COMPUTATIONAL NEUROSCIENCE
Research group at the University of Tartu

Introduction to Computational Neuroscience

Lecture 5: Data analysis II

Lesson	Title
1	Introduction
2	Structure and Function of the NS
3	Windows to the Brain
4	Data analysis
5	Data analysis II
6	Single neuron models
7	Network models
8	Artificial neural networks
9	Learning and memory
10	Perception
11	Attention & decision making
12	Brain-Computer interface
13	Neuroscience and society
14	Future and outlook: AI
15	Projects presentations
16	Projects presentations

Basics

Analyses

Models

Cognitive

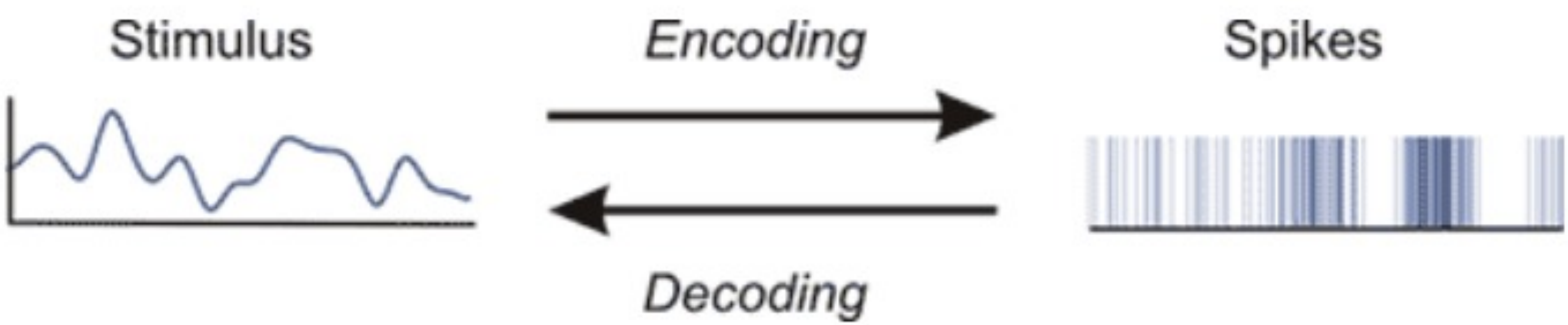
Applications

What is real?

"What is real? How do you define real? If you're talking about what you can hear, what you can smell, taste and feel, then real is simply electrical signals interpreted by your brain." *Morpheus to Neo*

The link between stimulus and neural response

can be studied from two different perspectives:



External world

Activity inside your brain

Learning objectives

- Understand the concepts of neuronal encoding and decoding
- Describe some candidates for neural codes
- Describe some read-out strategies and their applications

Neuronal encoding

Neuronal decoding

Neuronal encoding

Neural code

Tuning curves

Some possible codes

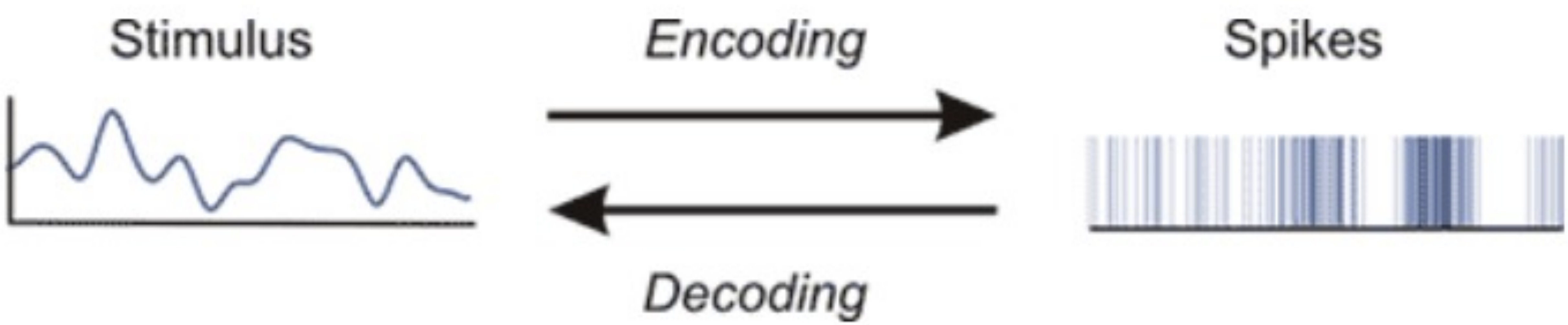
Neural encoding

Encoding: discovering the map from stimulus to response

$$s_1 \rightarrow r_1 \quad s_2 \rightarrow r_2 \quad s_3 \rightarrow r_3 \quad s_{NEW} \rightarrow ?$$

How information about a stimulus is transformed into patterns of action potentials?

Given a stimulus, predict the neuronal response



Encoding and decoding

In mathematical terms:

$P(R|S)$ **Encoding** $P(S|R)$ **Decoding**

Encoding and decoding

In mathematical terms:

$P(R|S)$ **Encoding** $P(S|R)$ **Decoding**

Bayes theorem relates encoding and decoding:

Encoding and decoding

In mathematical terms:

$P(R|S)$ **Encoding** $P(S|R)$ **Decoding**

Bayes theorem relates encoding and decoding:

$$P(S,R) = P(S|R)P(R) = P(R|S)P(S)$$

Encoding and decoding

In mathematical terms:

$P(R|S)$ **Encoding** $P(S|R)$ **Decoding**

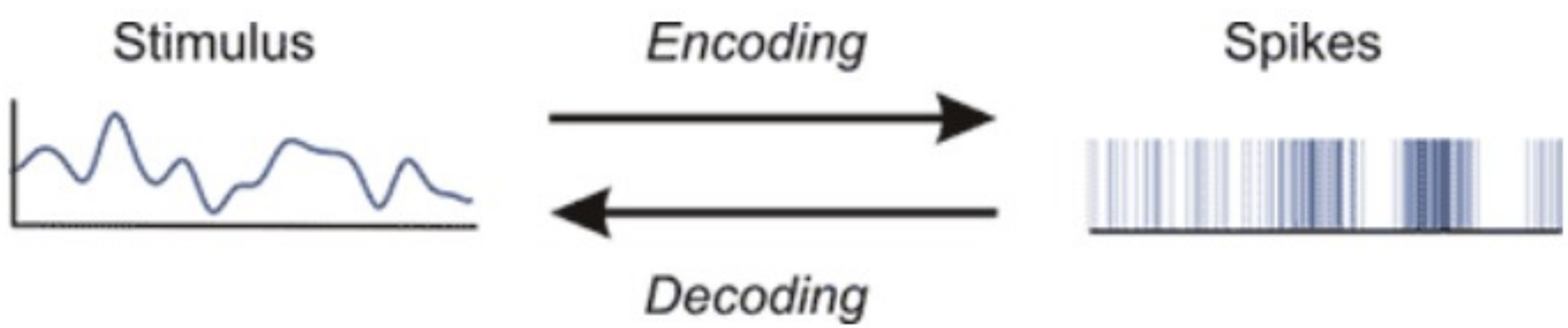
Bayes theorem relates encoding and decoding:

$$P(S,R) = P(S|R)P(R) = P(R|S)P(S)$$

$$\boxed{P(S|R)} = \frac{\boxed{P(R|S)}P(S)}{P(R)}$$

Neural code

Investigating the neural code is like building a dictionary



1 Translate from the external world (sensory stimuli or motor action) to internal neural representation

2 Translate neural representations to external world

3 Similar to dictionaries, one-to-many and many-to-one representations are possible

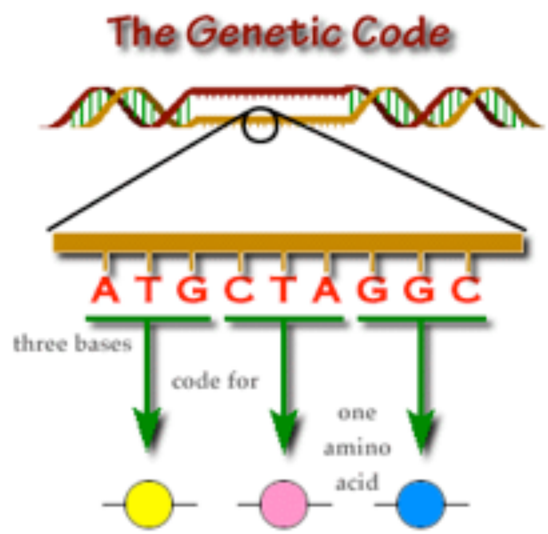
Neural code

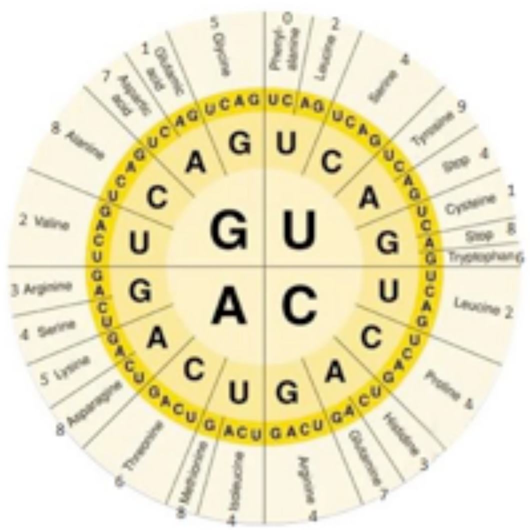
Two really hard problems for revealing the neural code:

1 Both stimuli and neural response are high-dimensional signals

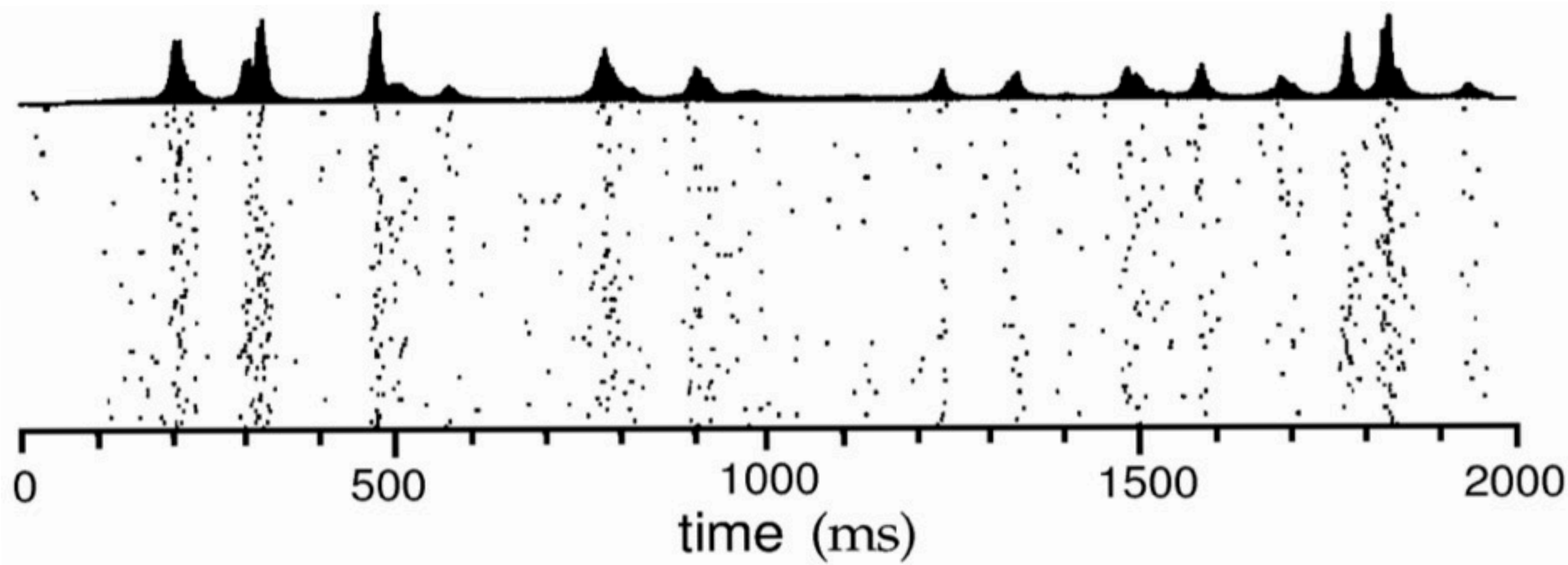
2 Noise

Compare to how simple is the **genetic code**: 4 letters, each ordered sequence of 3 letters determine 1 aminoacid

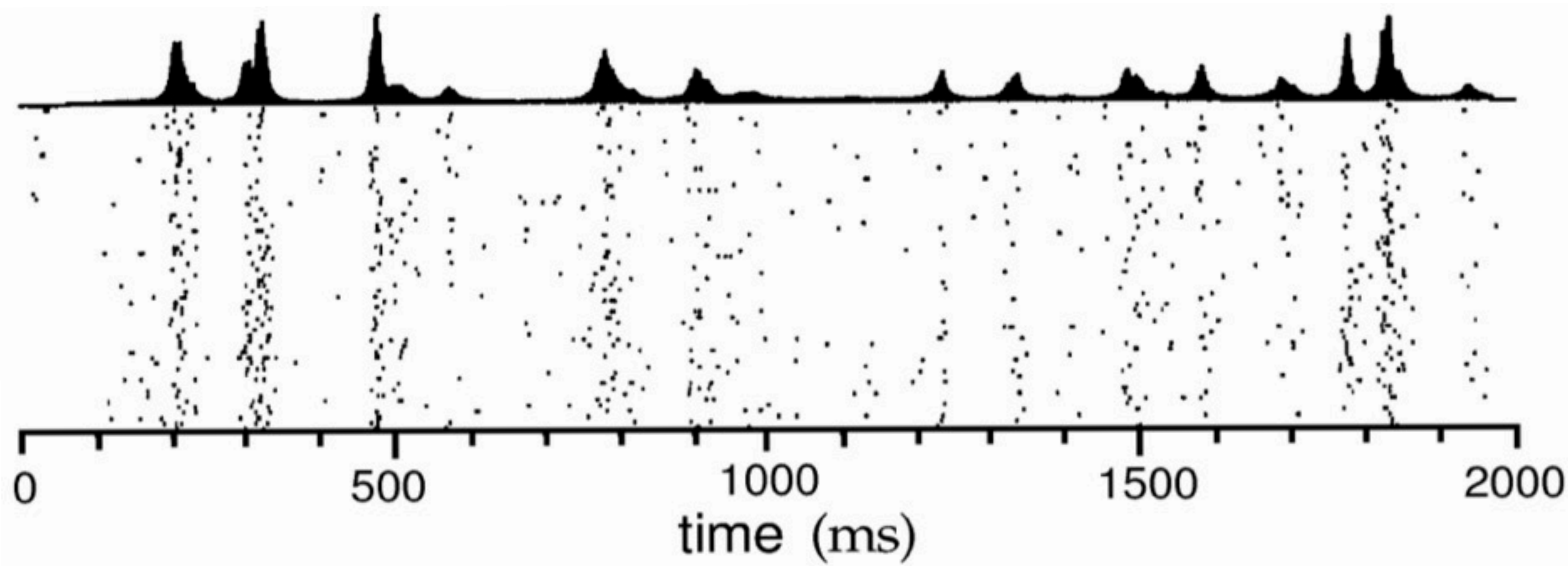




Relation stimulus-response

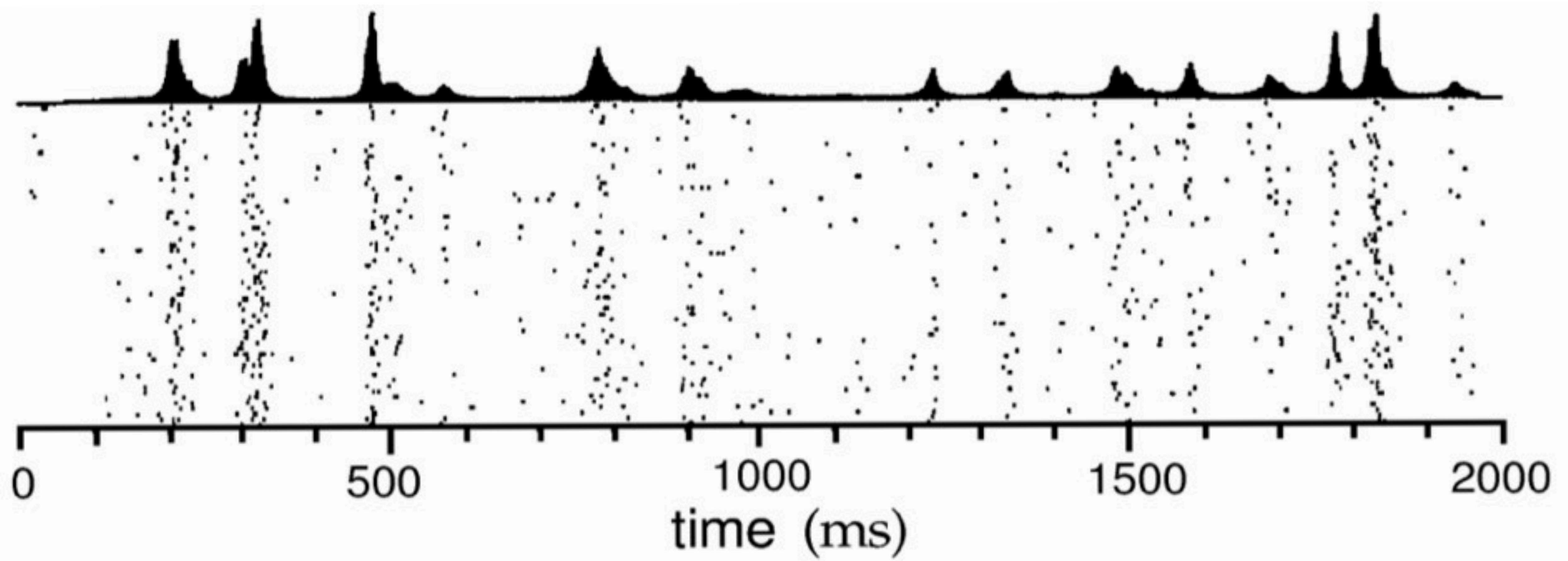


Relation stimulus-response



Difficult to characterize! Neural responses are stochastic:

