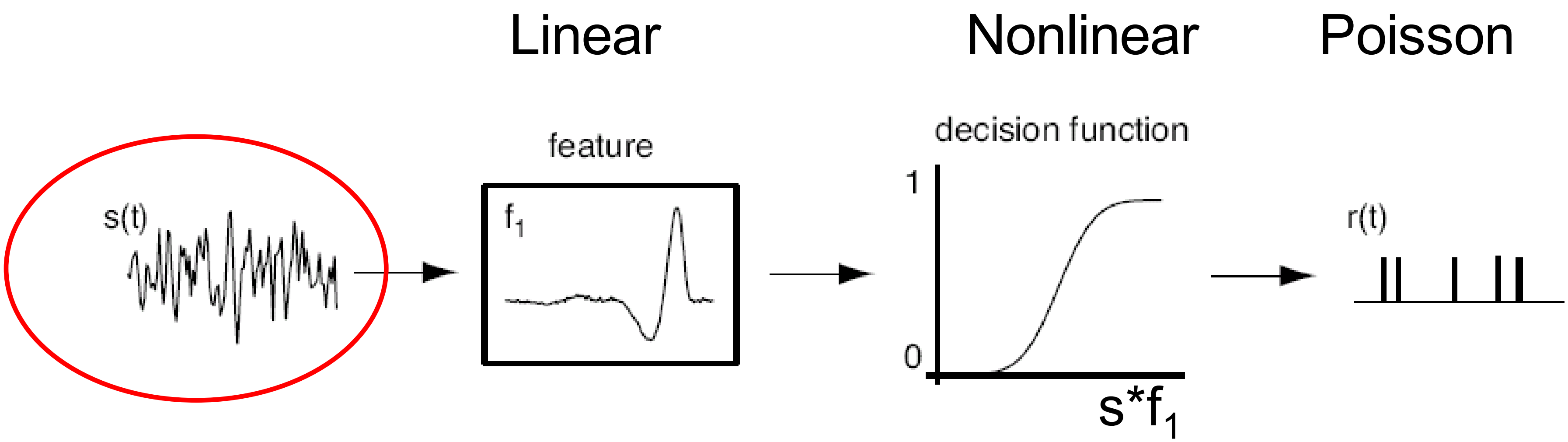


In an experiment:

- We know the input stimuli

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

Basic coding model: temporal



In an experiment:

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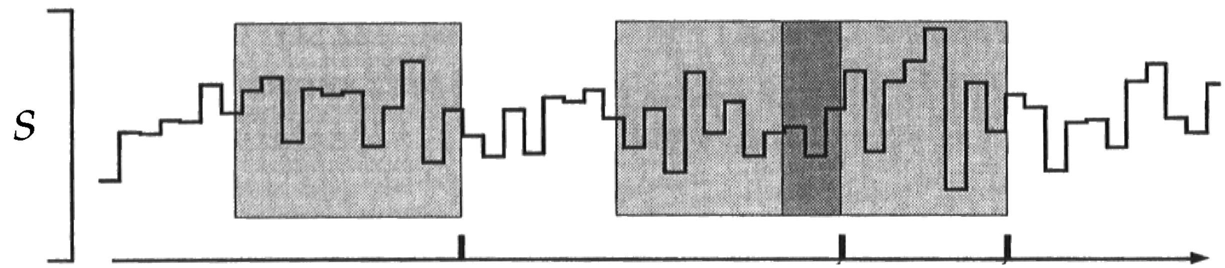
Or at least we have control over input stimuli
What stimuli should we use??? Random stimuli

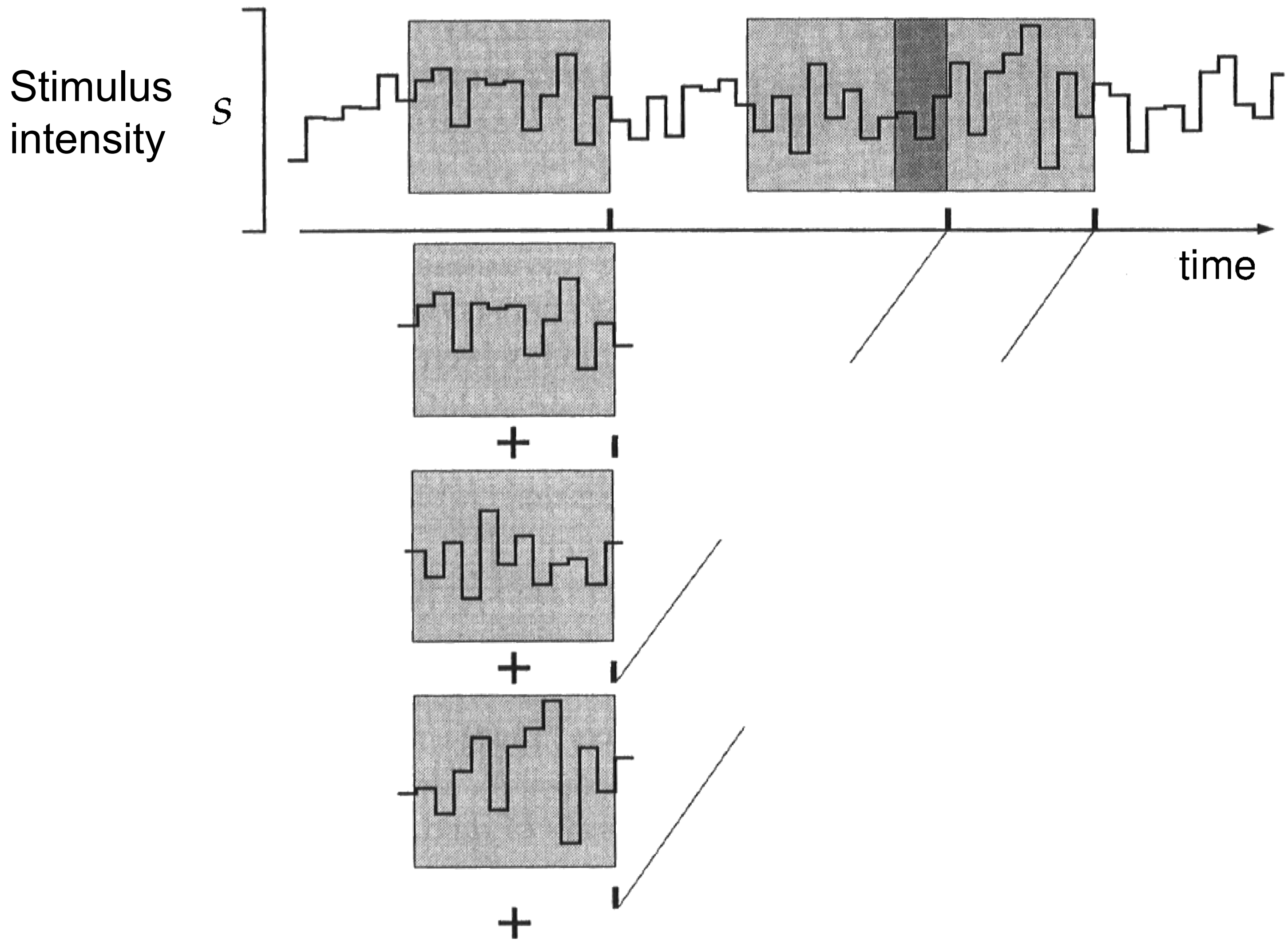
Spike-triggered Average (STA)

