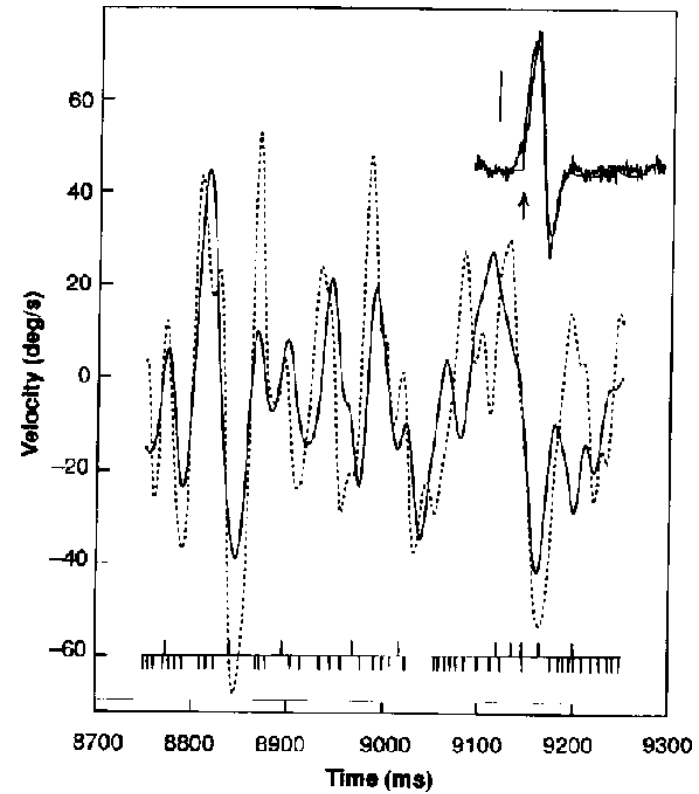


Most popular hypotheses

- A) **Rate codes:** Exact firing times are not important. Just the number of action potentials carries information.
- B) **Population codes:** The information is in the neural population, not in single neurons.
- C) **Spike time codes:** The timing of spikes is important

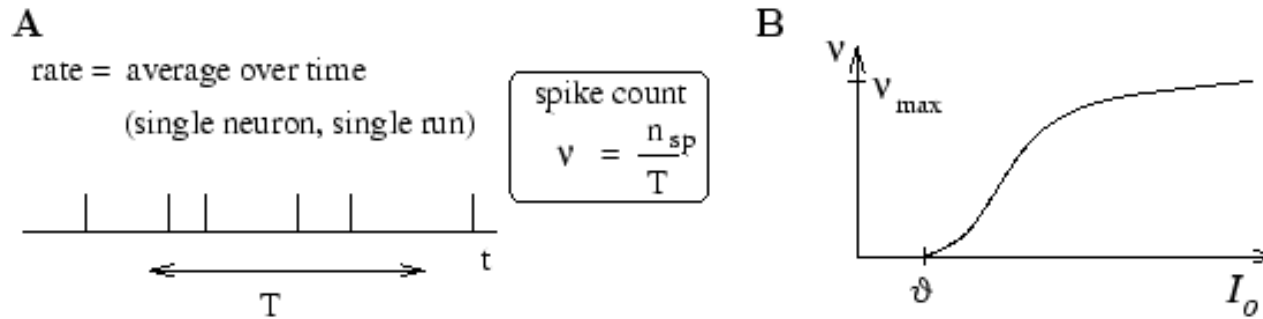


Count spikes. One can consider the mean over

A1 time: the rate of the neuron.

A2 experiments: instantaneous rate

A3 a population of neurons: leads to rate-based population codes.



T is on the order of 100 to 500ms.

ν is the firing rate

$\nu = g(I_0)$: g is the gain function.

Note: The firing rate in this sense can only change on the time scale of T .

Tuning curve of a neuron: How does the neuron respond to a systematic change of a stimulus?

E.g., temperature sensitive receptors respond to a cooling of the skin under 34°C.