Relation stimulus-response



Difficult to characterize! Neural responses are stochastic:

1 Levels of arousal and attention

2 Stochastic nature of biophysical processes

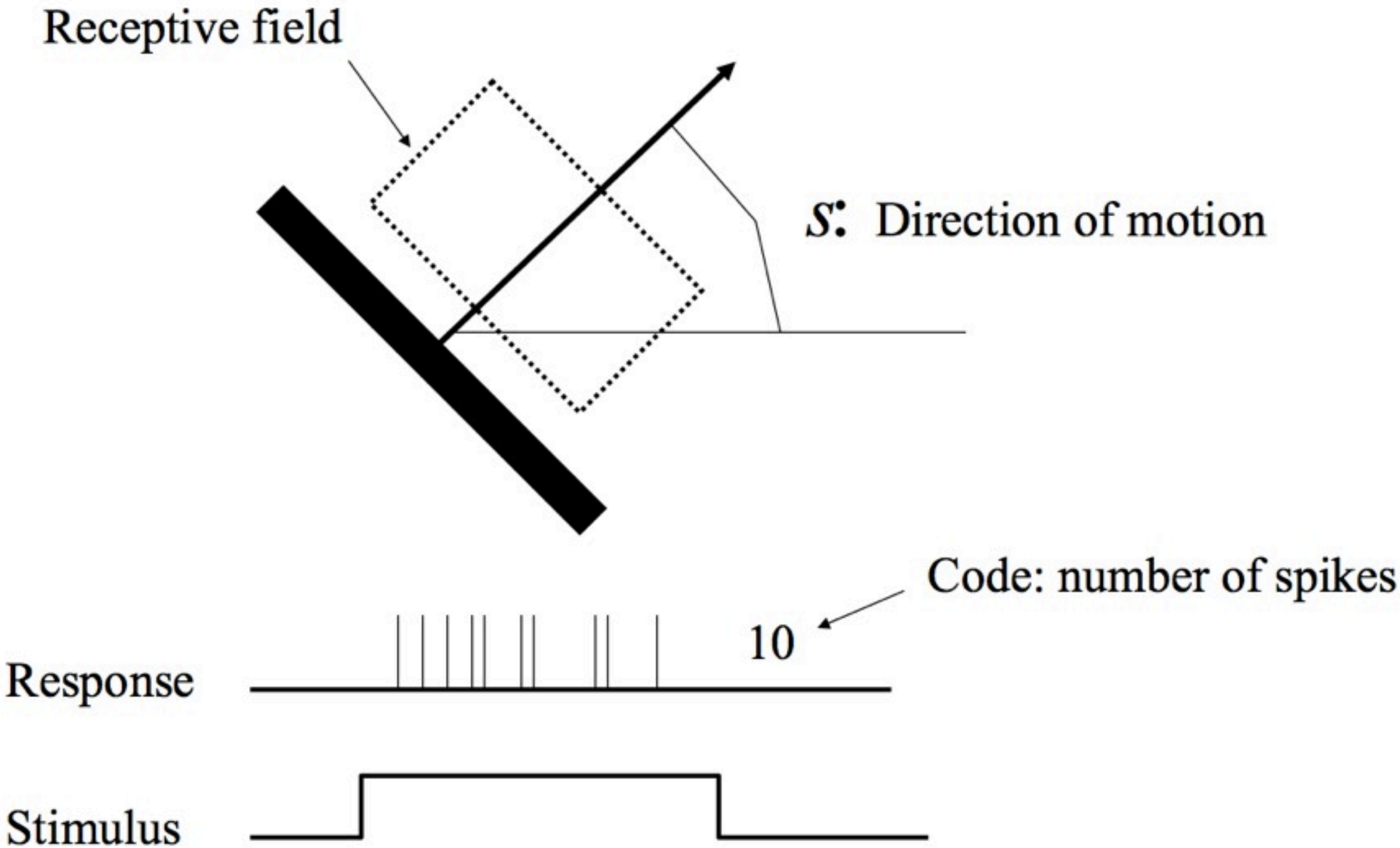
3 Other parallel cognitive processes

4 Large networks can be chaotic

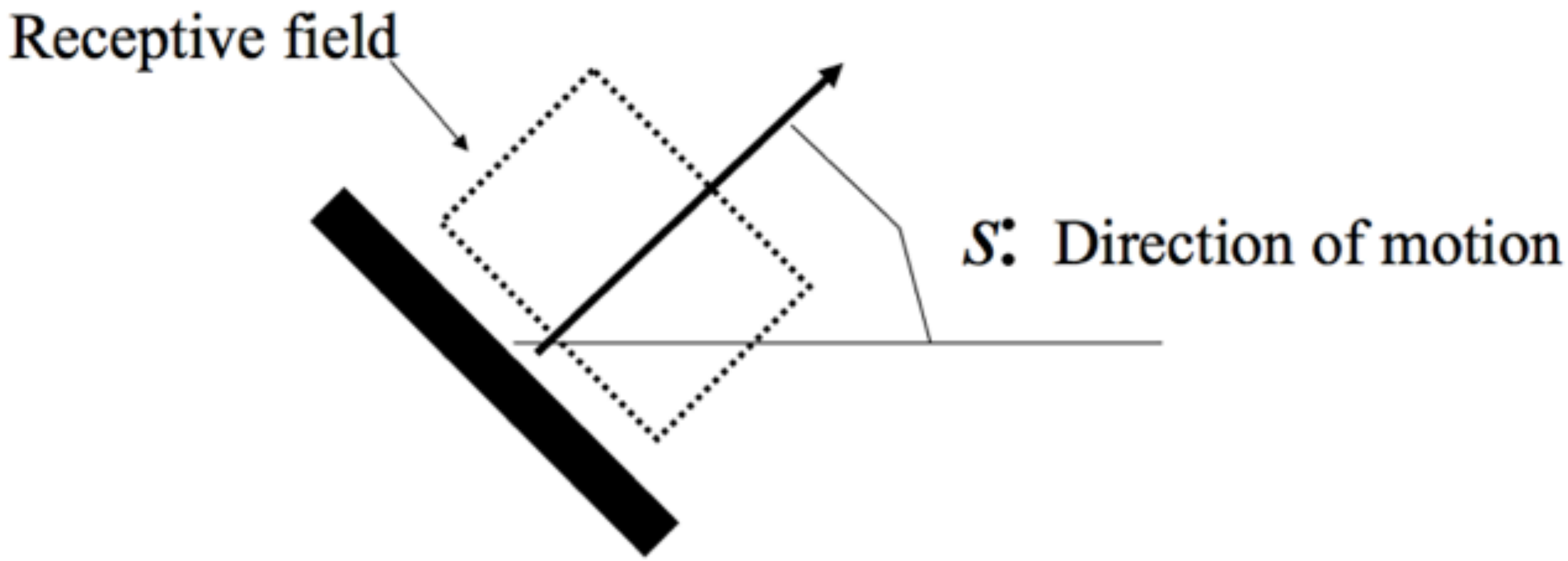
...

Deterministic model unlikely, we should seek a **probabilistic** one

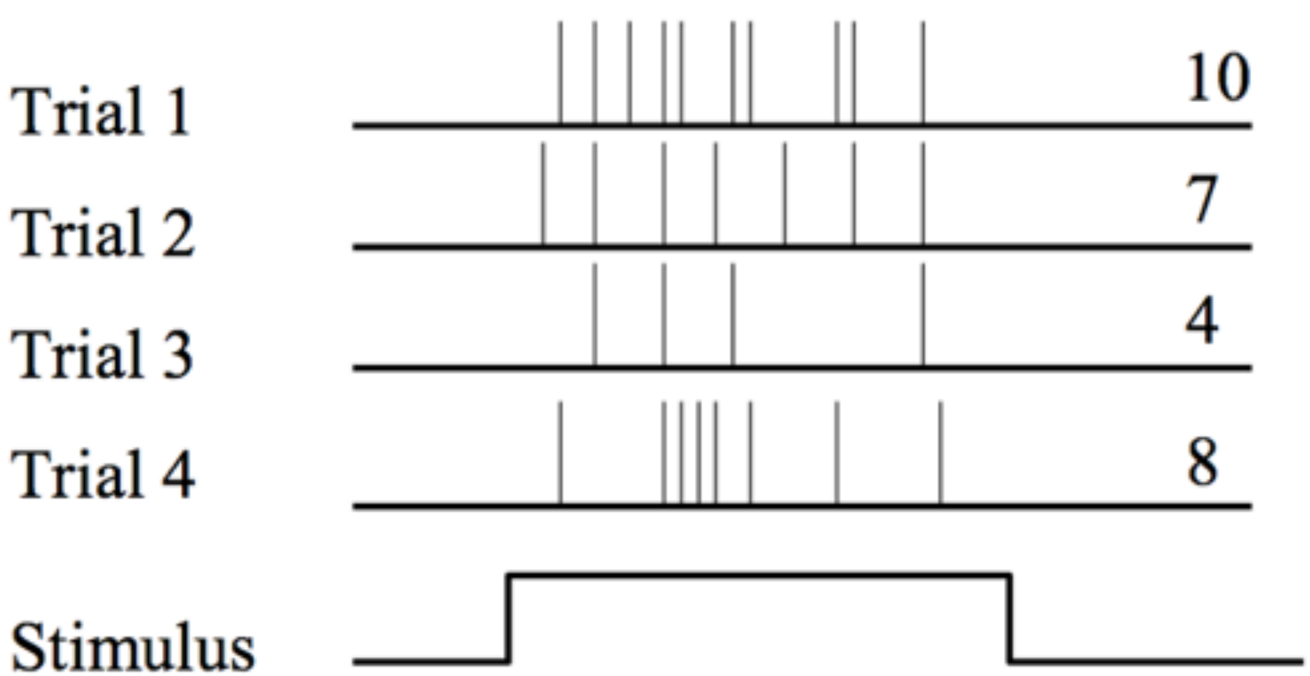
Tuning curve (example 1)



Tuning curve (example 1)

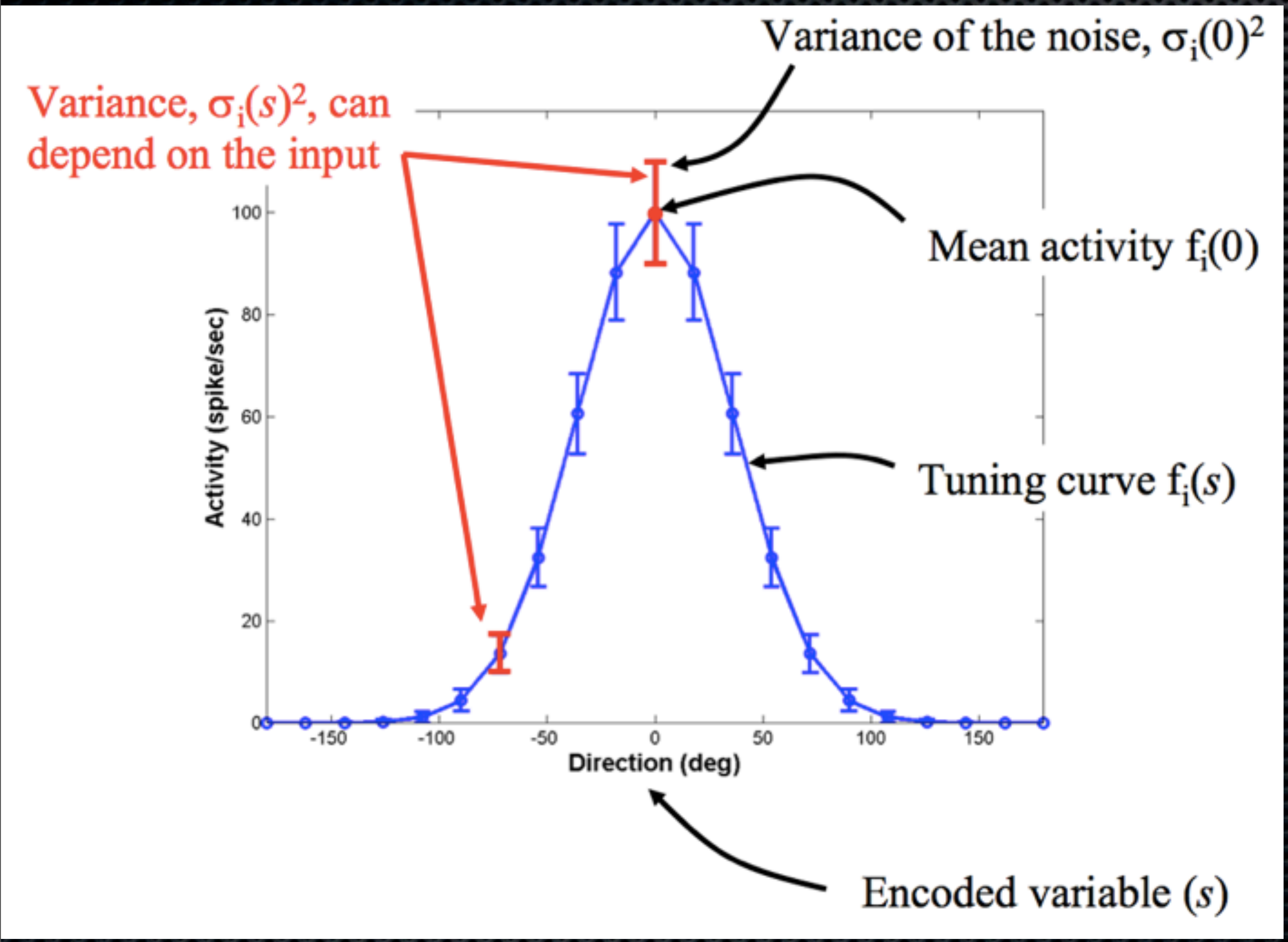


Different trials yield slightly different activity



Variability (noise?) typically follows a Poisson distrib.