Stimulus
intensity



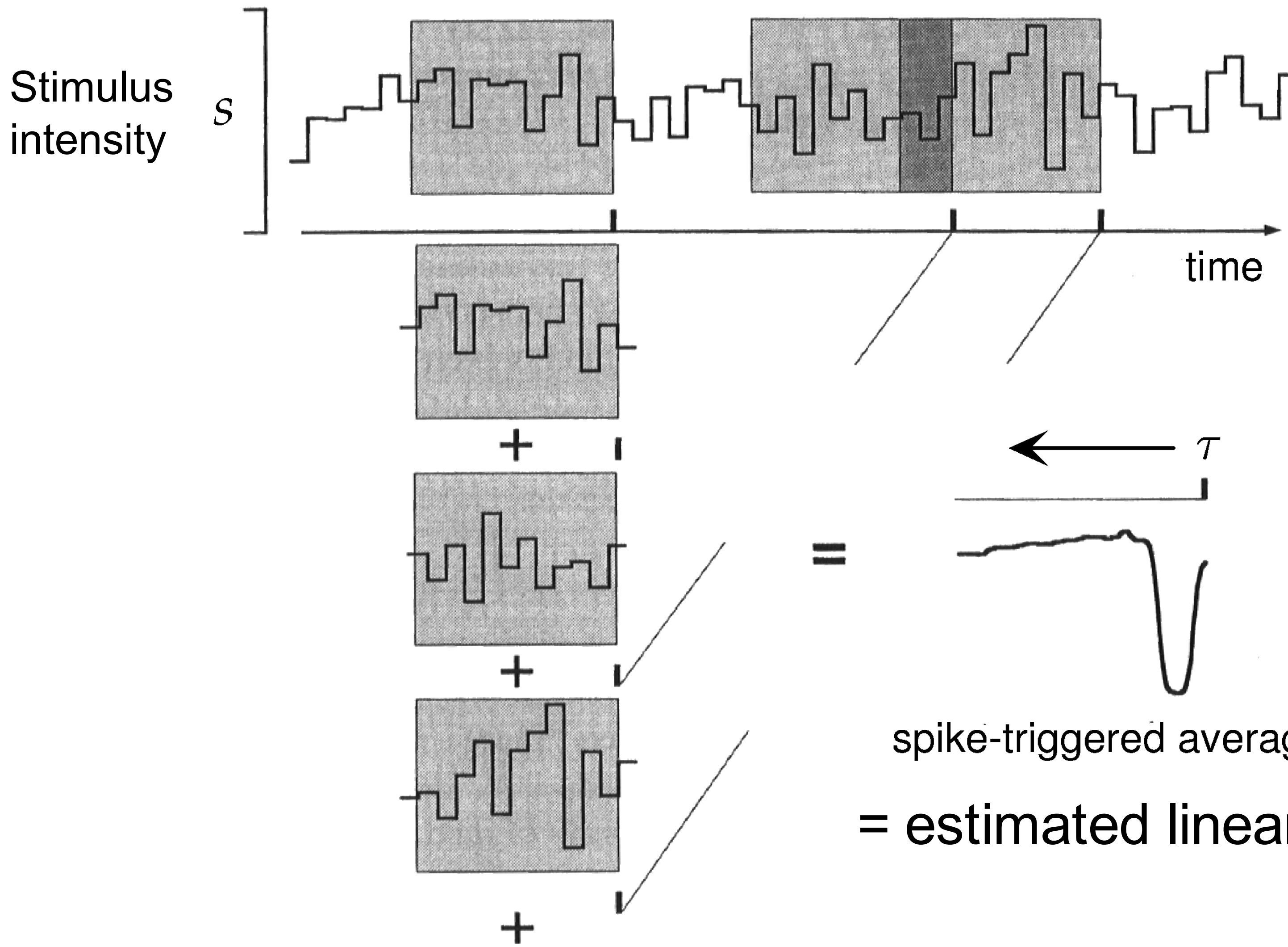
From Dayan and Abbott textbook; 2001

Spike-triggered Average (STA)



From Dayan and Abbott textbook; 2001

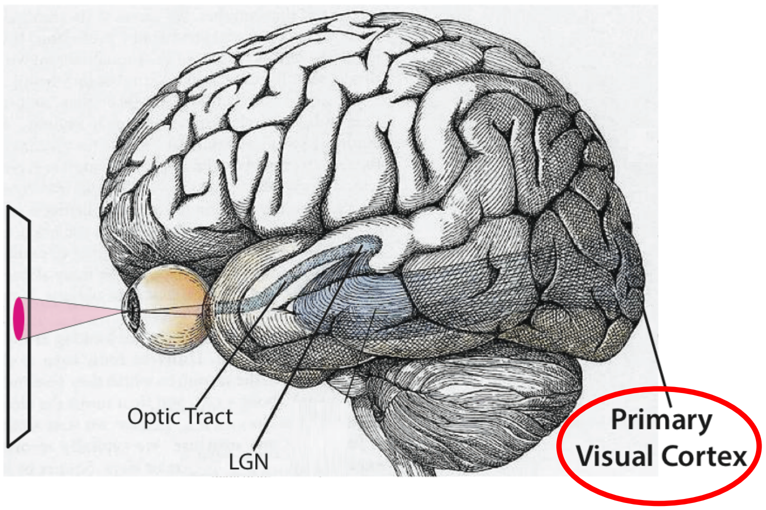
Spike-triggered Average (STA)

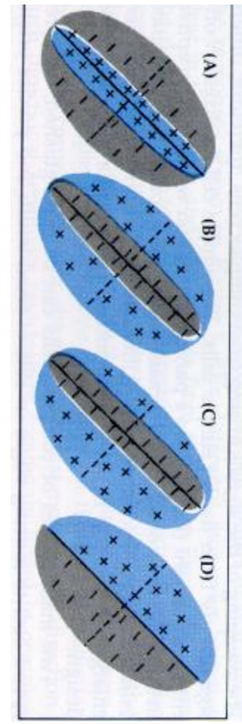


= estimated linear filter

From Dayan and Abbott textbook; 2001

Primary Visual Cortex Receptive Fields



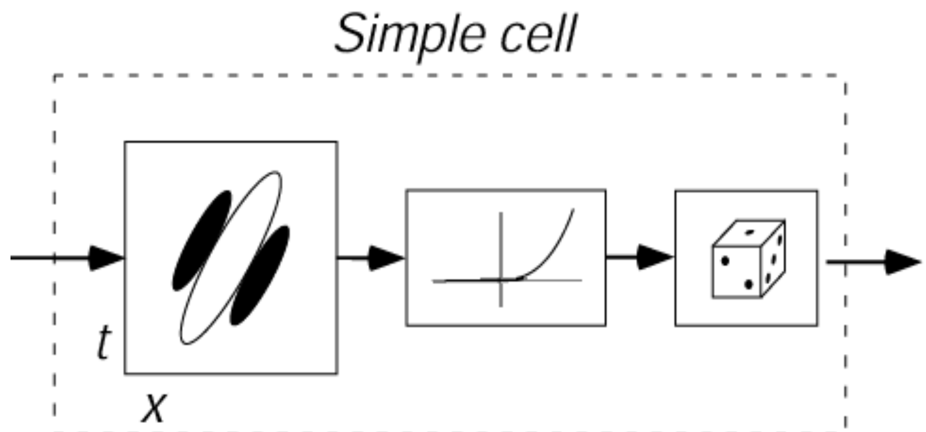


(From Nicholls et al., 1992)

Examples of receptive fields in primary visual cortex (V1)

Spike-triggered average (STA)