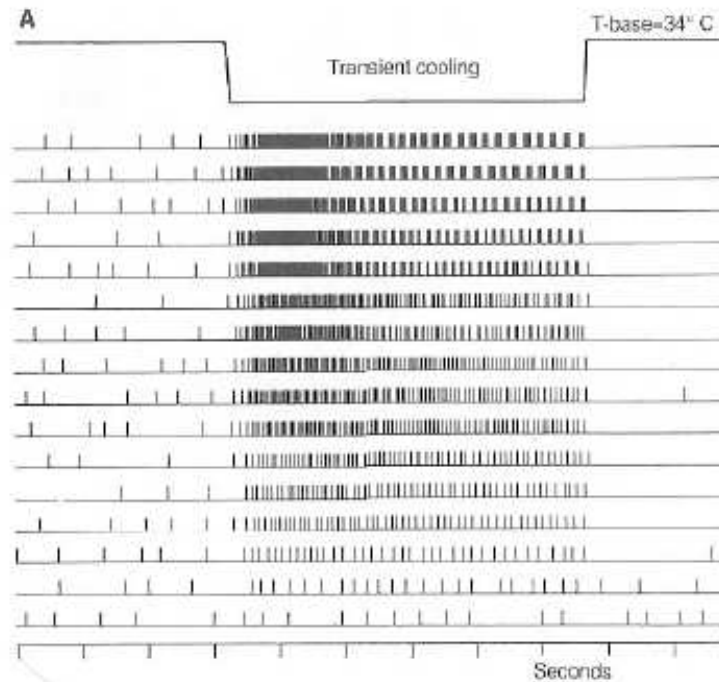


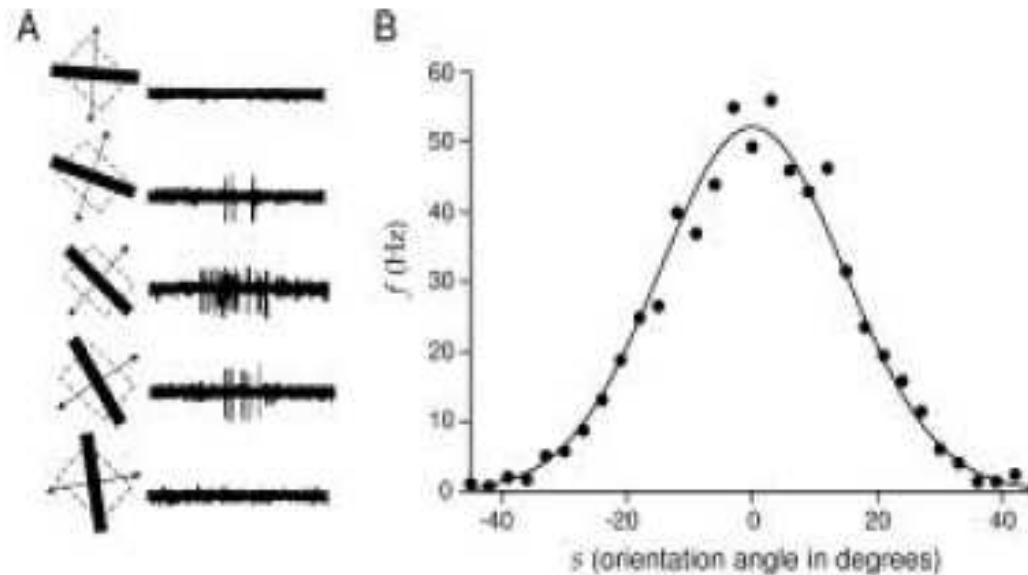
FIGURE 24-4

Cold receptors discharge when the skin is cooled below 34°C.

A. The frequency of discharge of a single cold fiber of a monkey increases with progressively greater cooling. (Adapted from Darian-Smith et al., 1973.)

Orientation tuning in visual cortex.

Let s be one parameter of a stimulus. We denote the average firing rate of a neuron in as a function of s as $f(s)$.