Tuning curve (example 1)

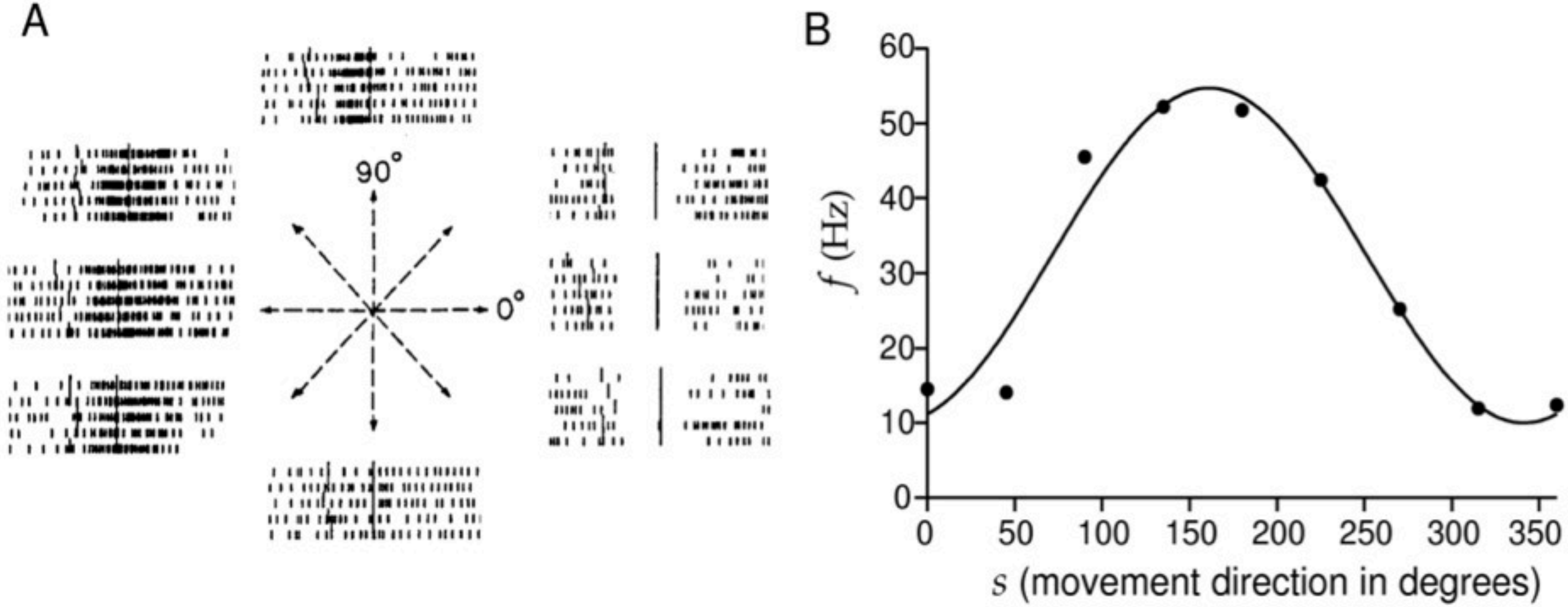


We repeat for different orientations to obtain a **tuning curve**

$$r = f(s) + n(s)$$

$$p(n|s) \longrightarrow p(r|s)$$

Tuning curve (example 2)

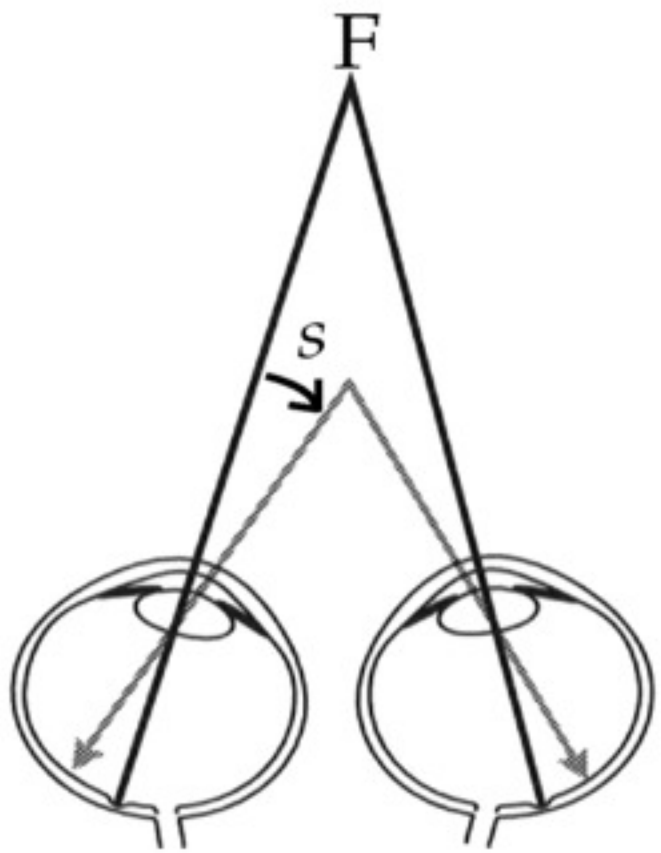


Neuron in monkey primary motor cortex (M1)

Sensitive to **reaching angle** (arm)

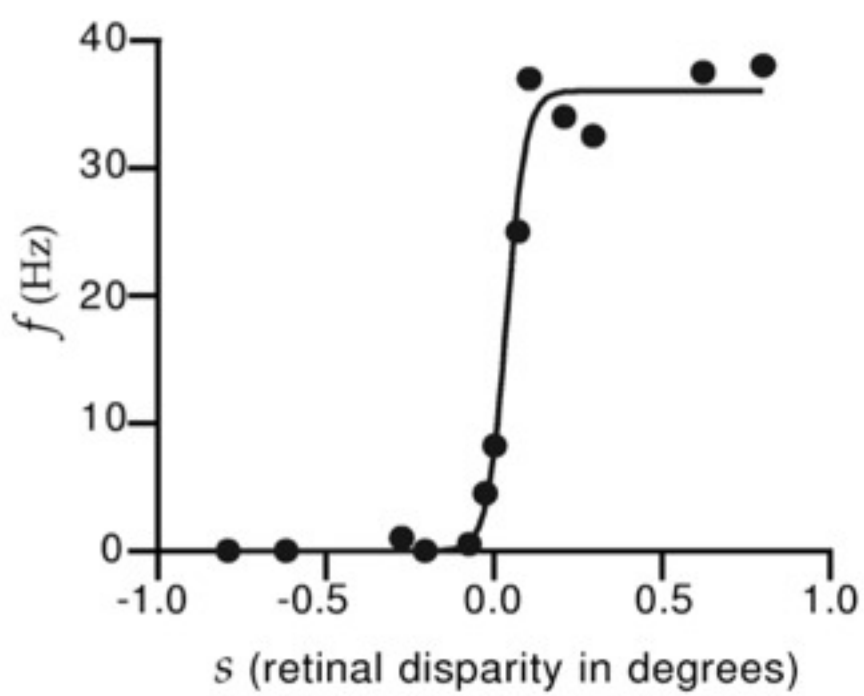
Cosine tuning curve with baseline firing rate (10 Hz)

Tuning curve (example 3)



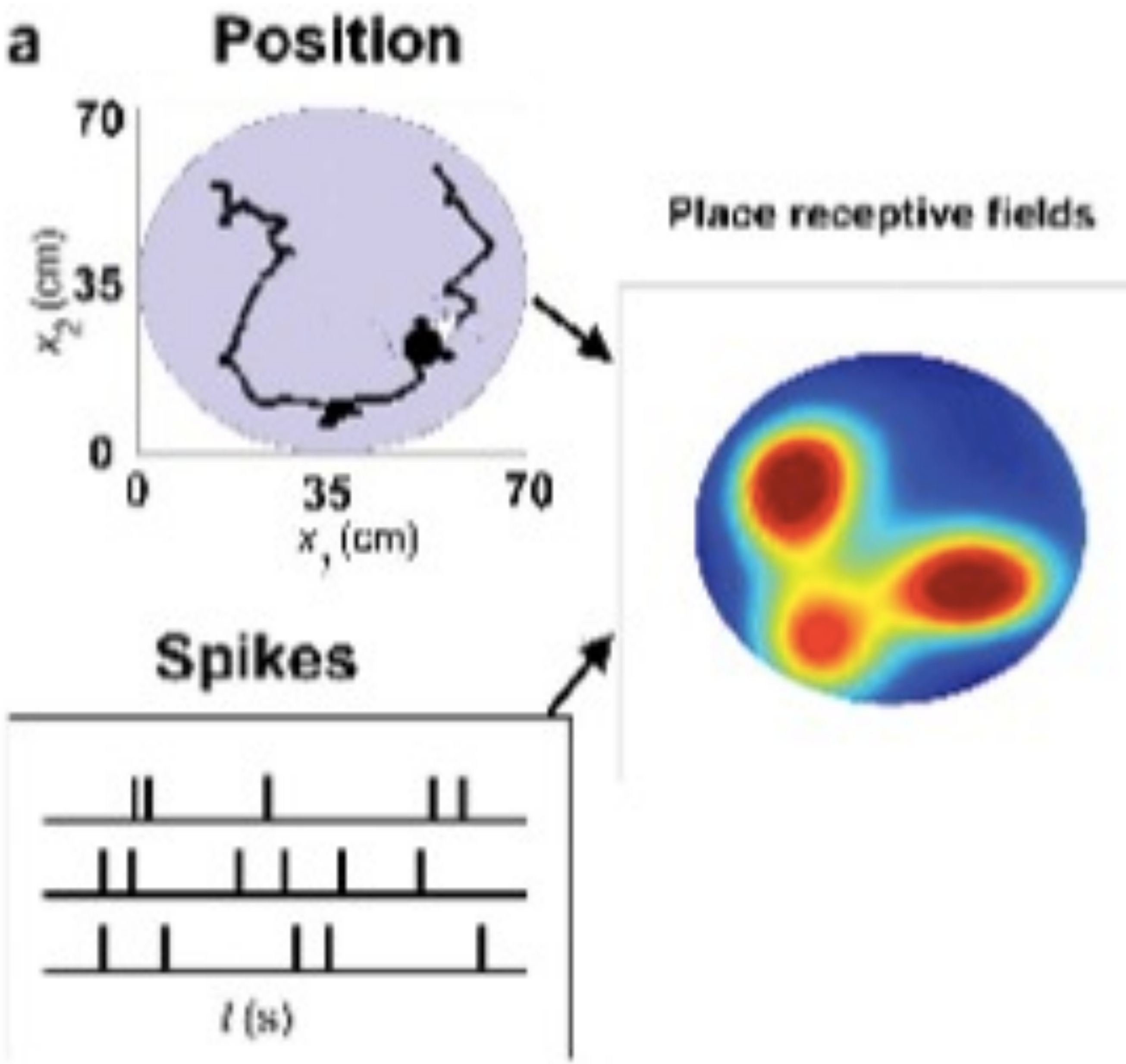
Retinal disparity: difference in the retinal location of an image between the two eyes

Some neurons in primary visual cortex (V1) are sensitive to retinal disparity



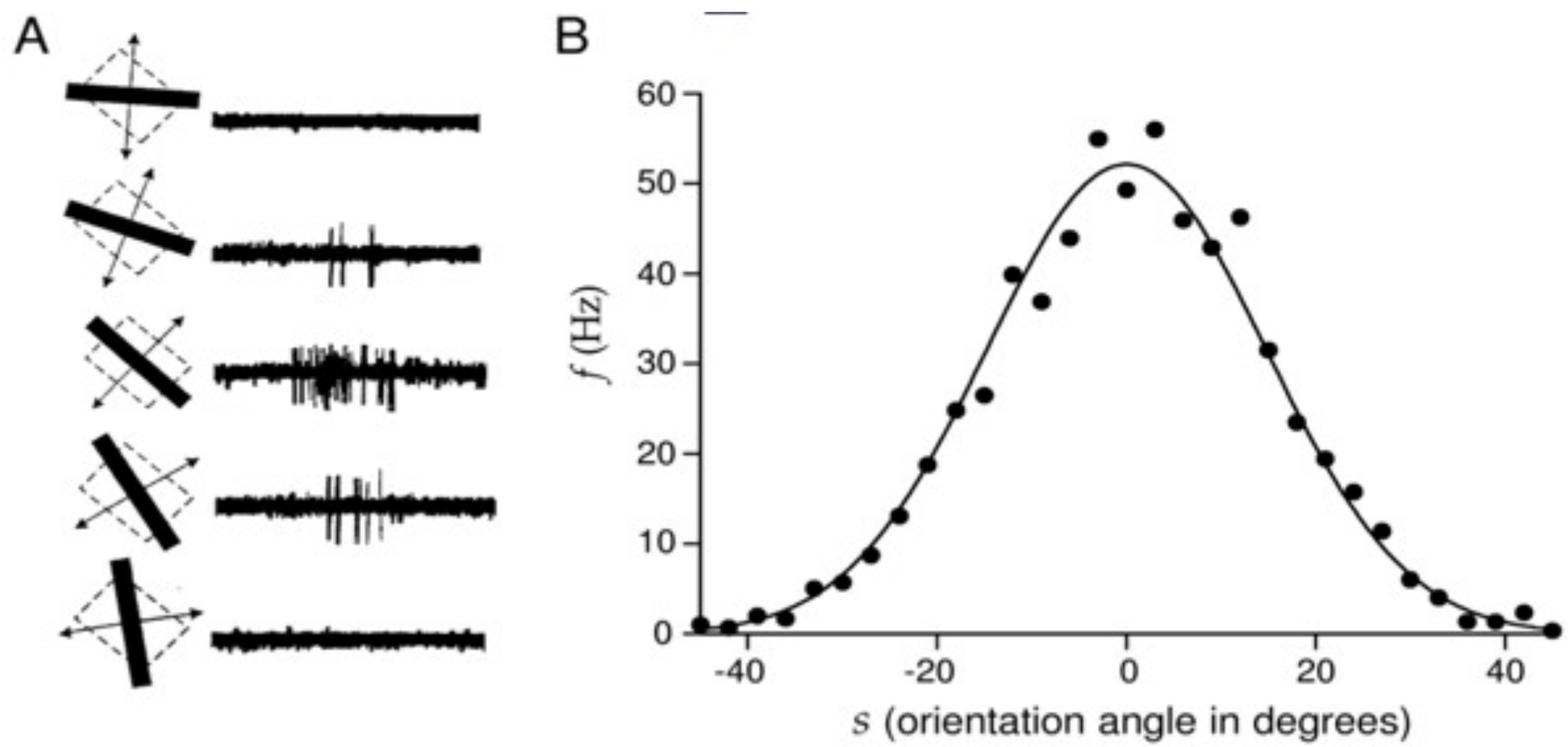
What could be the purpose of these neurons?

Tuning surface (example 4)



Some neurons in the hippocampus region can be **sensitive to the location** of the animal: they are named **place cells**

Tuning curve (summary)



Used to **characterize the sensitivity of neurons** in visual or other sensory areas **to a variety of stimulus parameters**

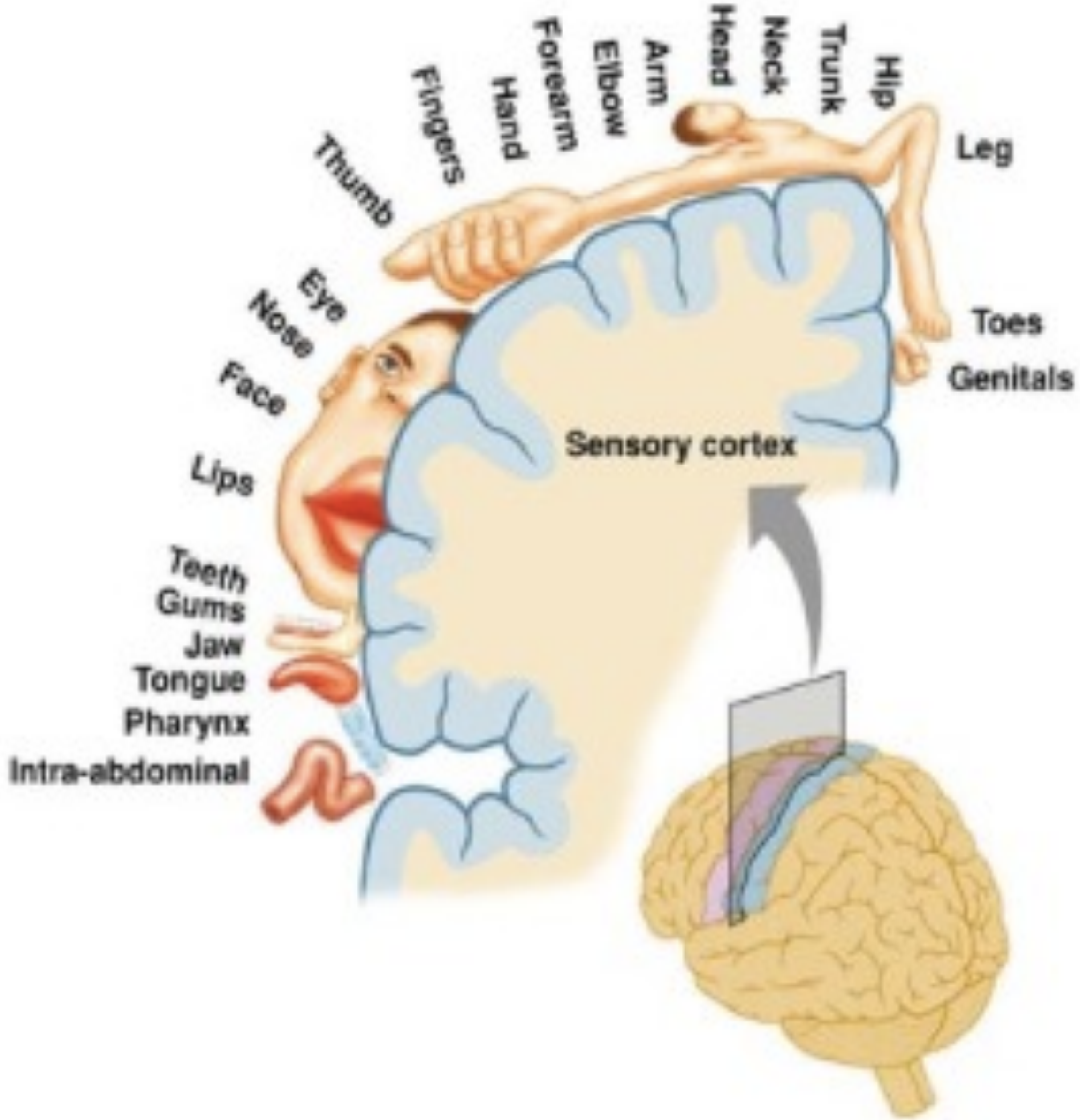
Measure the impact of a single stimulus attribute ***s***, on the average neural response ***r*** $\longrightarrow$ ***r = f(s)***

Correspond to firing rates, they are **measured** in spikes/s or **Hz**

How do neurons encode information?