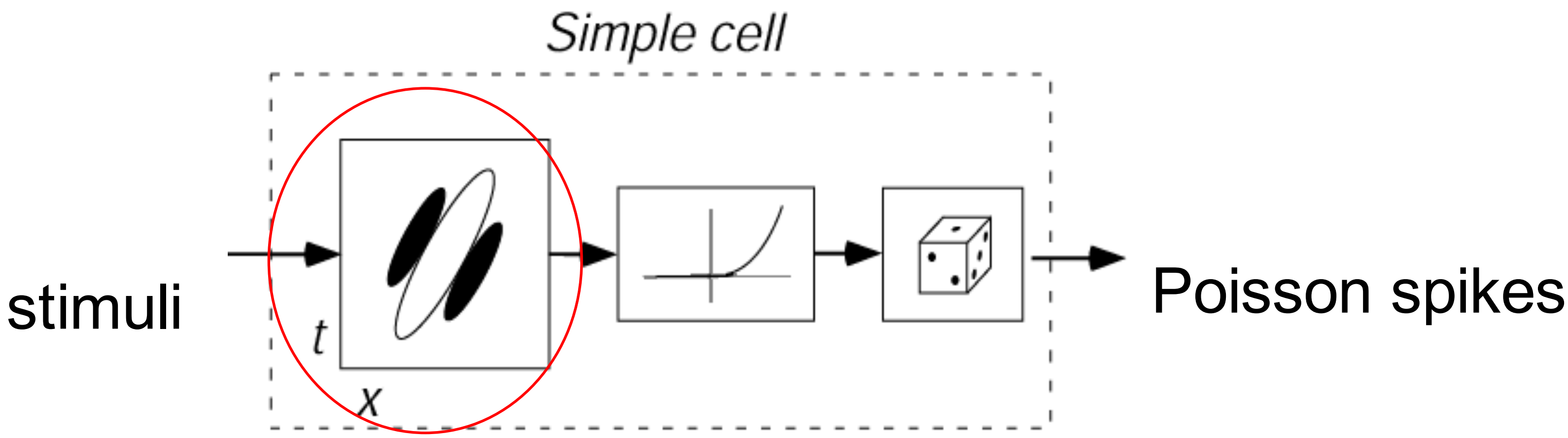
stimuli



Poisson spikes

Linear, Nonlinear, Poisson encoding model

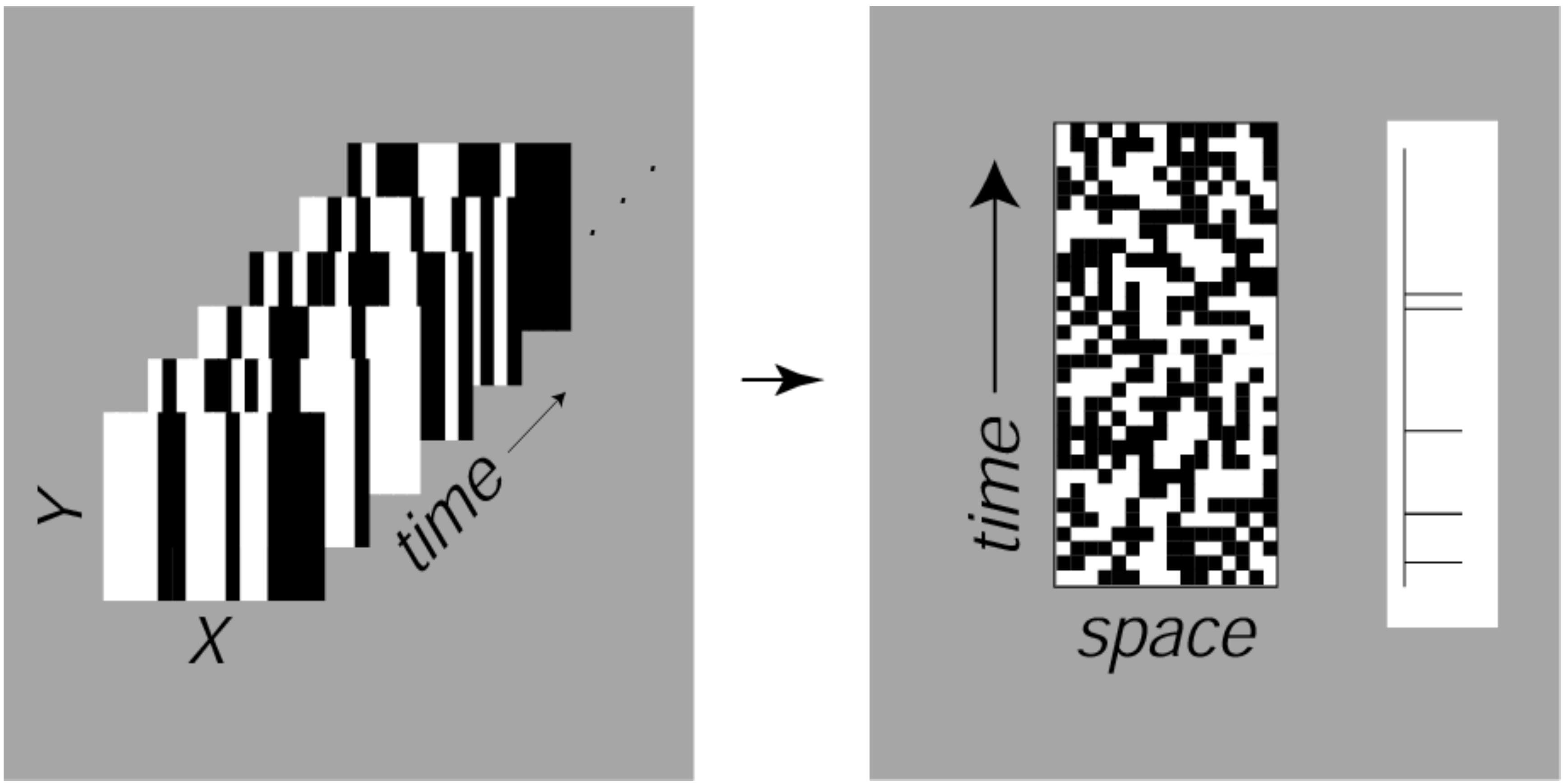
Spike-triggered average (STA)



Linear, Nonlinear, Poisson (LNP) encoding model

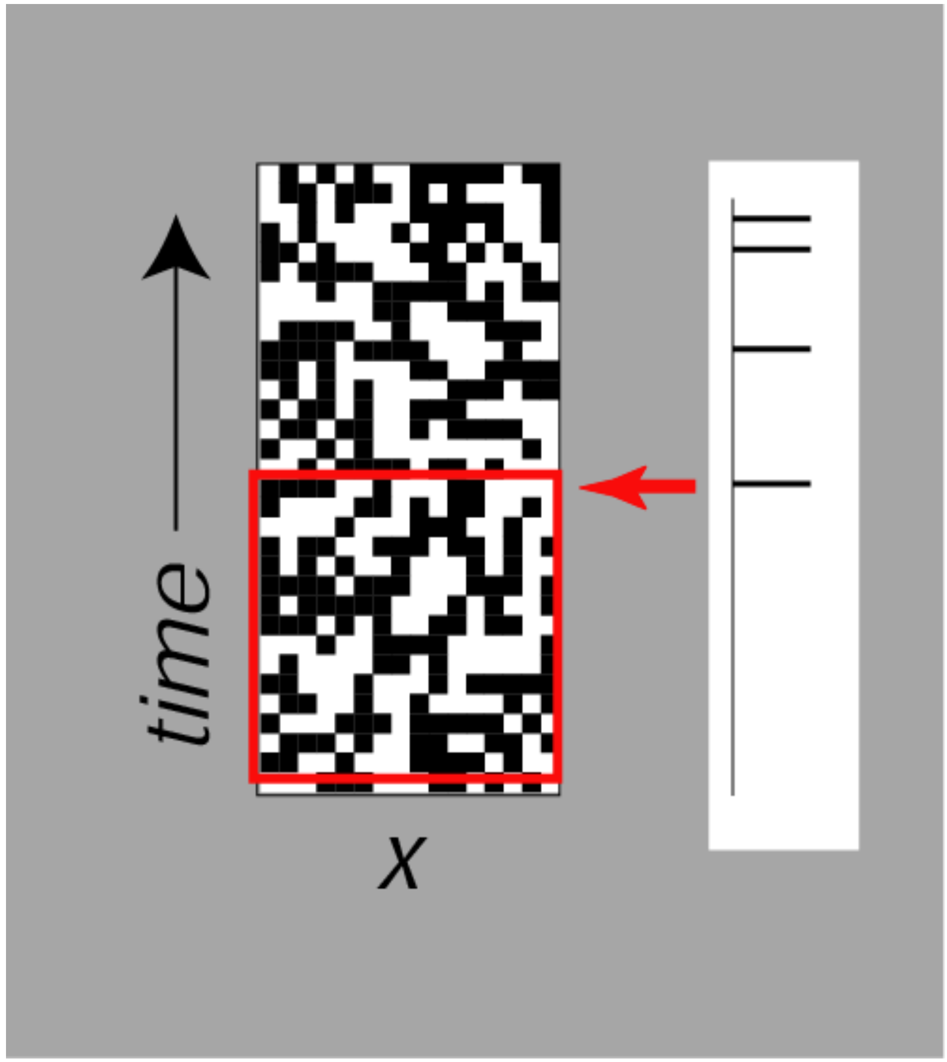
We would like to characterize the linear receptive field or filter (and the nonlinearity; later) for a neuron…