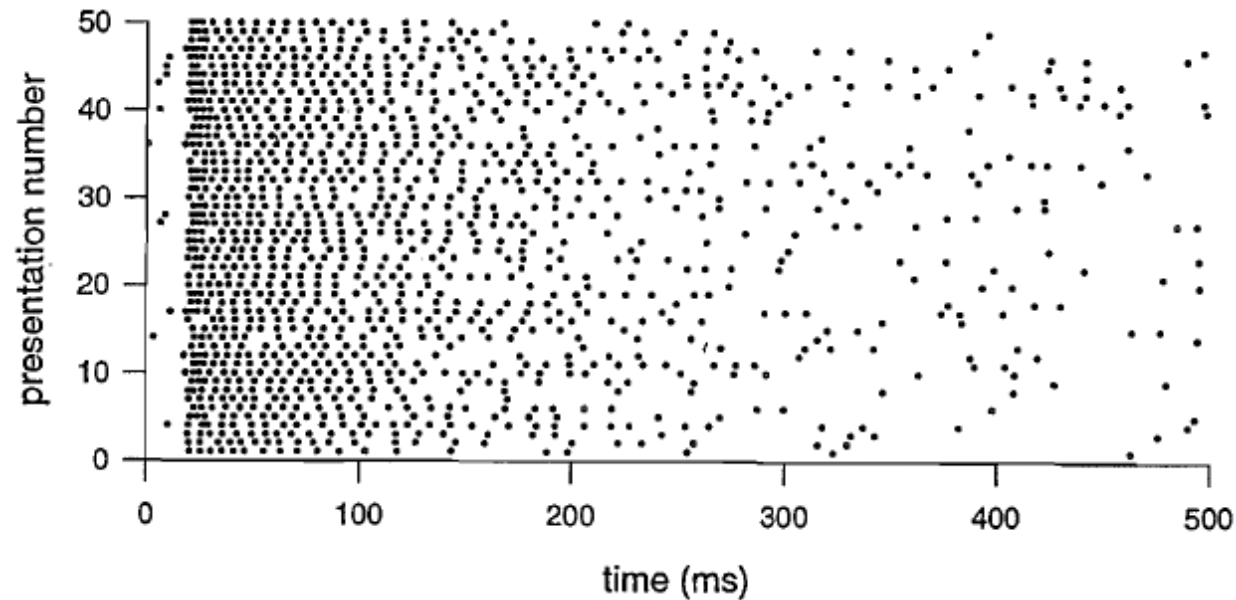


The data can be fitted in the following way:

$$f(s) = r_{max} \exp\left(-\frac{1}{2} \left(\frac{s - s_{max}}{\sigma_f}\right)^2\right).$$

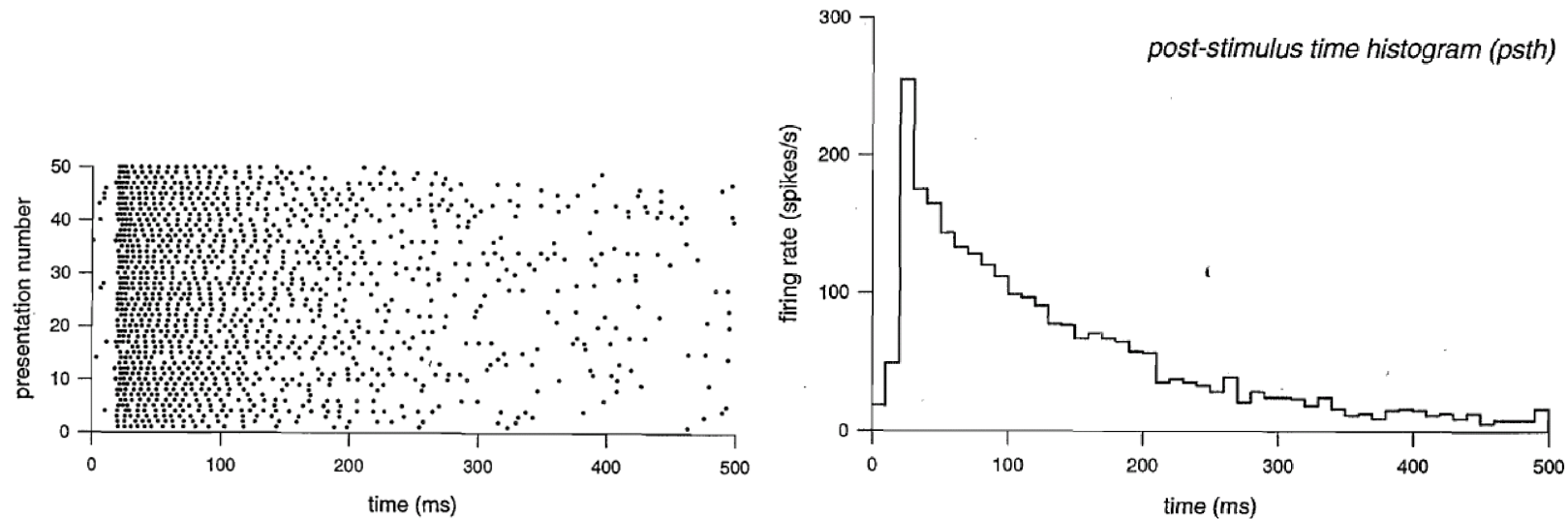
Setup:

- We present a stimulus S at time $t = 0$.
- We measure the response of a neuron for several such presentations.



We see that the response is stochastic.

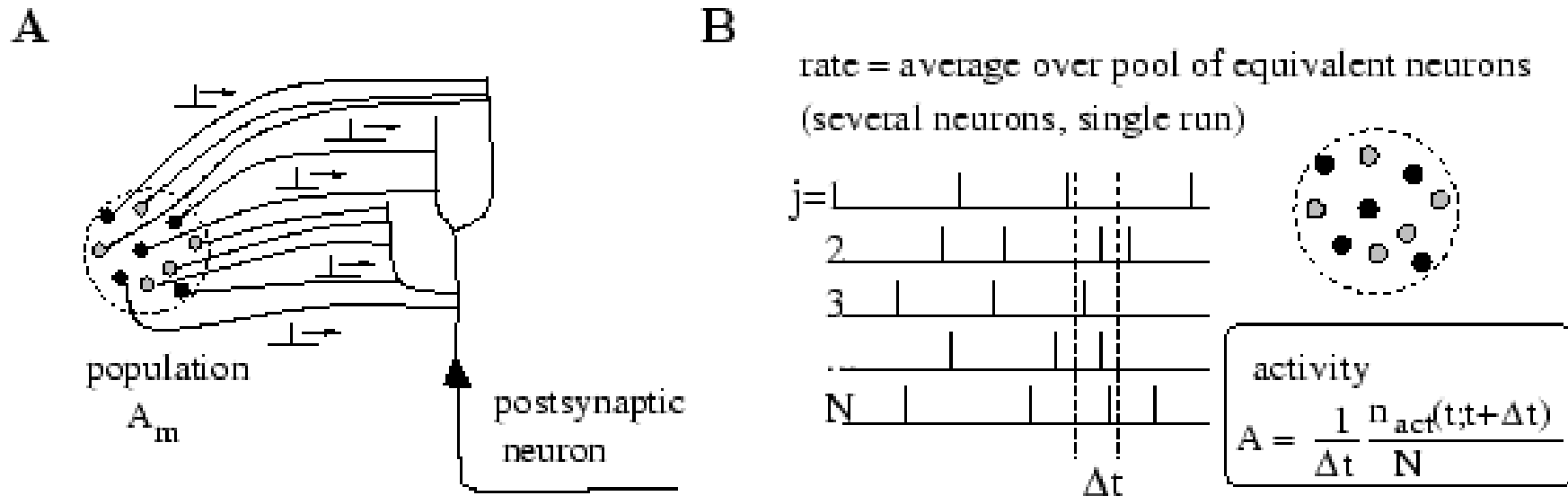
We describe the average response with the *instantaneous rate* $r(t)$:



In an experiment, one counts the number of spikes that occurred in a time window $[t, t + \Delta t]$. The resulting plot is called the *peri-stimulus time histogram (PSTH)*.

$$p(t) = p\{\text{spike in } [t, t + \Delta t]\} \quad r(t) \approx \frac{p(t)}{\Delta t}.$$

Δt is on the order of several ms.