Which characteristics of spike trains can we use to code information?

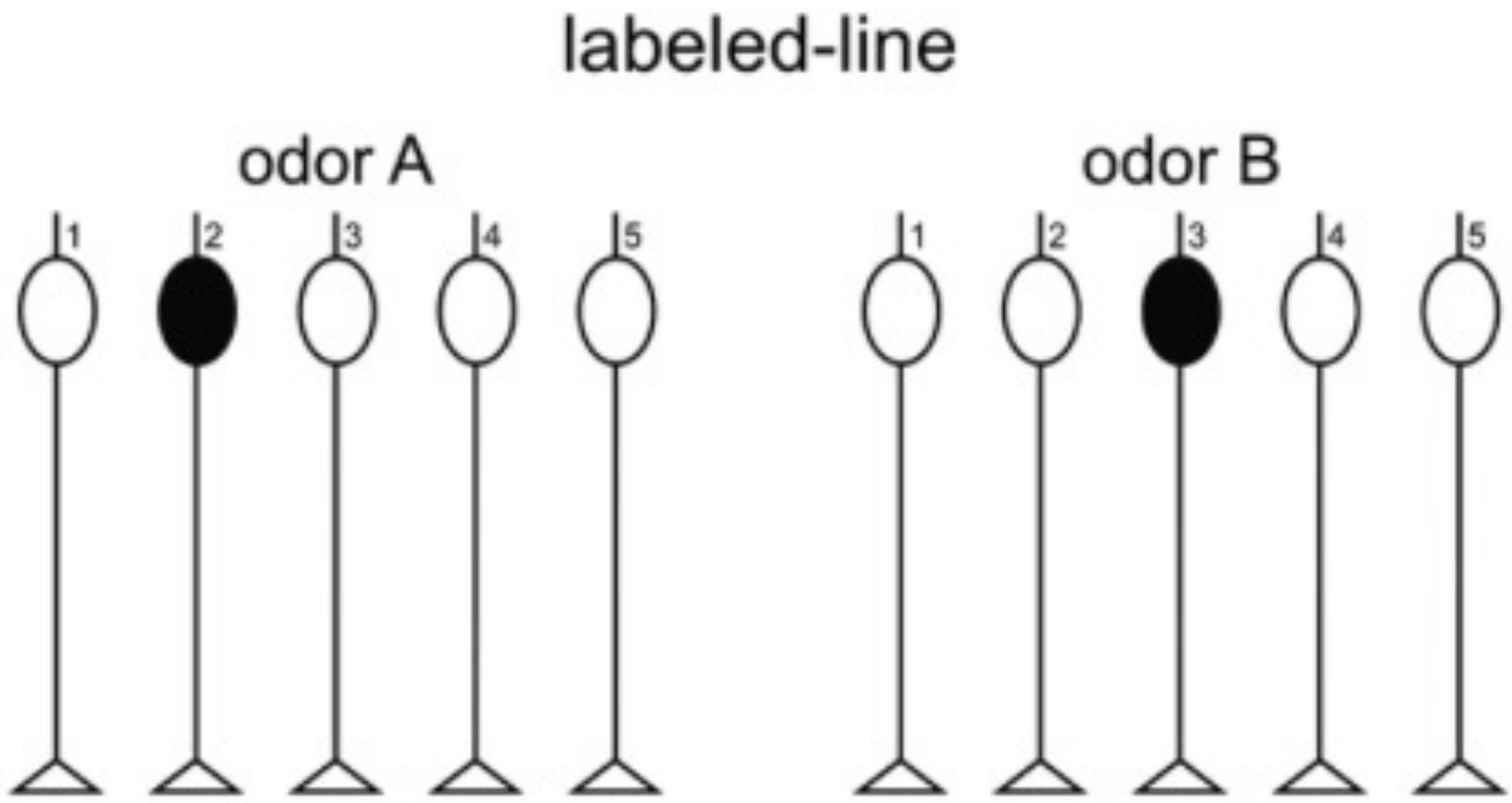
Labeled line code



Maps maintain an orderly representation of the stimulus

Pathways carrying sensory information are specific, forming a "labeled line" regarding a particular stimulus

Labeled line code



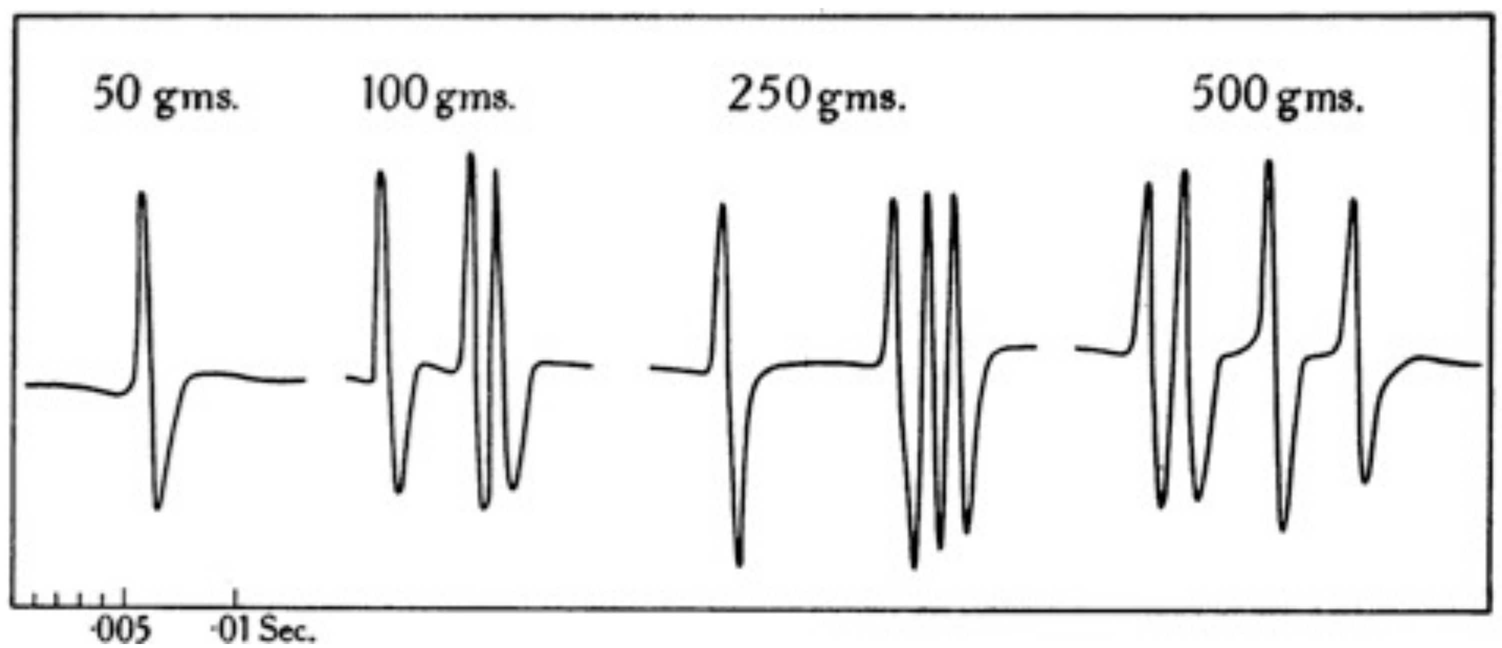
Odor is **coded in the identity of the neuron activated**

No further processing is needed for decoding

Low capacity

Rate code

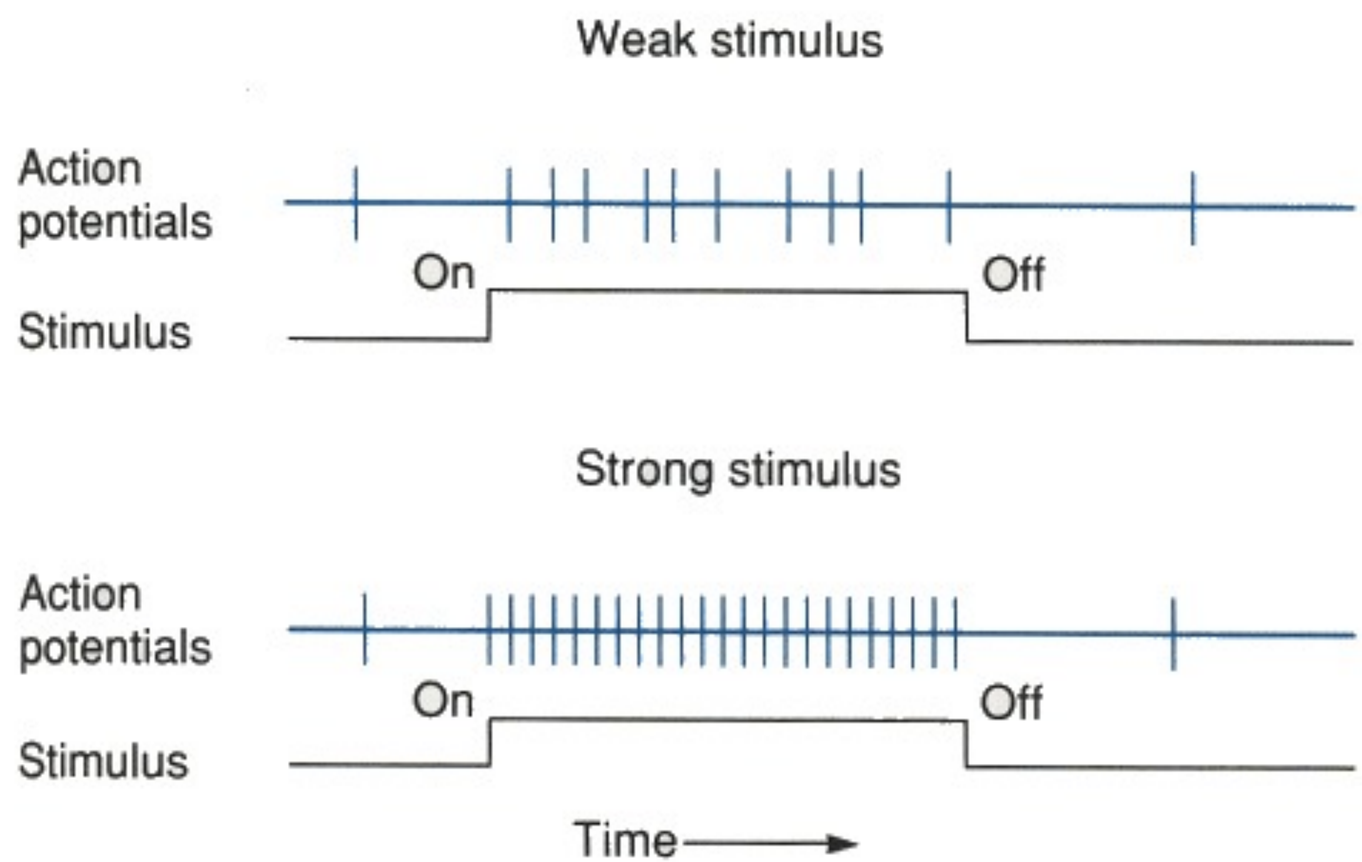
The classic ⟶ Adrian & Zotterman (1926)



Information about the stimulus is contained in the firing rate (frequency) of the neuron

In most sensory systems, the firing rate increases, generally non-linearly, with increasing stimulus intensity

Rate code



The standard tool for describing the properties of sensory and cortical neurons, in part due to the ease of measuring

Not efficient and **slow** but **robust**

Temporal code

Rate code neglects all the information possibly contained in the exact timing of the spikes (temporal code)

	String 1		String 2	
Rate code	000111000111	=	001100110011	6
Temporal code	000111000111	≠	001100110011	6

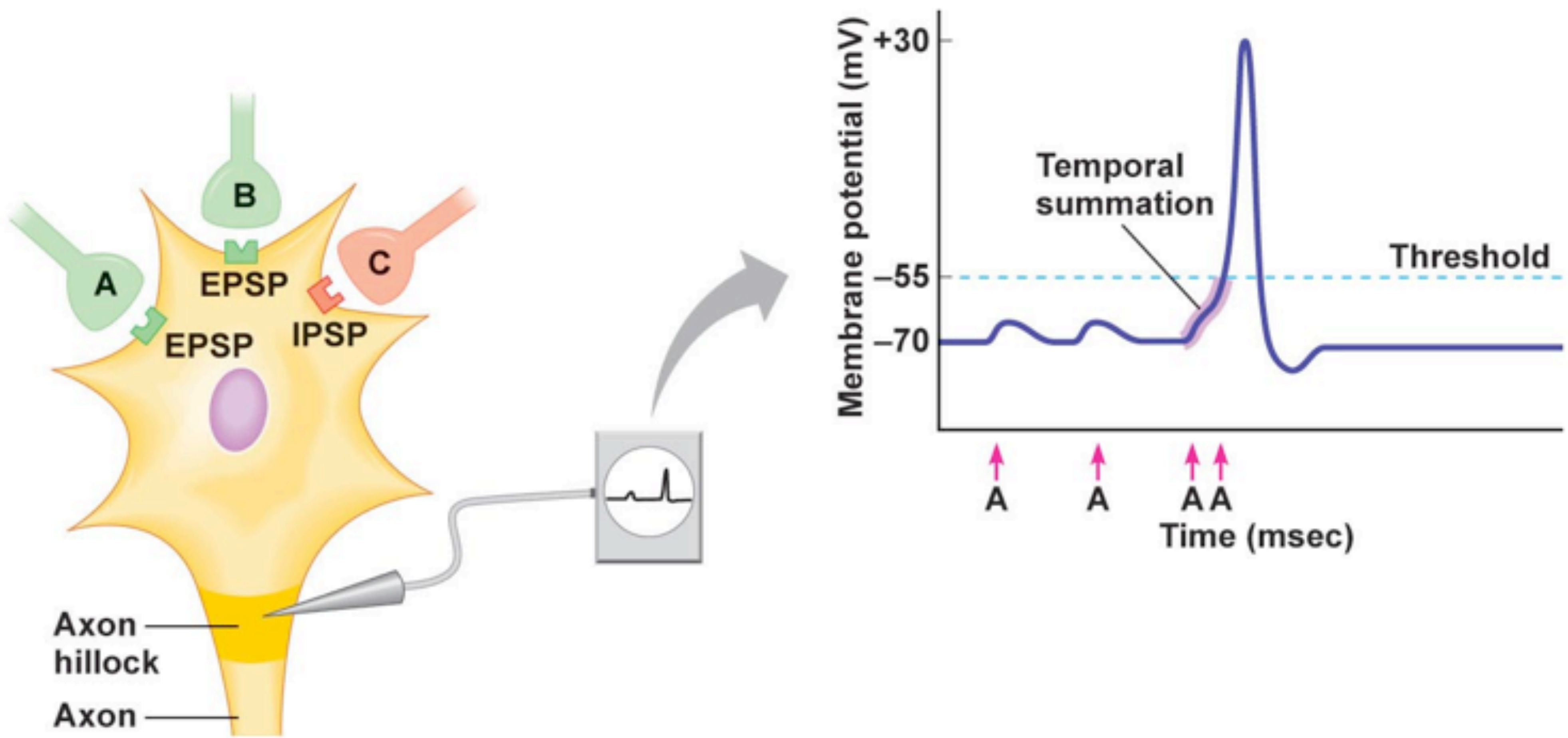
Recent studies suggest that spike timing on a millisecond time scale can be a significant element of neuronal coding

Temporal code

Temporal code 000111000111   001100110011

How could a neuron distinguish these two inputs?