Spike-triggered Average (STA): example



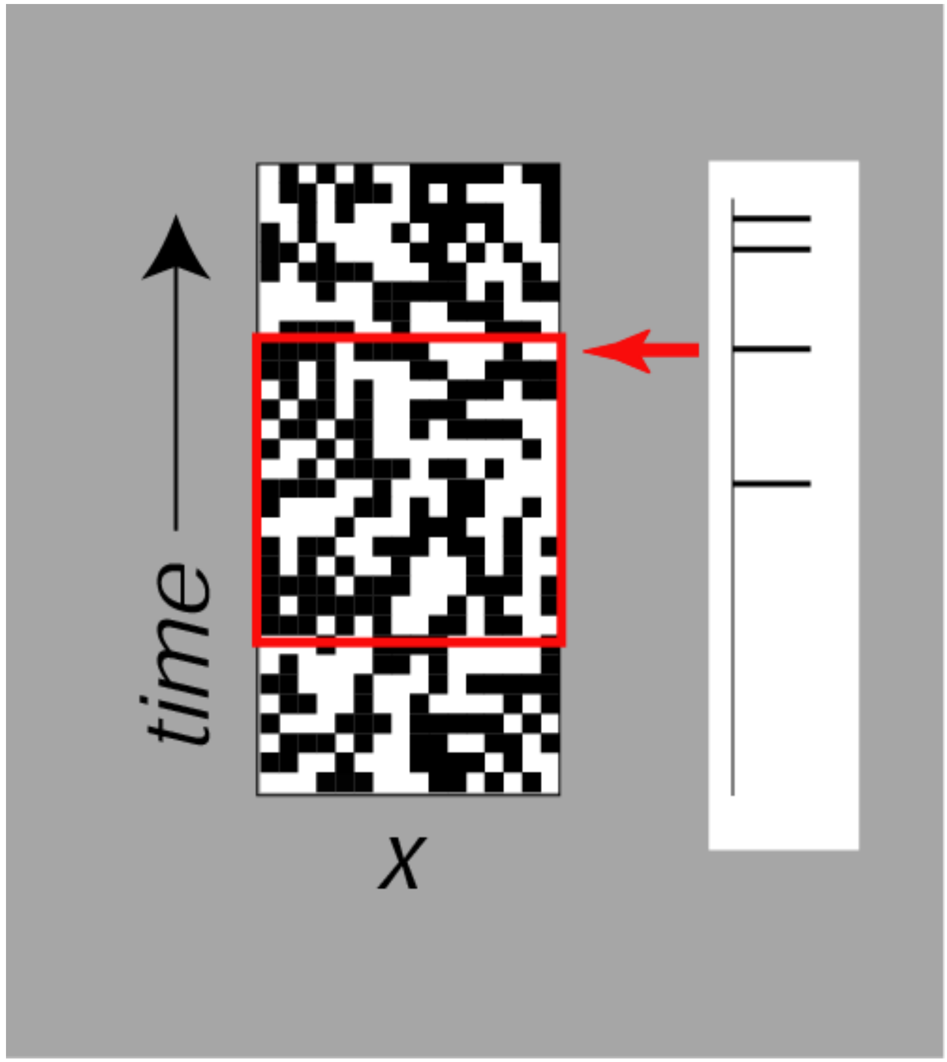
From Nicole Rust

Spike-triggered Average (STA): example



From Nicole Rust

Spike-triggered Average (STA): example

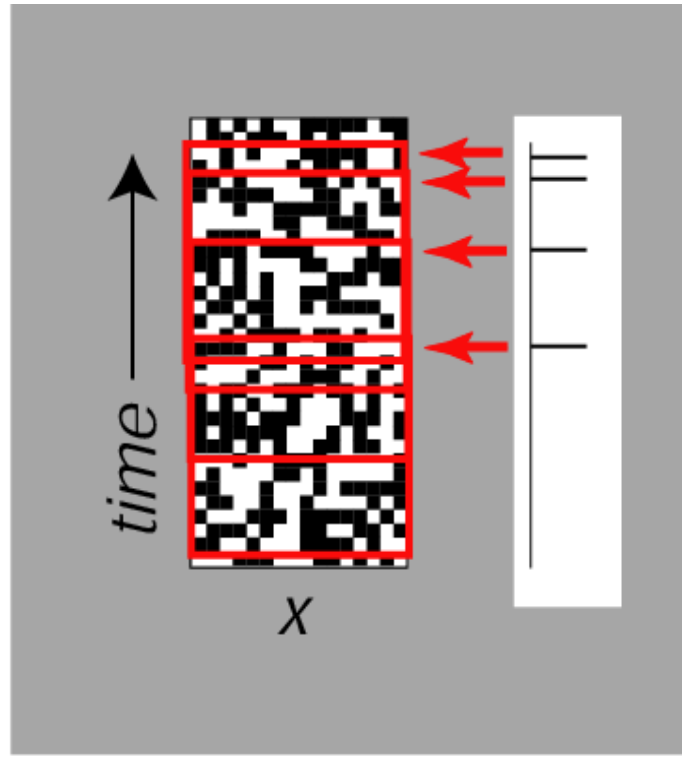


From Nicole Rust

Spike-triggered Average (STA) : example

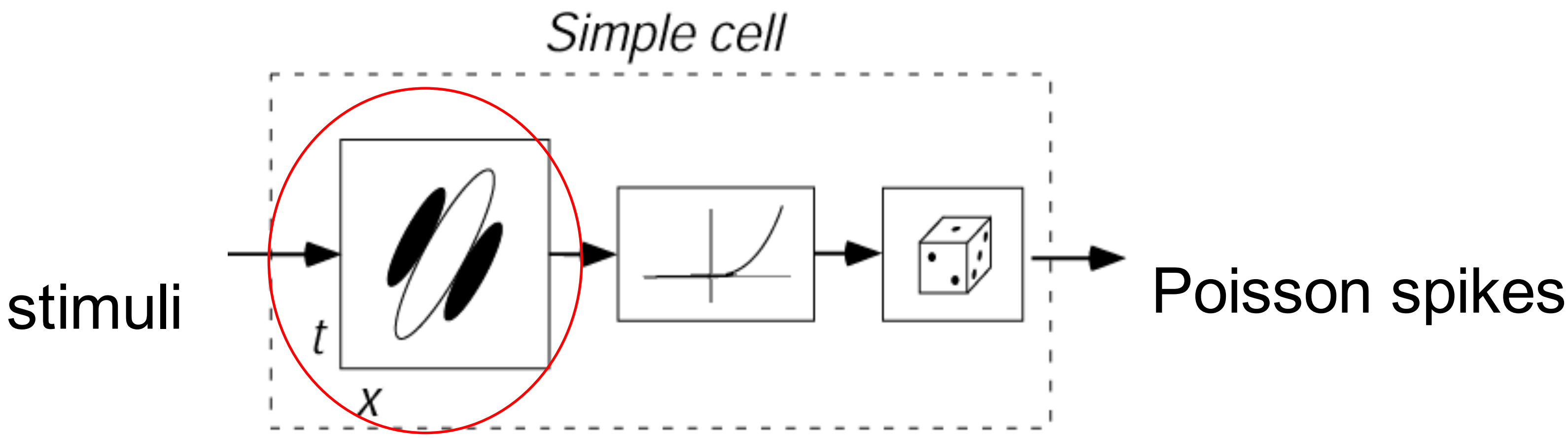
STA

Average of spike-triggered stimuli



From Nicole Rust

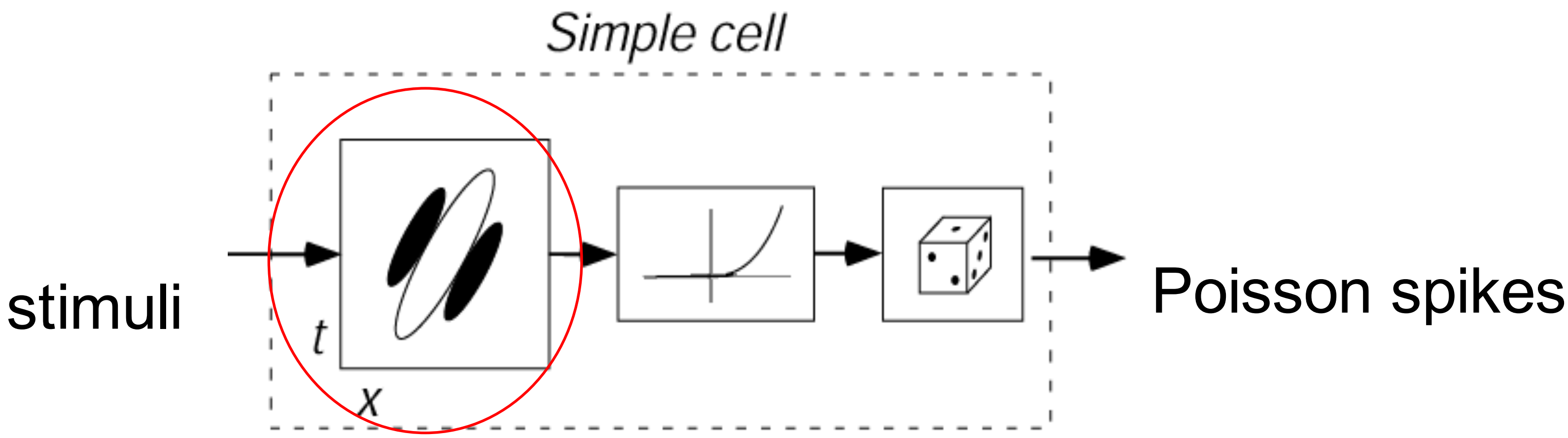
Spike-triggered average (STA)