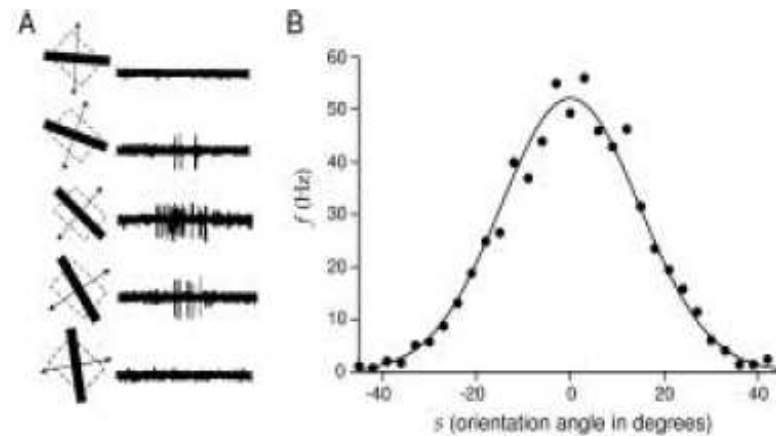


Assumption: All neurons of a population have identical input-output connections and the neurons are spiking stochastically and independently from each other (given the input).

The activity of a population can change fast. However, the assumptions are unrealistic.

The paradigm of population coding denotes in general the idea that a neuronal population collectively codes the stimulus in some simple way.

Why are tuning curves so broad (non selective)?



Three possibilities to code a parameter space (e.g. different orientations). Only variant C is used in the brain.

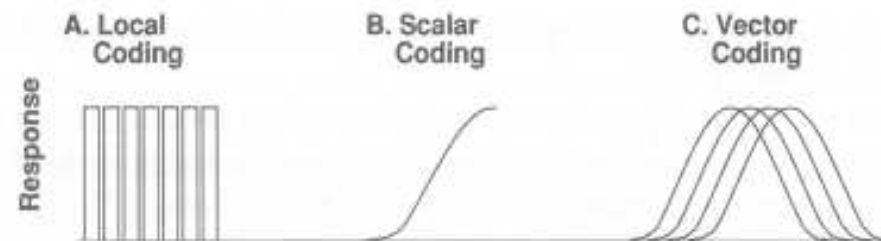
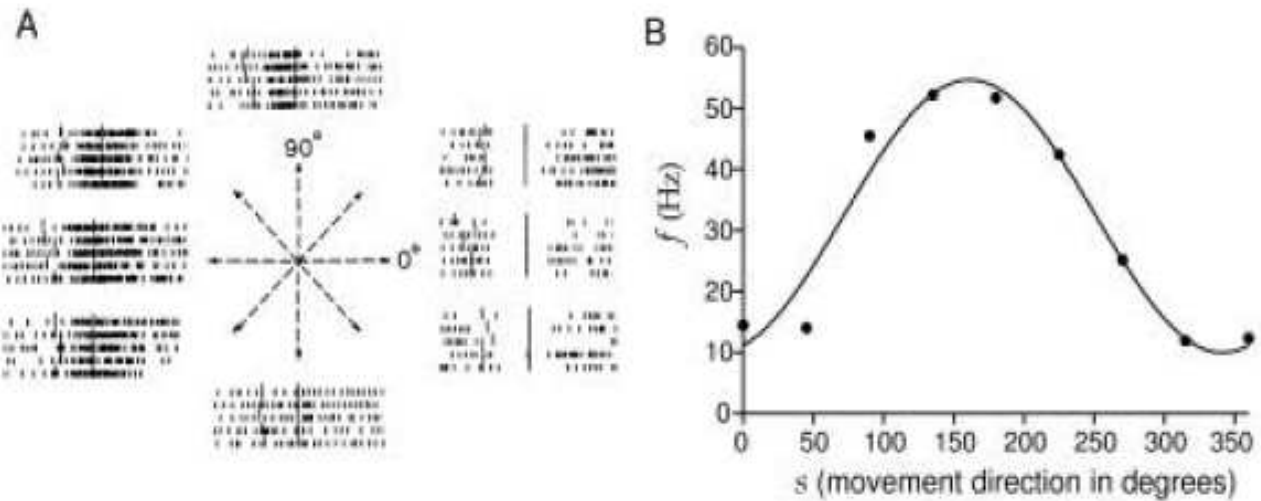
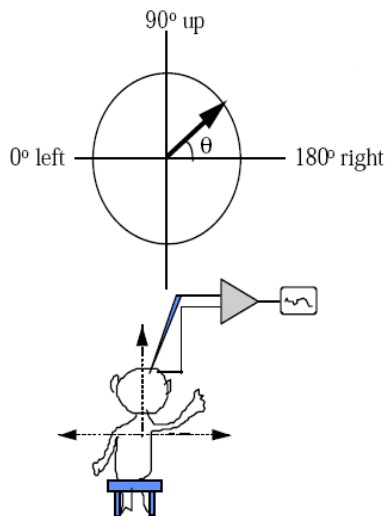
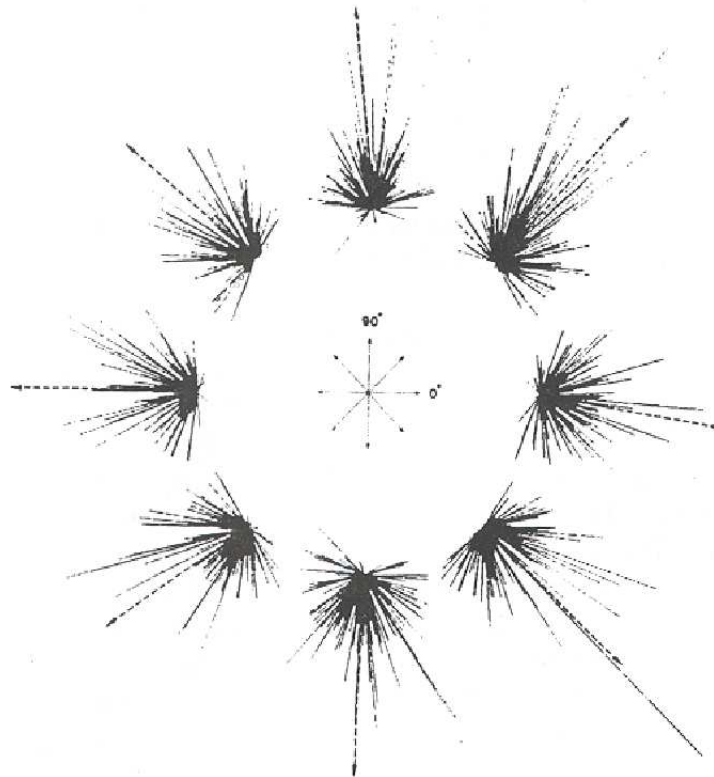