Temporal summation



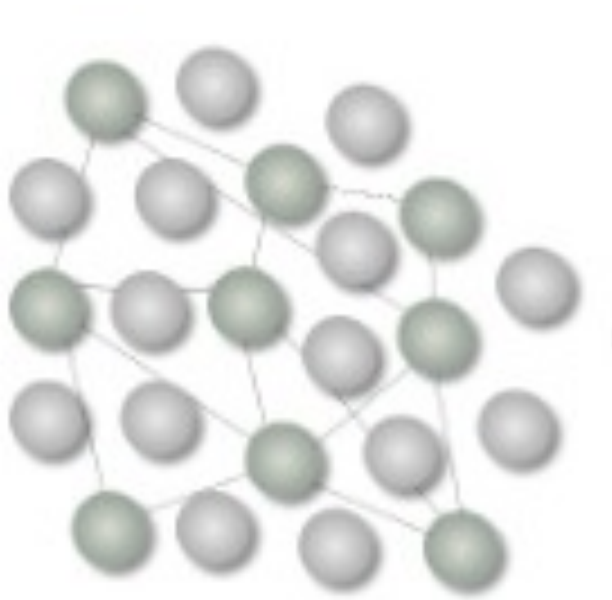
Temporal code

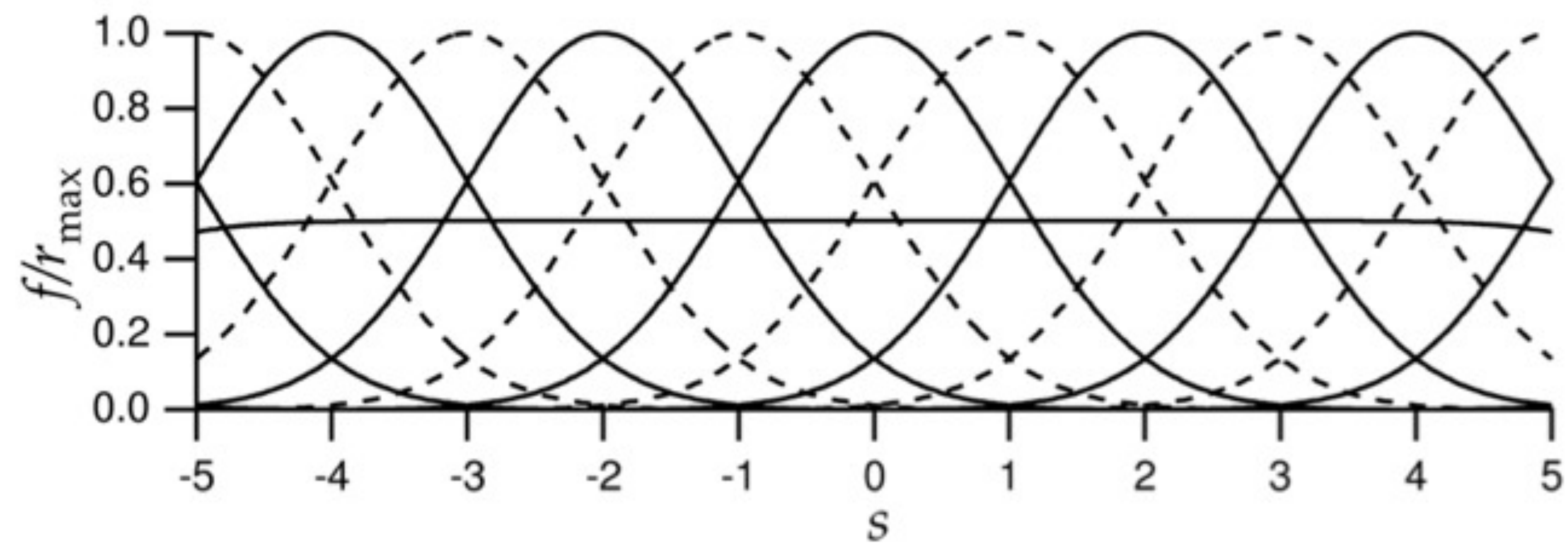
As there is no absolute clock in the brain, the information must be carried either in relative timing of spikes between neurons or with respect to ongoing brains oscillations

Examples: **1)** latency of the first spike after stimulus onset, 2) phase of an oscillation during firing, 3) sequences of firing

Population code

Represent stimuli by using the joint activities of a number of neurons

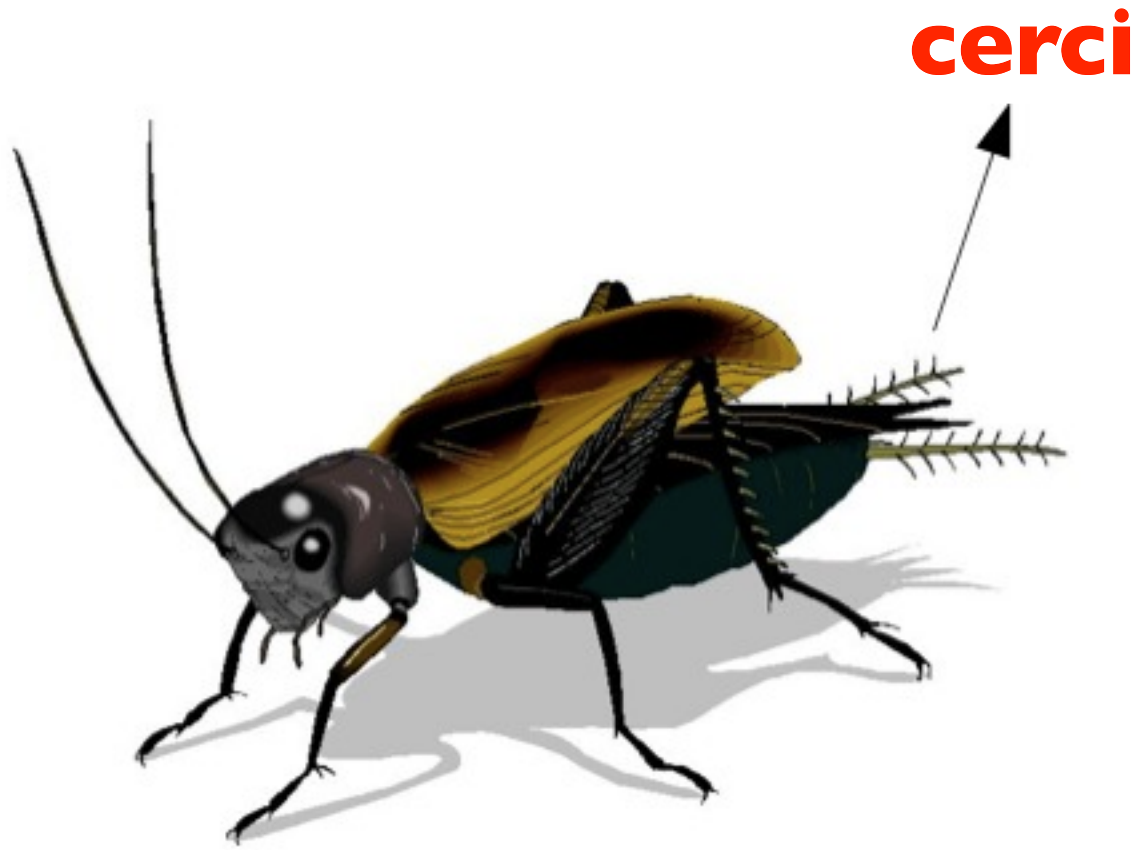




Each neuron has a distribution of responses (is sensitive) over some set of inputs, and the responses of many neurons is combined to determine some value about the inputs

Population code

System: the cercal system of the cricket



Senses air direction as a warning for approaching predators

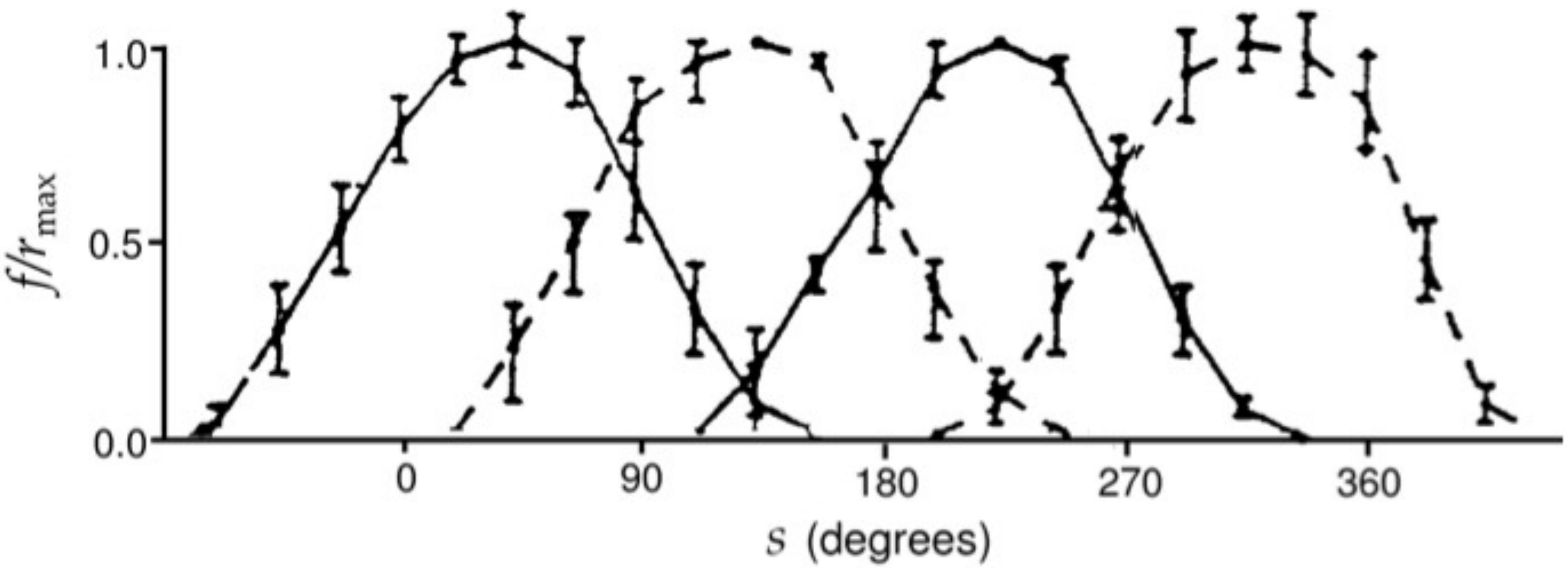
Sensory neurons project to interneurons

At low air-speed **information is encoded by just 4 inter-neurons**

No single neurons responds to all wind directions, **multiple neurons respond to any wind direction**

Population code

System: the cercal system of the cricket



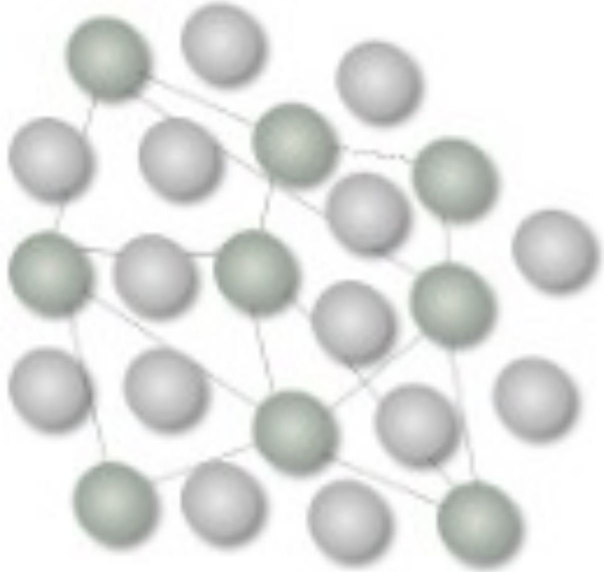
These 4 neurons are sensitive to the angle of wind

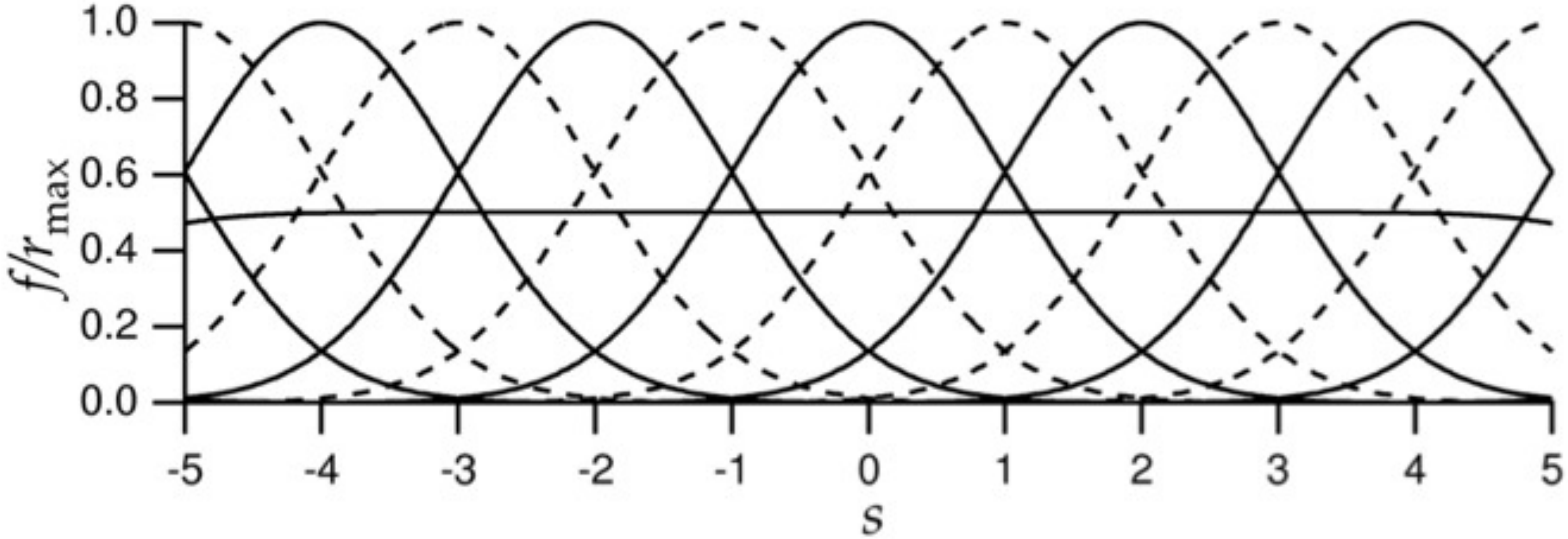
Preferred directions $\mathbf{c_a}$: -135°, -45°, 45°, 135°

Note: rate code also assumed

Crickets are cartesian!

Population code





By using a large number of neurons to represent information:

1. **Reduction of uncertainty** (& fast)

2. **Immune** to fluctuations existing in **single neuron's signal**

3. Ability to represent a number of **different attributes simultaneously**

THE neural code?

Q:

What kind of code do neurons use to represent sensory information and communicate with each other?

Is precise timing important (temporal code) or are firing rates (rate code) enough?

Which variability is noise and which information?