Linear, Nonlinear, Poisson (LNP) encoding model

Will estimate of Linear always work??

Spike-triggered average (STA)



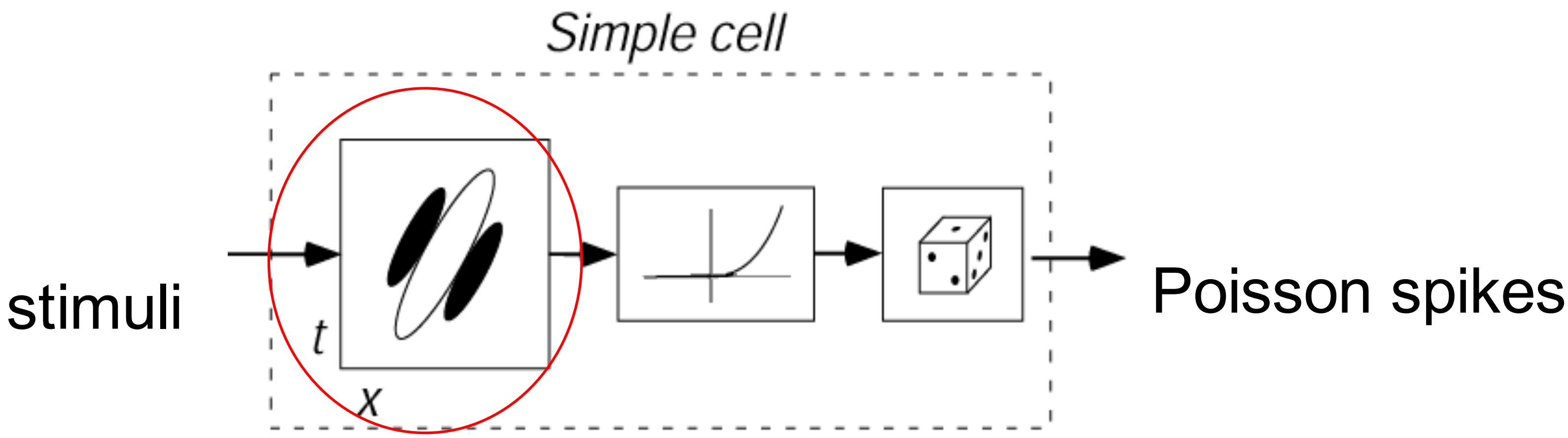
Linear, Nonlinear, Poisson (LNP) encoding model

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)



Linear, Nonlinear, Poisson (LNP) encoding model

Can we generalize the model?

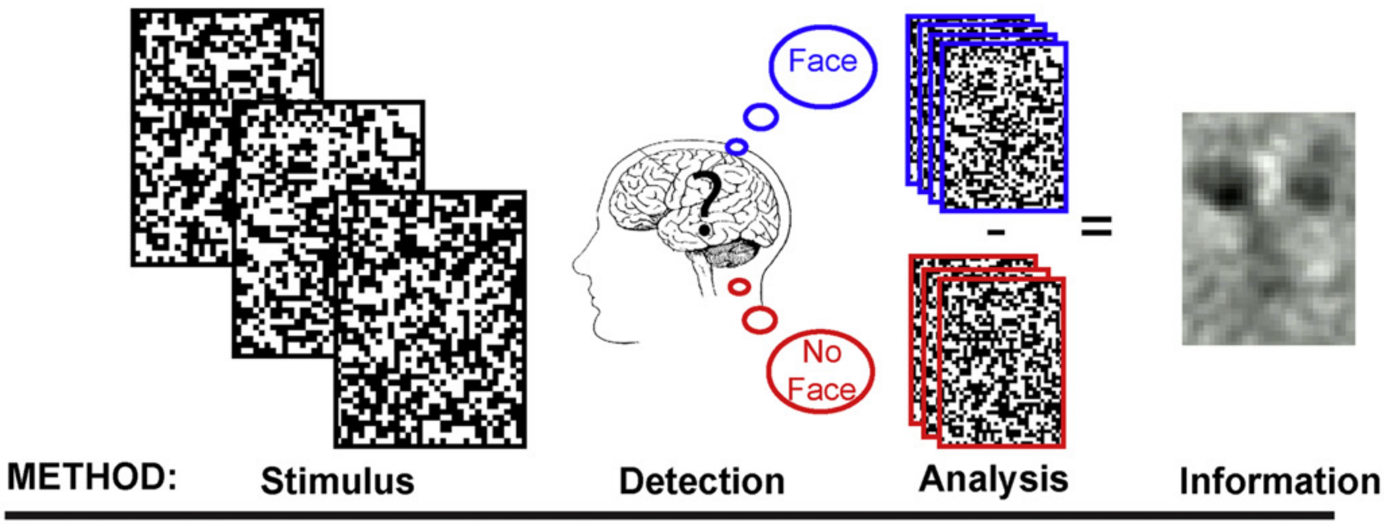
- More filters
- Other metrics of spike versus non spike ensemble beyond the mean