A:

Probably, we should talk about the neural codes of the brain, where **different codes** (rate, temporal, population, ?) interact and are used to a **different degree in different regions** of the brain (and different animals)

Some principles for codes

1. Efficient coding hypothesis: Neural codes minimize the number of spikes (cost) needed to transmit a given signal

Neurons in the visual (or auditory) system are optimized for coding images (or sounds) from their natural environment

To investigate neural codes we should test with **natural stimuli**

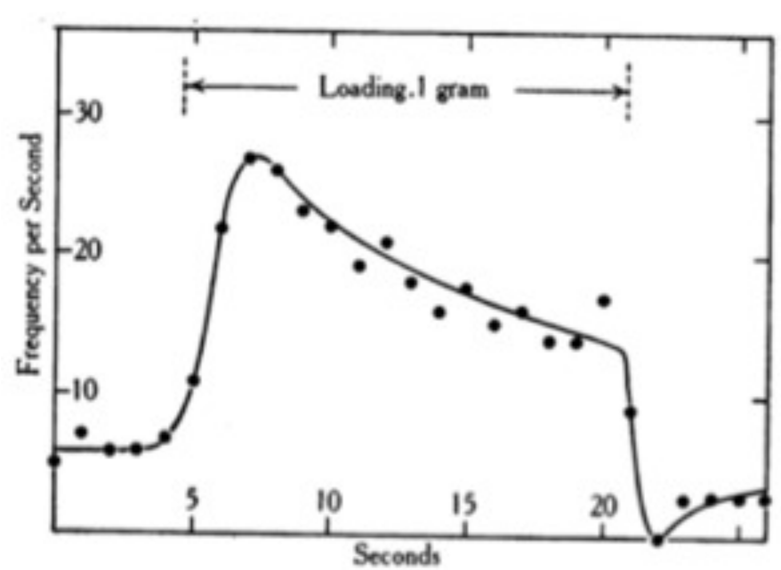
Some principles for codes

1. Efficient coding hypothesis: Neural codes minimize the number of spikes (cost) needed to transmit a given signal

Neurons in the visual (or auditory) system are optimized for coding images (or sounds) from their natural environment

To investigate neural codes we should test with **natural stimuli**

2. Adaptive coding: Neural codes adapt to the regularities of stimuli



Neuronal decoding

Read-outs and information theory

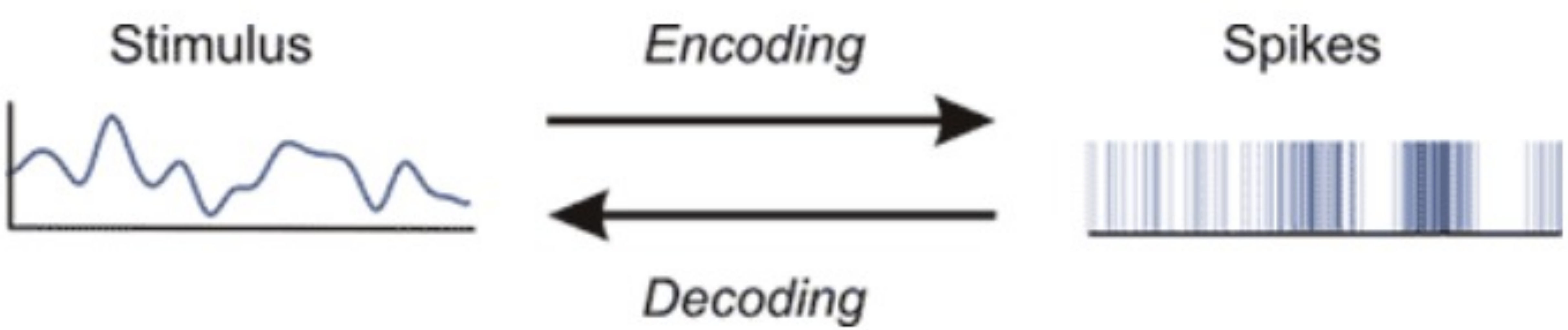
Estimators

Neural decoding

Decoding: opposite map, from response to stimulus

Given a response, what was the stimulus?

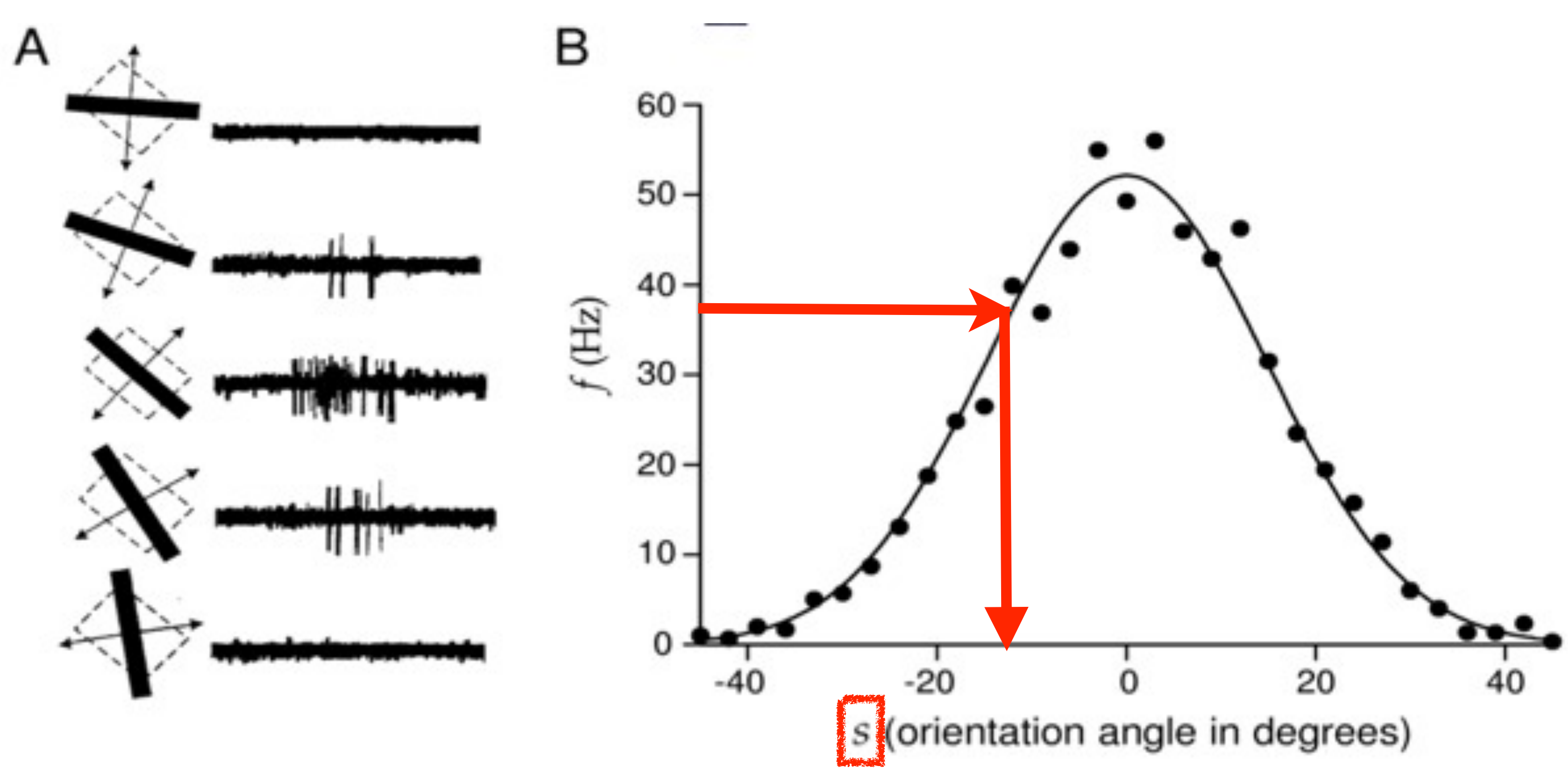
Given a firing pattern, what will be the motor behavior?



Neural decoding

How to determine what is going on in the real world from the cortical dynamics?

Using the responses of one or more neurons to identify the stimulus



Why?

Fundamental

A lot of information processing in the brain consists of routing or discarding information...

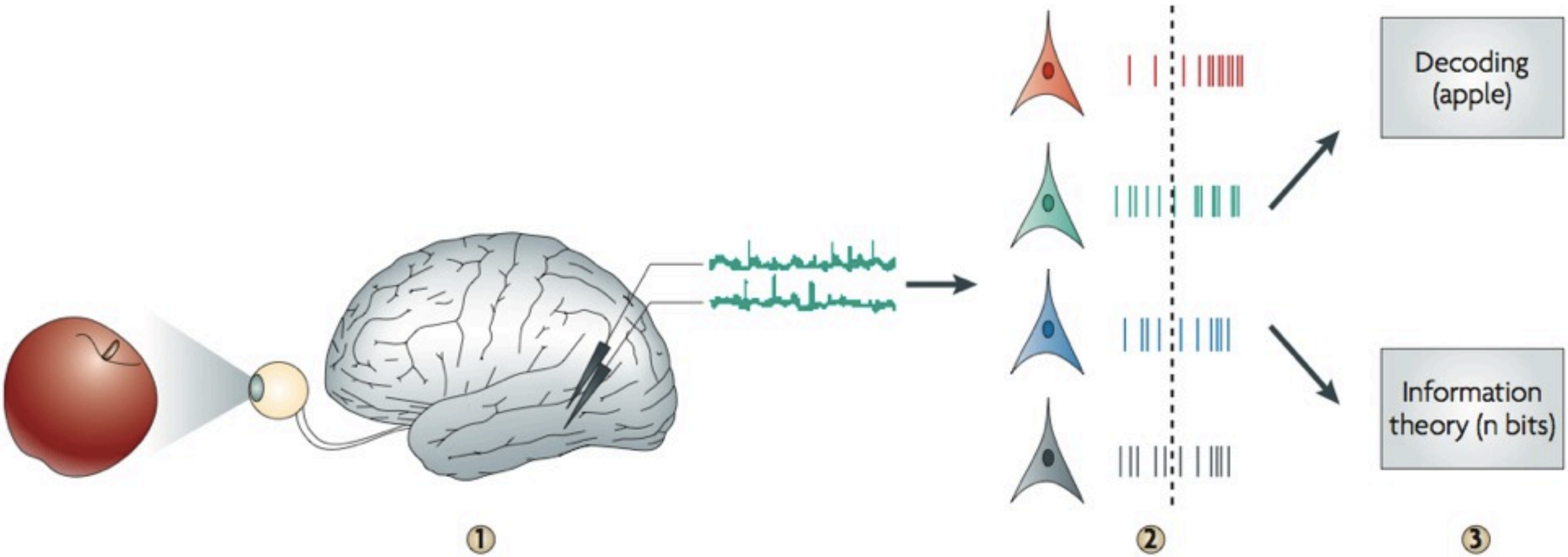
What aspects of a stimulus are important for each brain area?

Practical

Neural prosthetics (ex. neural signals into movements)

Infer subjective human experience directly from brain activation

Read-Outs & Information Theory



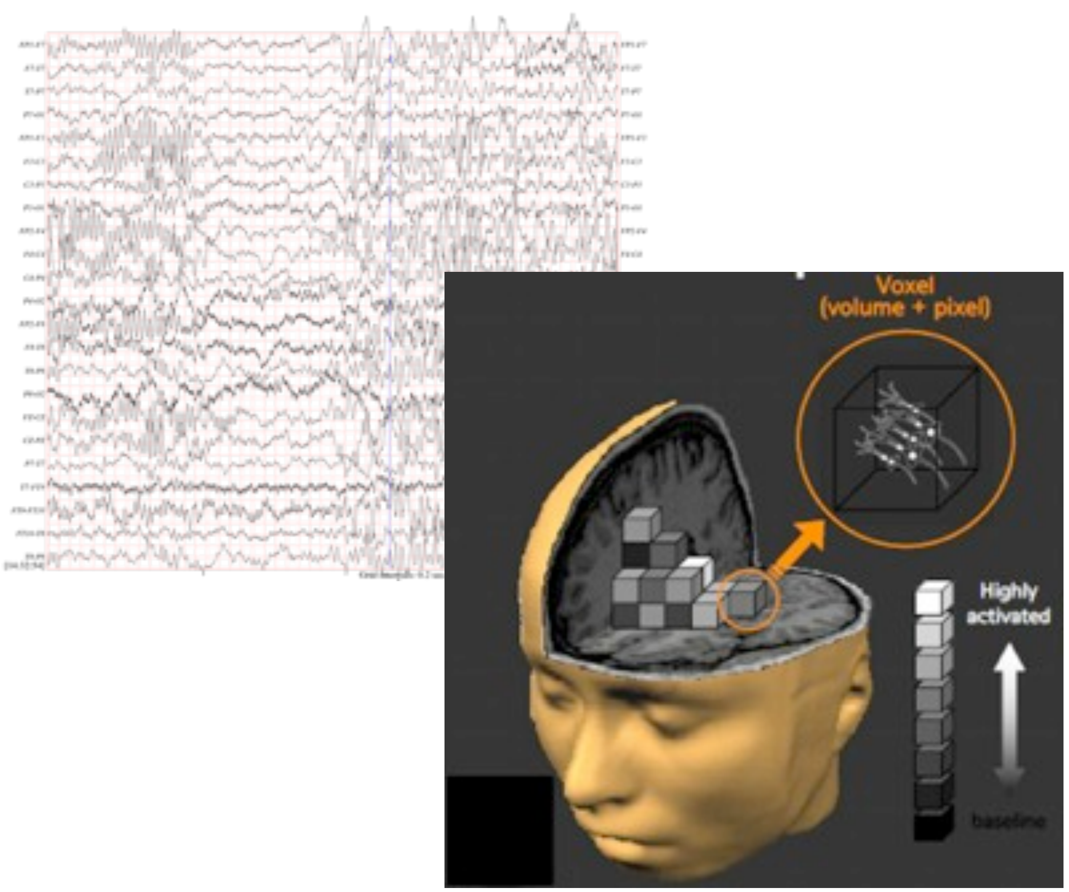
RO: predict which stimulus or behavior elicits an observed neural response (ex., classifiers in % accuracy)

IT: reduction of uncertainty about the stimulus obtained by knowing the neural response (ex., mutual information in bits)

Machine Learning: algorithms that learn from data

- "Teaches" the algorithm with correct examples to learn the relation between neuronal signals *X* and behavior *Y* (or stimulus)

- What? Where? When?



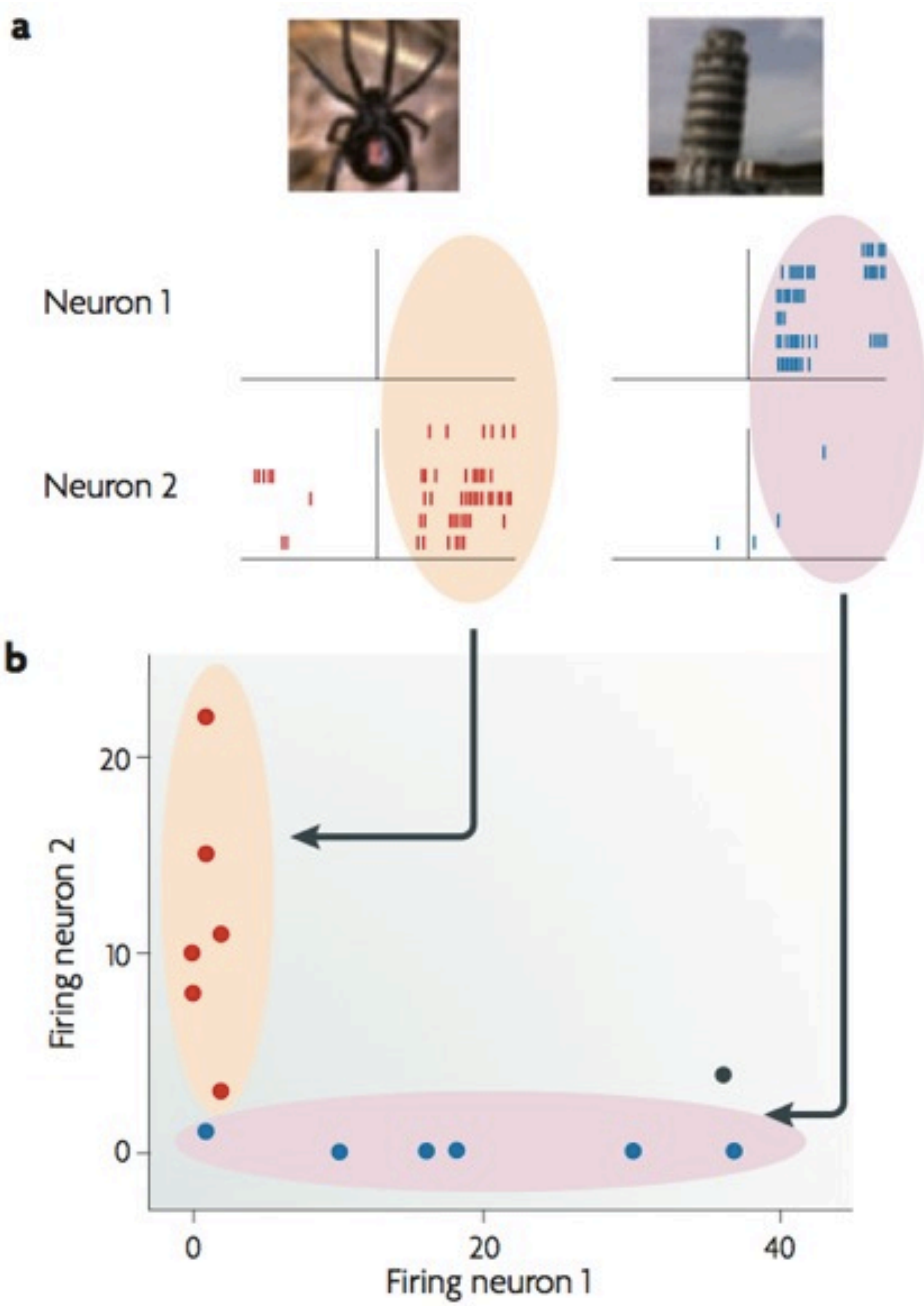
classifier

$f: X \rightarrow Y$

Y~
behavior, stimuli

X~ spikes, LFP, EEG, fMRI

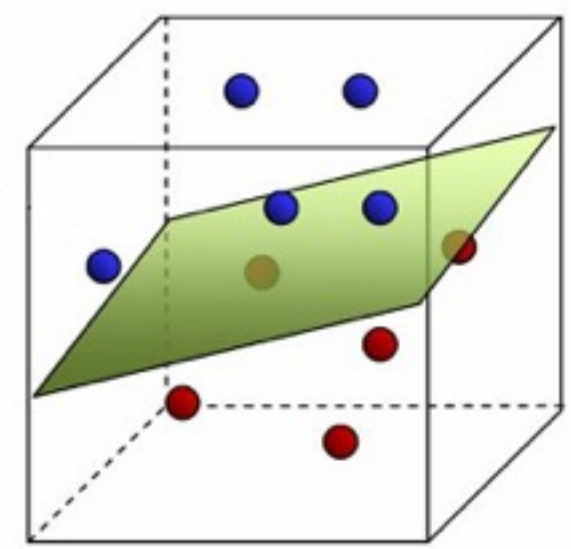
Read-Outs: the problem



Prediction: given the firing rate of the two neurons...which class was the stimulus?

Features: $\{\mathbf{r_1}, \mathbf{r_2}\}$

Labels: {**0**,**1**} (**animal**,**building**)



Machine learning

Read-Outs: formulation

Idea: train a classifier to discriminate between different classes of stimuli (or decisions) and used to predict novel examples

Features: can be firing rates in intracraneal recordings, power of oscillations in EEG, voxel activity in fMRI,...

$$\mathbf{x} = (x_1, x_2, ..., x_v)$$

Classifier: a function f(.) that takes the values of the observed features (ex., voxels) and predicts to which class *y* the observation belongs

$$y = f(\mathbf{x})$$

Read-Outs: training & test

Training data

A classifier has a number of parameters that have to be learned

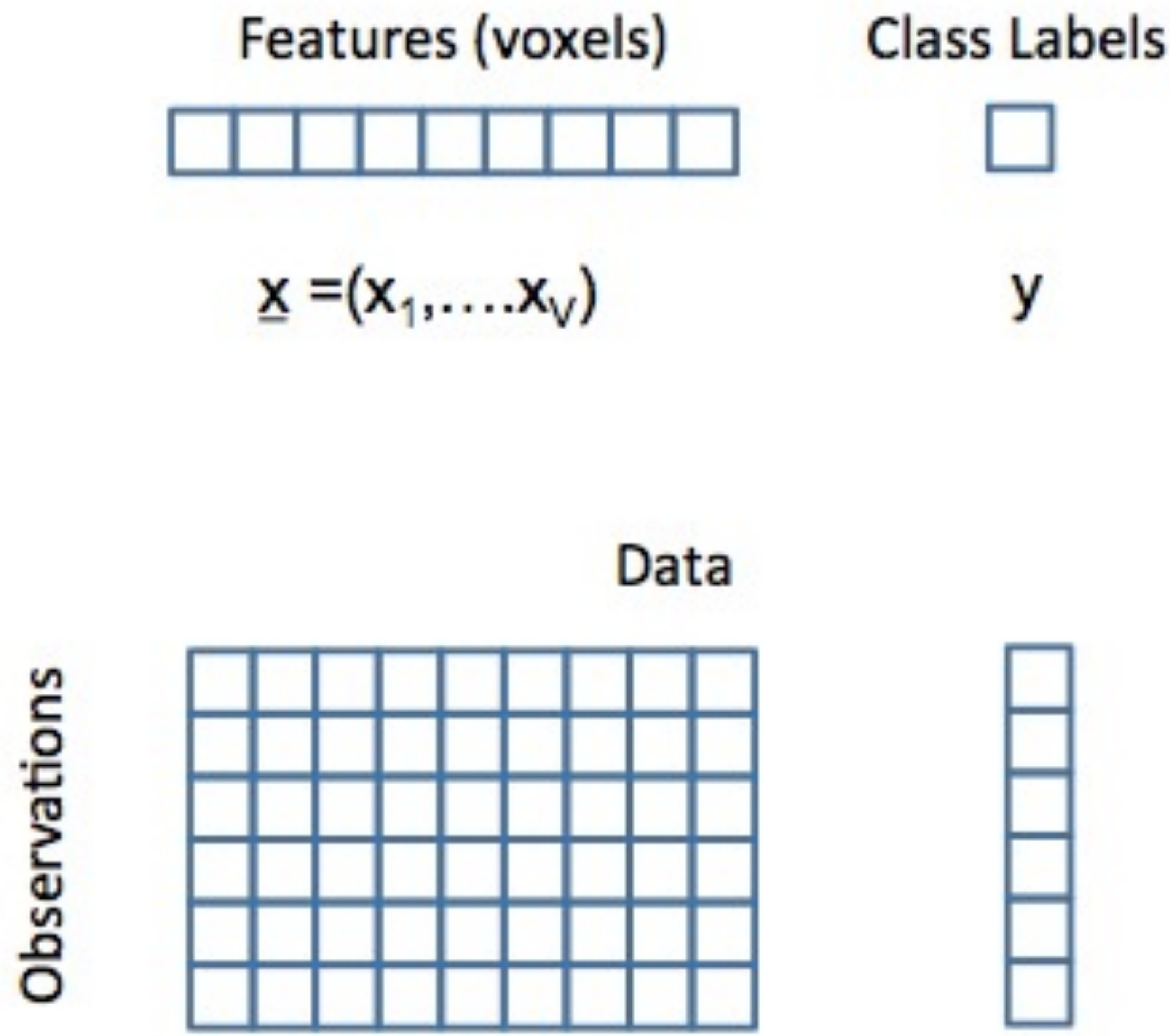
A learned classifiers models the relation between features and class labels in the training data set

Test data

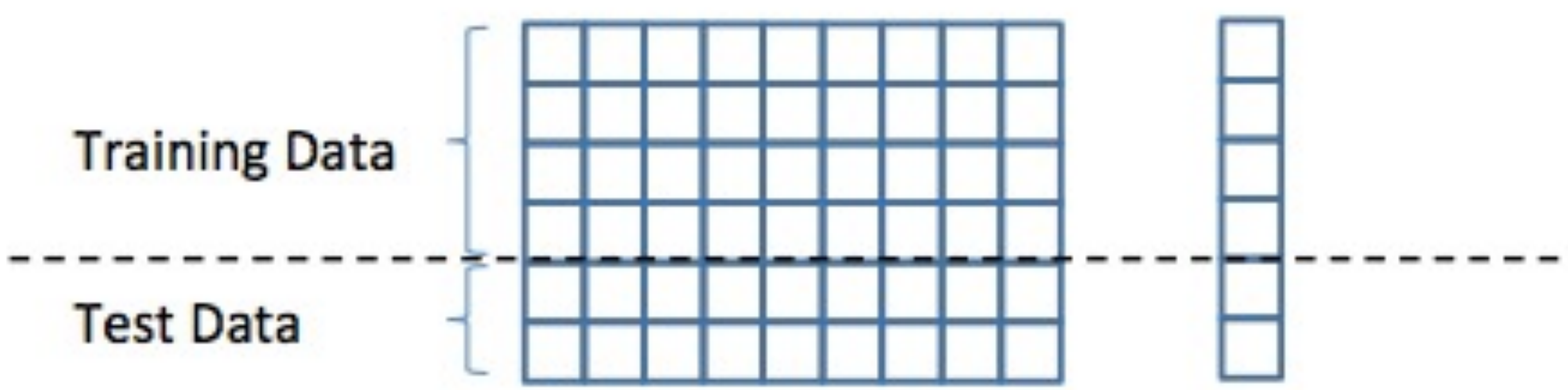
If the classifiers truly captures the relation between features and labels, it should predict the class label for data it has not seen before

Once trained the classifier is evaluated using an independent set of observations (test data)

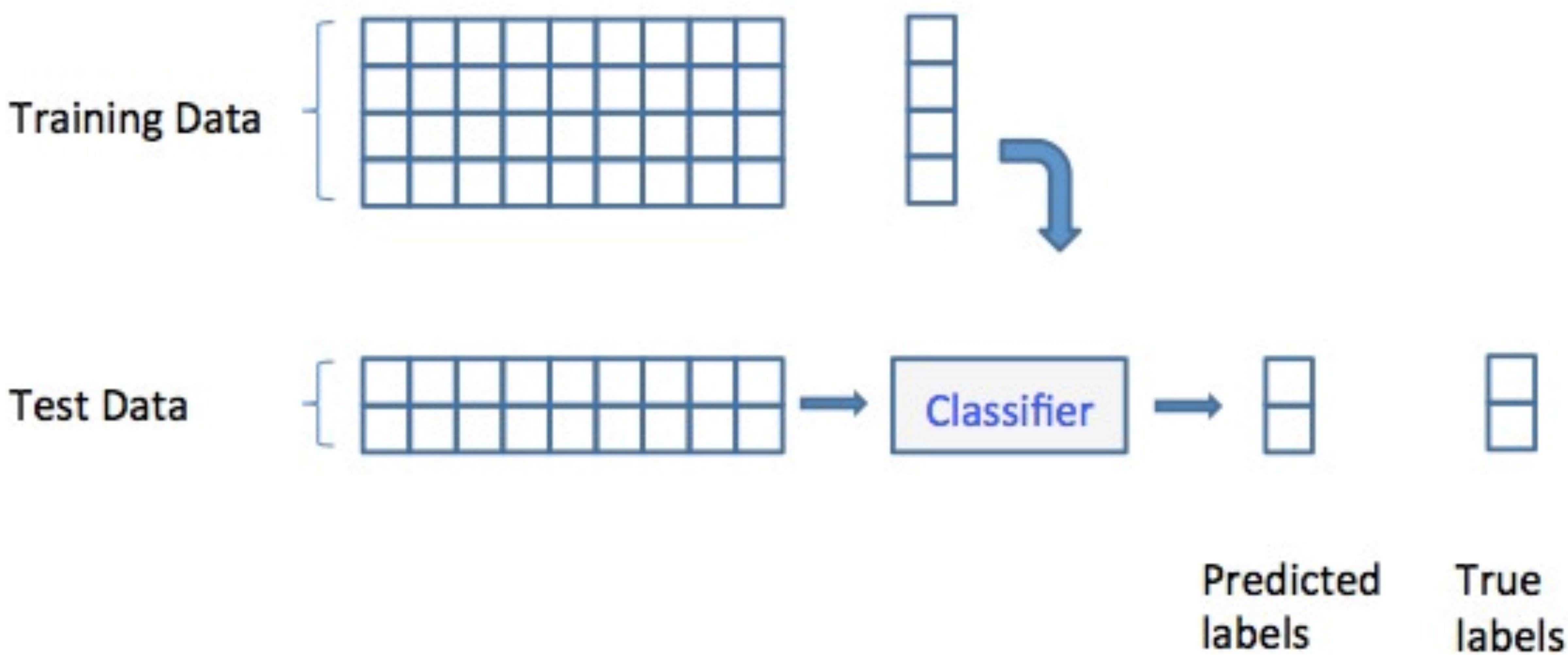
Read-Outs: illustration



Read-Outs: illustration

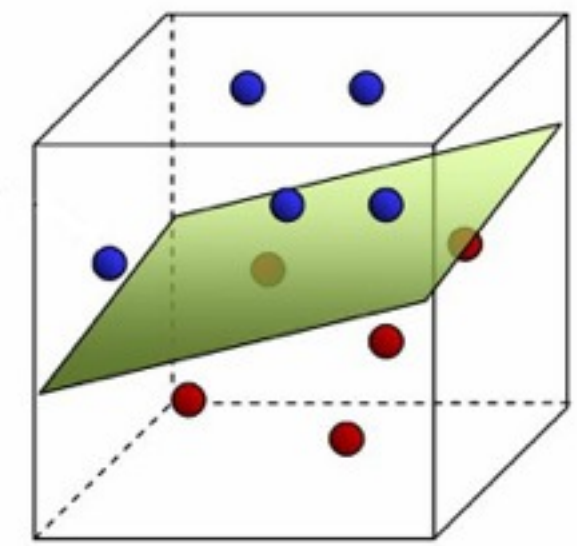


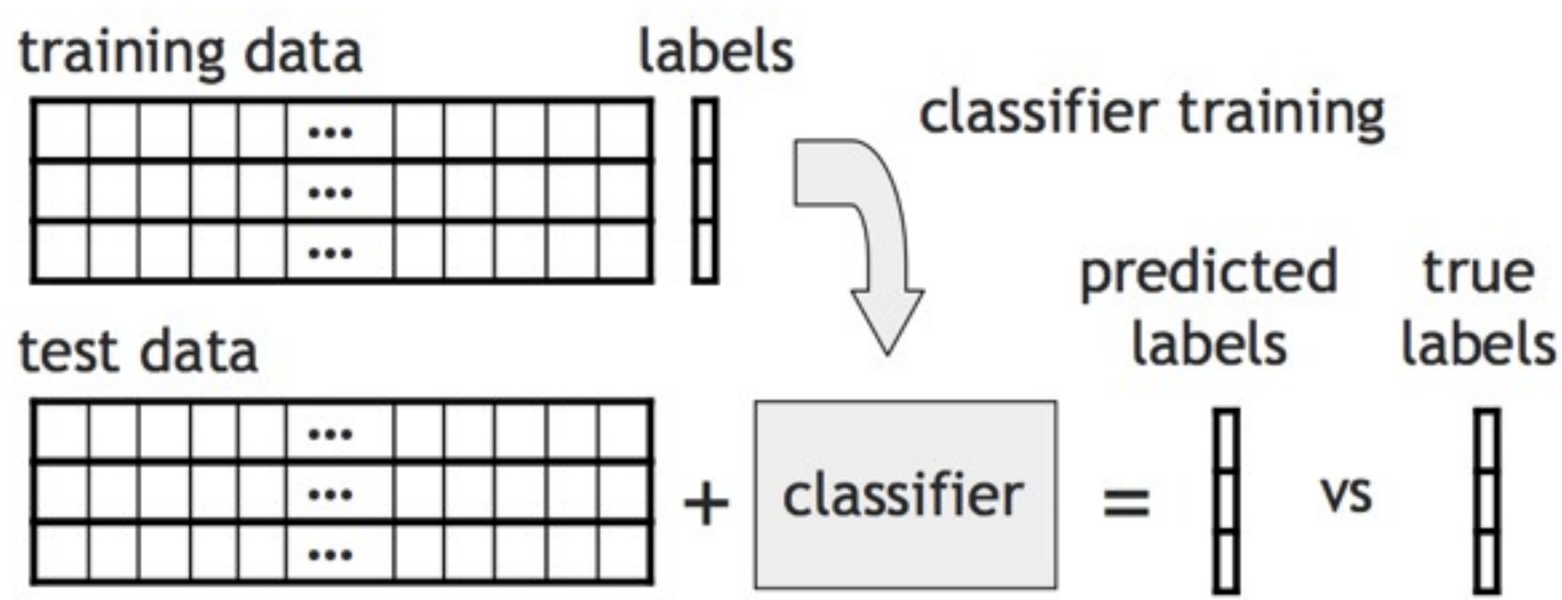
Read-Outs: illustration



Read-Outs: summary

1. Defining features and classes
2. Feature selection
3. Choosing a classifier
4. Training and testing a classifier
5. Examining results