(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"

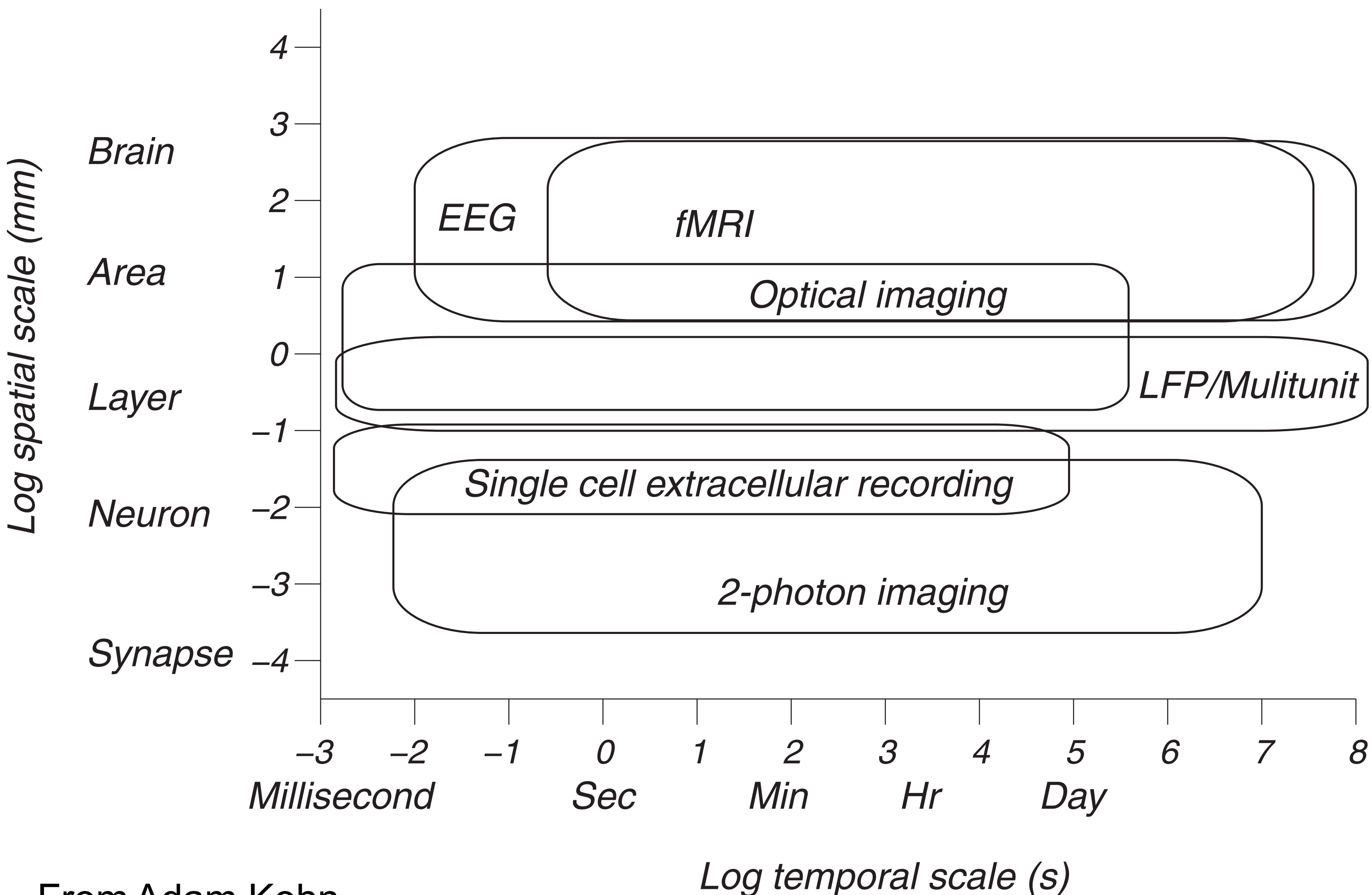


- Smith et al. Current Biology 2012: Subjects told that half the noise stimuli contain faces, although there are no faces…
- Approach useful beyond single neurons to other types of data (EEG, fMRI)

Summary

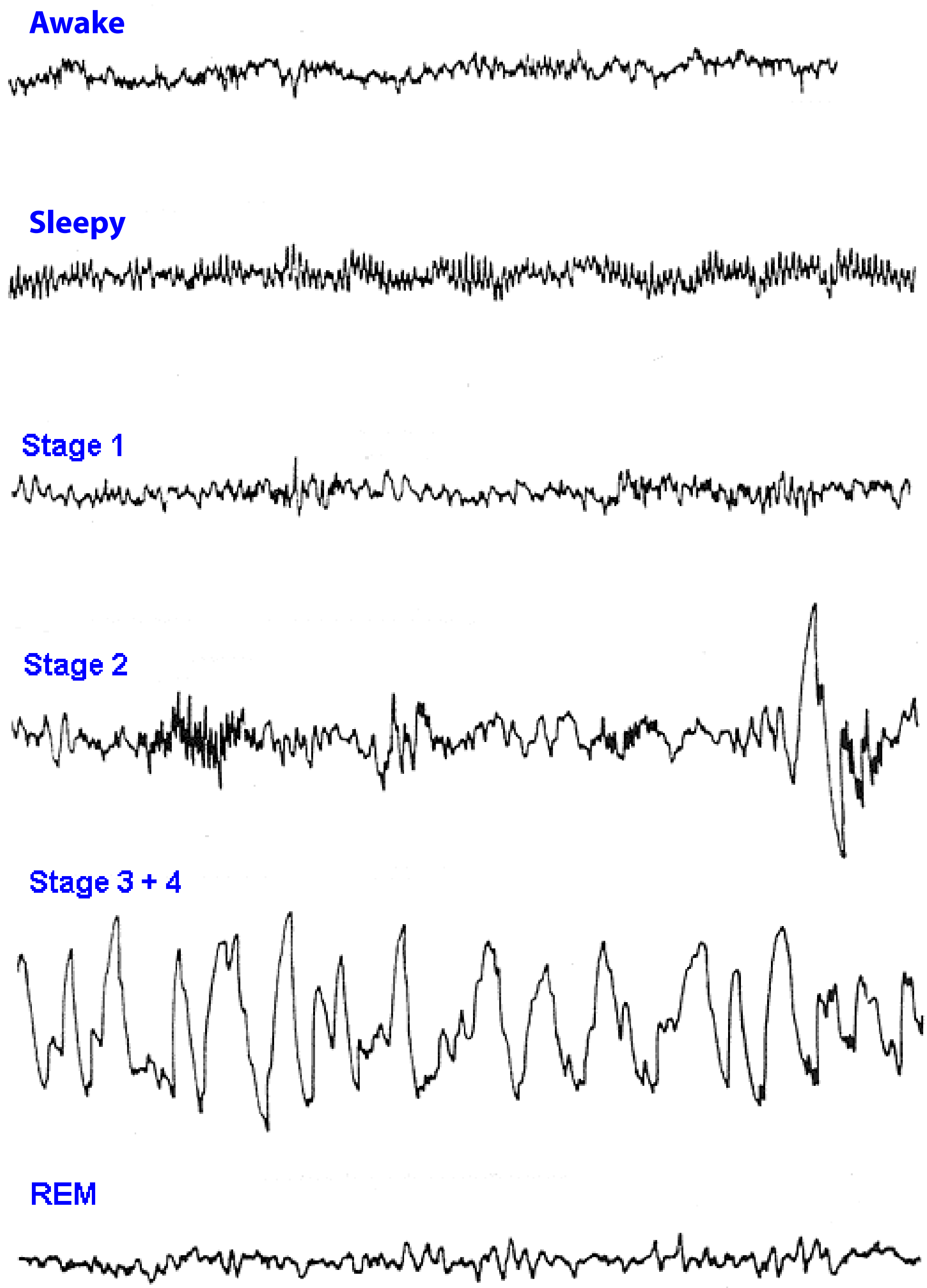
- Rate codes and temporal codes
- Characterize response properties of neurons: either we are lucky and know stimulus class neuron likes or use random stimuli (other work: “natural” stimuli)
- Simple encoding model: Linear, Nonlinear, Poisson. It’s a descriptive model of a neuron
- We’ve looked at estimating the Linear filter with Spike Triggered Average (later: limitations)
- Next: population codes
  Later: more sophisticated encoding models