Read-outs: choose a classifier

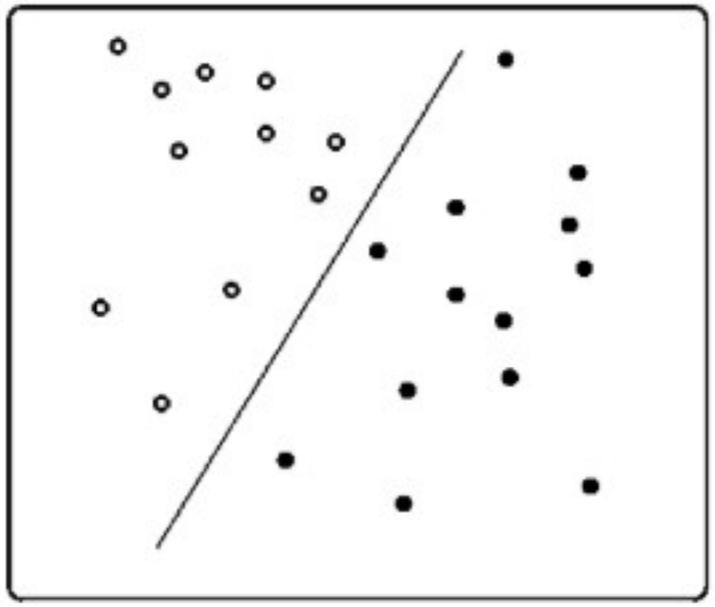
Linear:

Naive Bayes (NB)

Support Vector Machines (SVM)

Logistic Regression (LR)

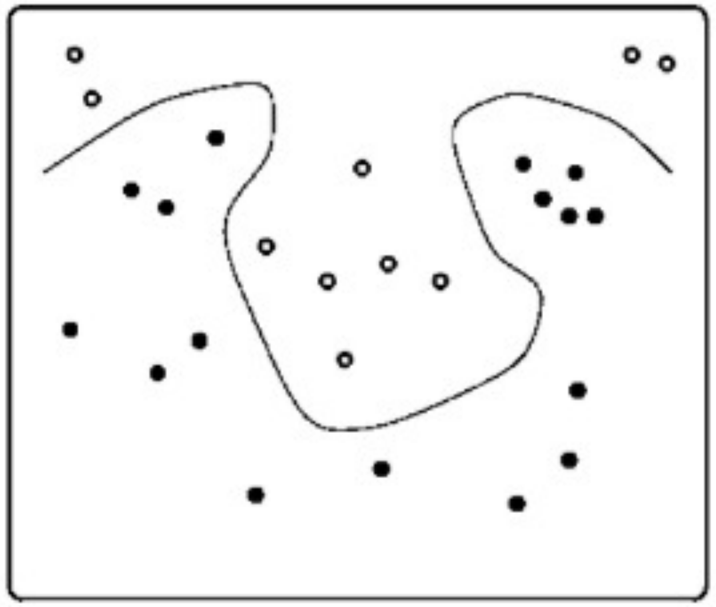
Linear Discrimination Analysis (LDA)



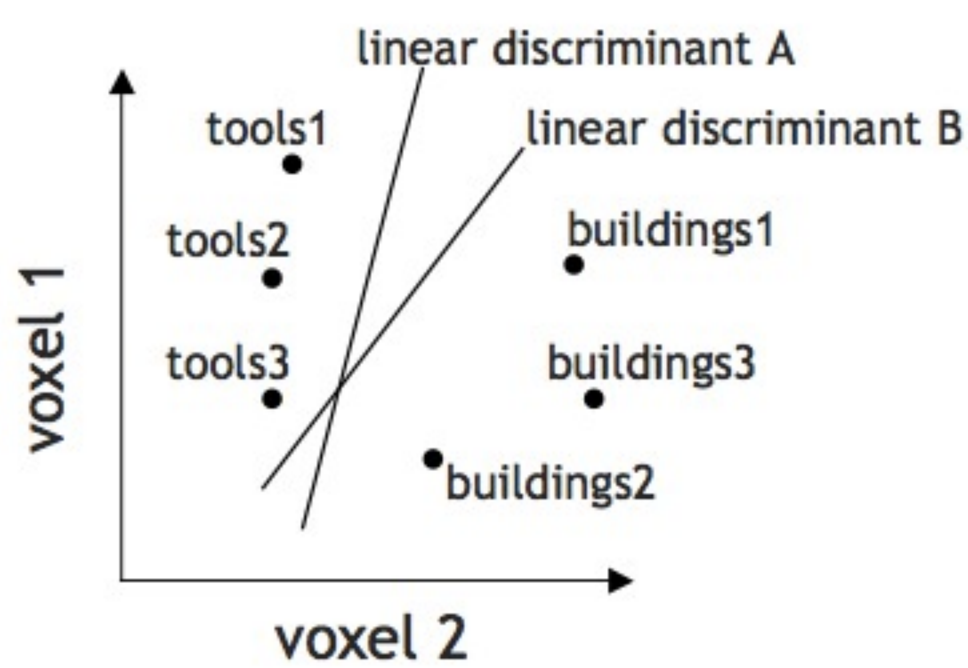
Non-linear:

Kernel SVM

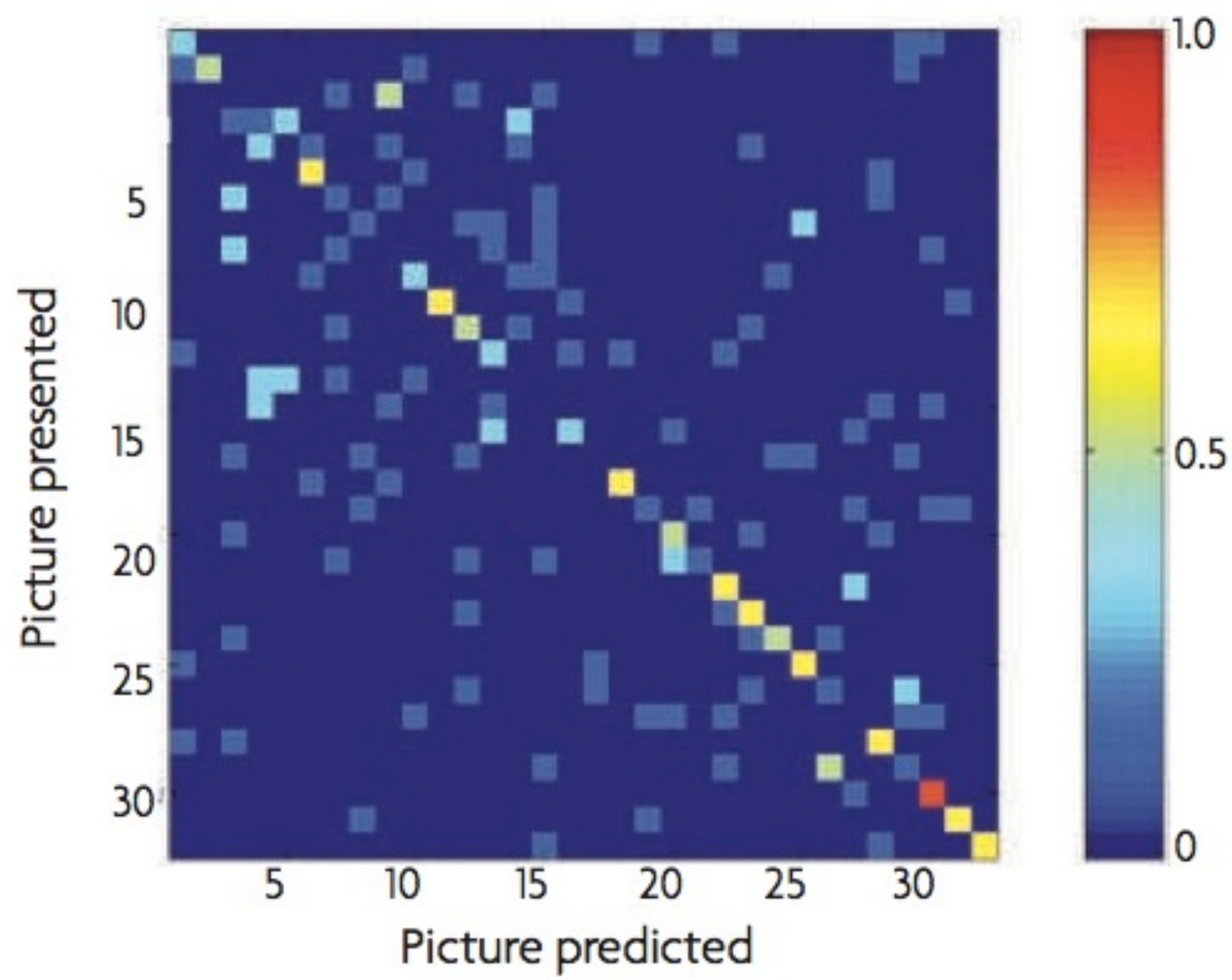
Artificial Neural Networks (ANN)



Read-outs: presenting results

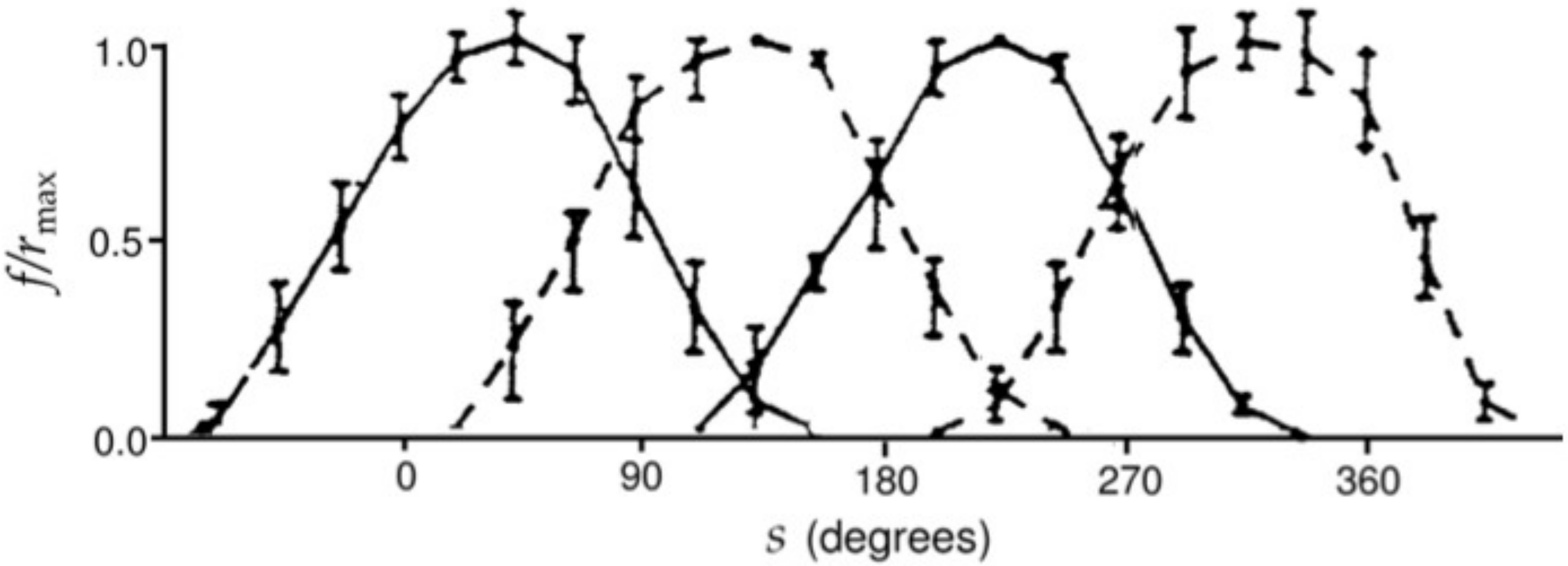


Confusion matrix



Estimators: back to the cricket

System: the cercal system of the cricket



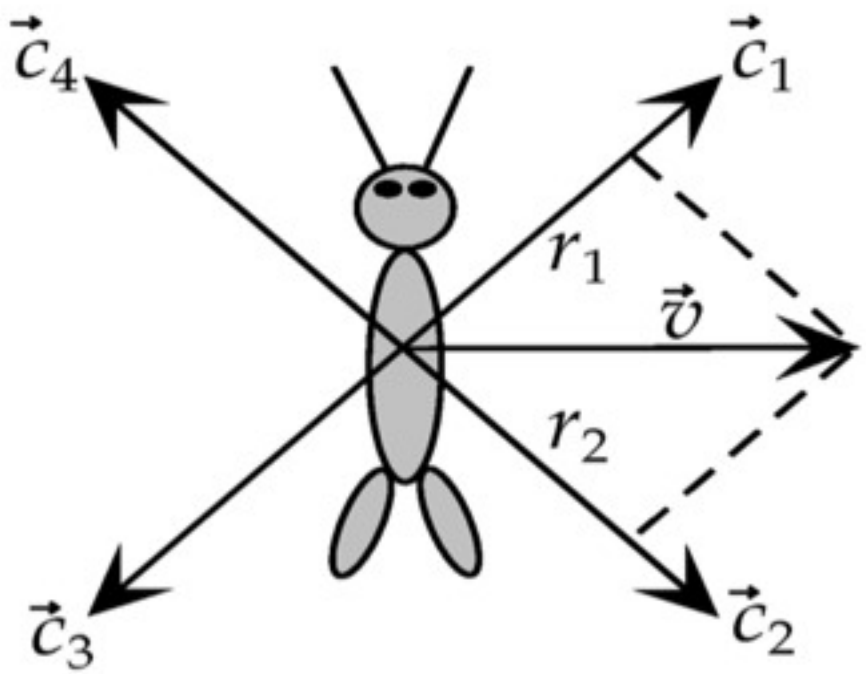
These 4 neurons are sensitive to the angle of wind

Preferred directions $\mathbf{c_a}$: -135°, -45°, 45°, 135°

Crickets are cartesian!

Estimators: population vector

An heuristic method to decode orientation (or any periodic variable) is to say that neuron **a** "votes" for a vector, $\mathbf{c_a}$, with a strength determined by its activity $\mathbf{r_a}$



$$\vec{v}_{\text{pop}} = \sum_{a=1}^{4} \left(\frac{r}{r_{\text{max}}} \right)_a \vec{c}_a$$

Similar results have been observed for arm reaching movements in monkeys

Estimation: optimal decoding

The vector method is not general nor optimal

Other methods than can be called "optimal" take into account the full probabilistic model of encoding:

Maximum likelihood estimator **Bayesian estimates**

$$P(r|s) \qquad\qquad P(s|r)$$

Estimation: ML estimator

Values of ***s*** for which $p(r|s)$ is high are the stimuli which are likely to have produced the observed activities ***r***; values of ***s*** for which $p(r|s)$ is low are unlikely

Maximum likelihood estimator

$$\boxed{\hat{s}_{ML}(r) = \arg\max_{s} p(r|s)}$$

Estimation: Bayesian estimator

Bayesian estimators combine the likelihood $p(r|s)$ with any prior information about the stimulus ***s*** to produce a posterior distribution $p(s|r)$

Bayesian estimator

$$p(s|r) = \frac{p(r|s)p(s)}{p(r)} \qquad p(r) = \sum_s p(r|s)p(s)$$

$$\boxed{\hat{s}_{MAP}(r) = \arg\max_s p(s|r)}$$

Summary

- Encoding deals with the way stimulus is map to neural activity
- Cortex faces the opposite problem (decoding): to infer real world stimulus from neuronal dynamics
- There are several plausible and non-mutually exclusive neural codes: rate, temporal, population...
- Decoding neural activity with read-outs is a useful tool for investigating neural processing and BCI

Lesson	Title
1	Introduction
2	Structure and Function of the NS
3	Windows to the Brain
4	Data analysis
5	Data analysis II
6	Single neuron models
7	Network models
8	Artificial neural networks
9	Learning and memory
10	Perception
11	Attention & decision making
12	Brain-Computer interface
13	Neuroscience and society
14	Future and outlook: AI
15	Projects presentations
16	Projects presentations

Basics

Analyses

Models

Cognitive

Applications