Measuring neural activity



From Adam Kohn

EEG



From Adam Kohn

fMRI: Voxel triggered

fMRI: Voxel triggered

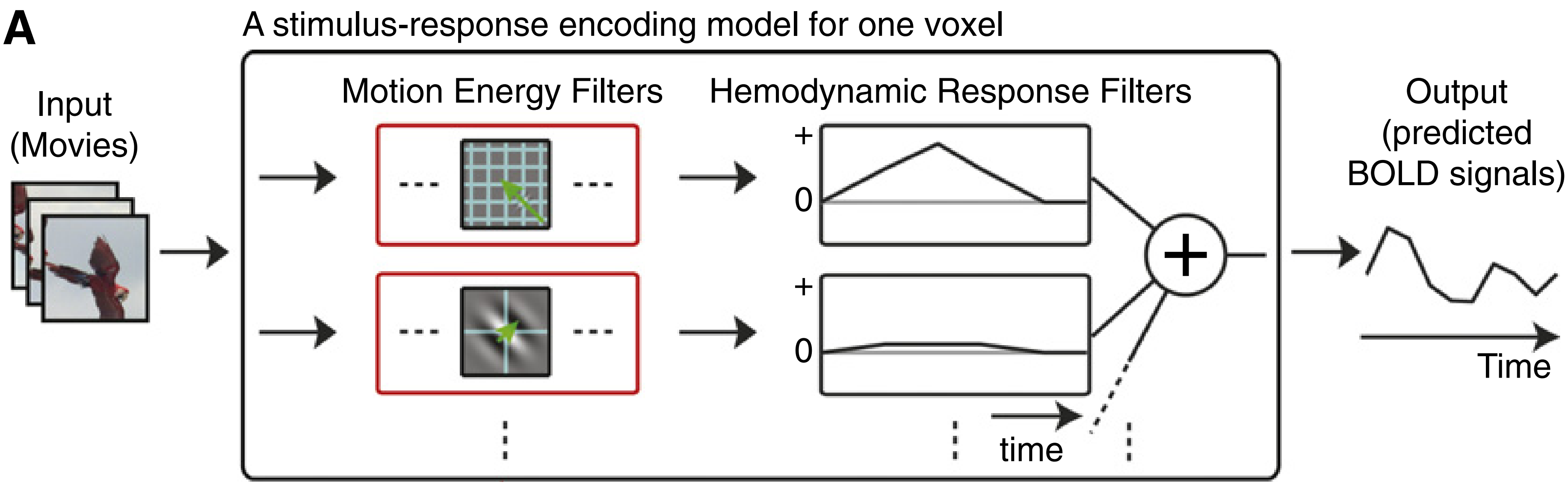
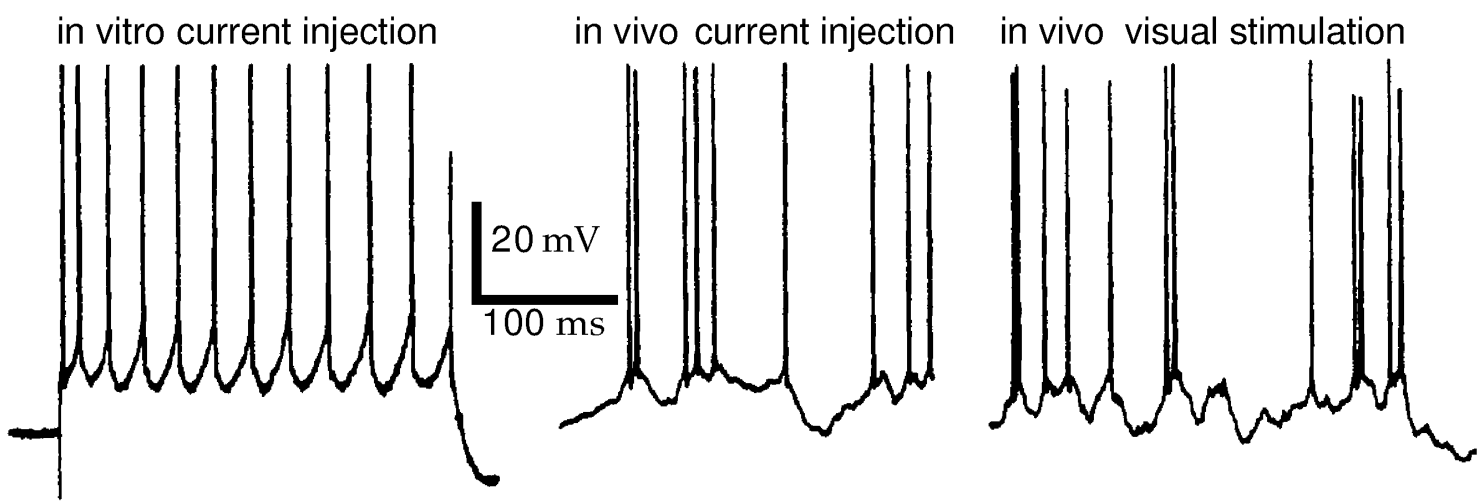


Figure 1. Schematic Diagram of the Motion-Energy Encoding Model

(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

Why are neurons noisy?

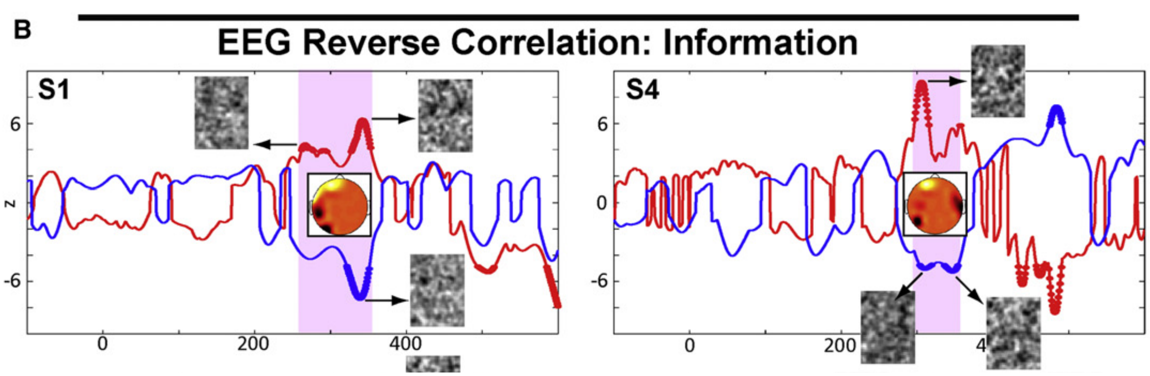


The spike generating mechanism is not noisy. Trial-to-trial variability comes about from fluctuations in input drive

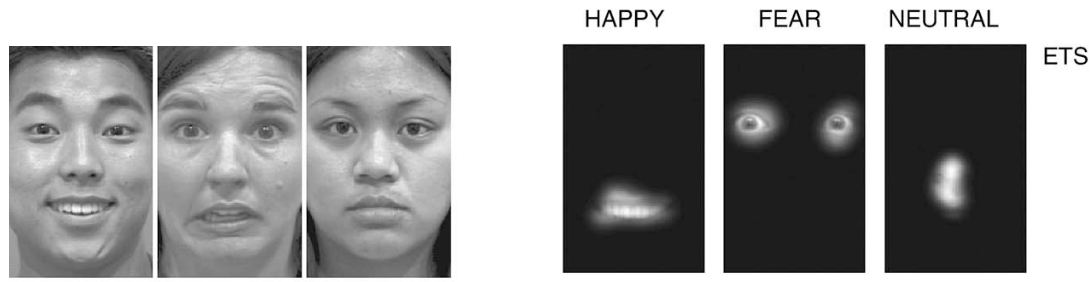
Figure from Dayan and Abbott textbook; 2001 (adapted from Holt et al., 1996)

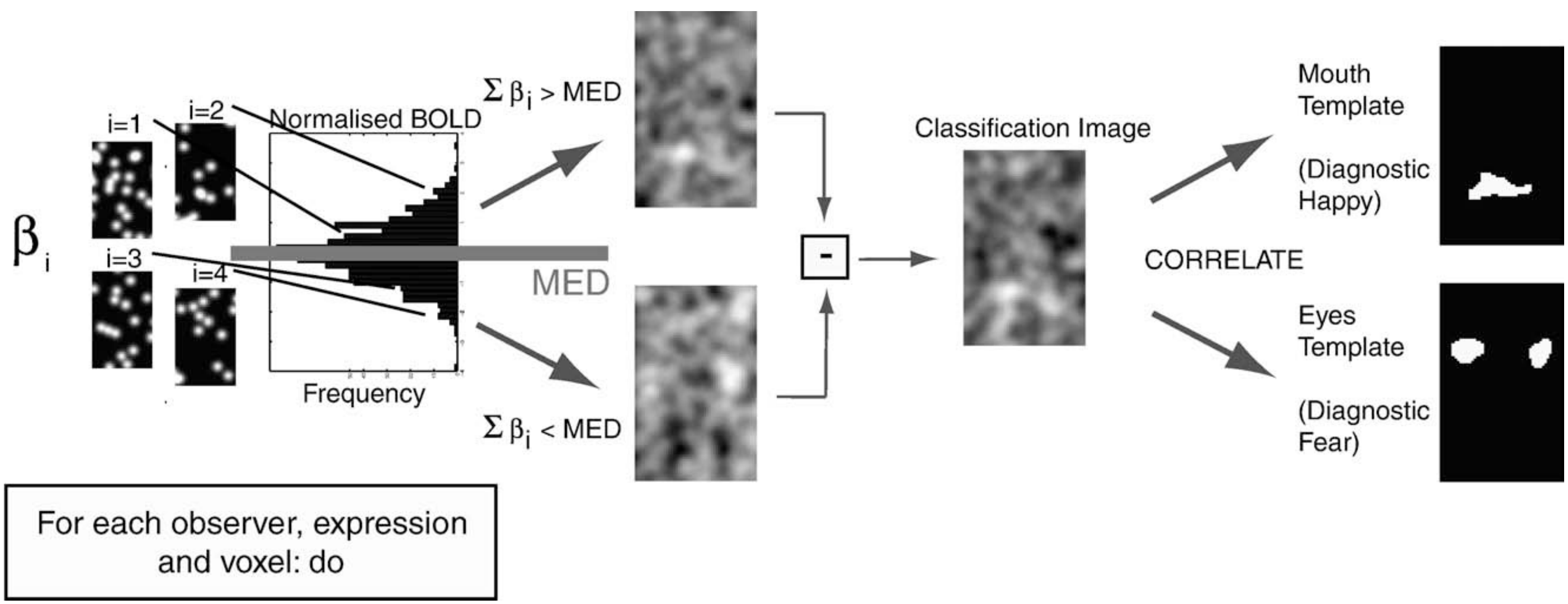
In Psychology: termed
"Classification Images"

"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"



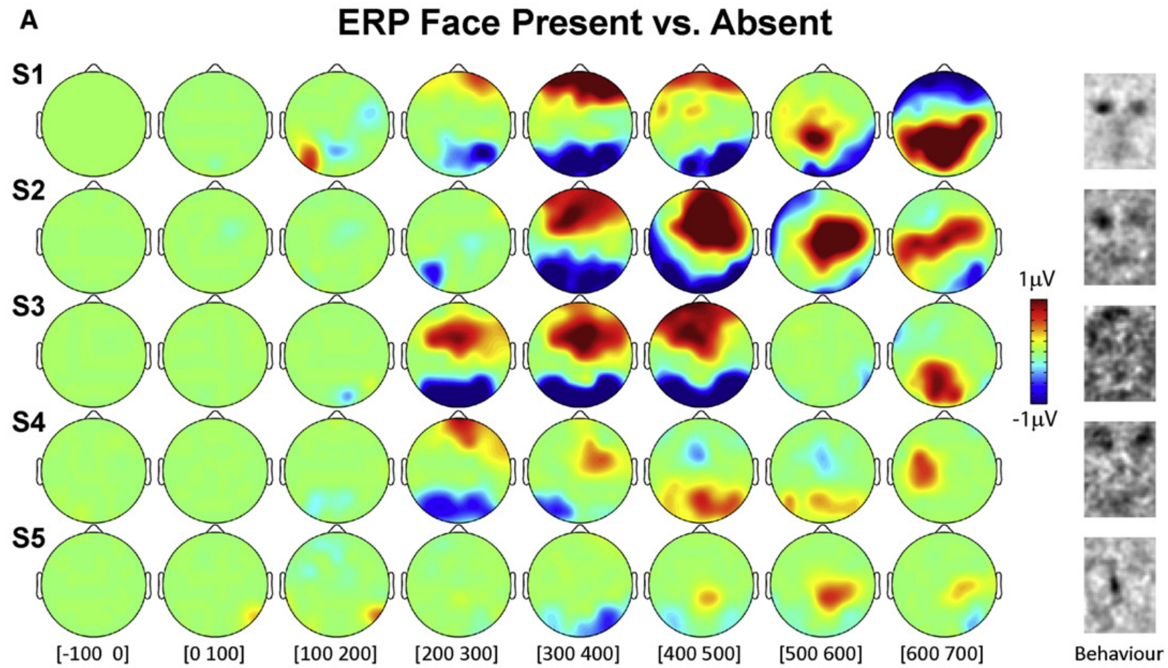
fMRI: Voxel triggered





Smith it el. 2008

In Psychology: termed "Classification Images"



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."