Figure 4.14 Three methods of encoding information. (A) Local coding: a separate unit is dedicated to each feature the system distinguishes. (B) Scalar encoding: features are encoded by the firing rate of a single neuron. (C) Vector coding: features are encoded in the pattern of activity in a population of units that have broad, overlapping tuning curves.

Single neurons code upcoming arm movements with broad tuning curves



If one draws a vector of the preferred direction for each neuron and weights it with the firing rate of that neuron, then one obtains a bundle of vectors. The geometric sum of these vectors is a reliable estimate of the future arm movement.



To be able to utilize the timing of a single spike, one needs a temporal reference frame.

Possible references:

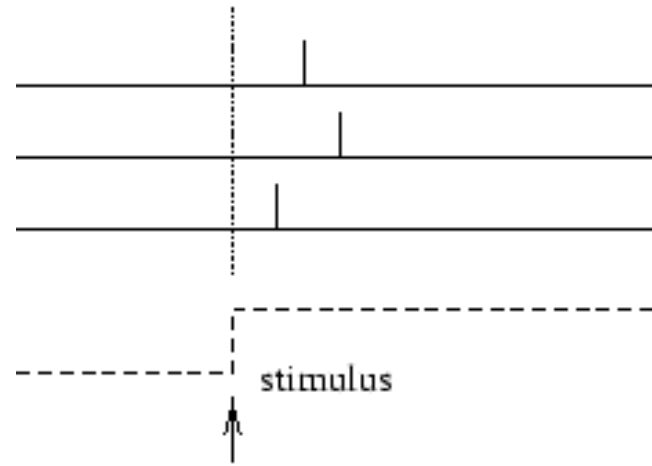
C1) Stimulus: Time-to-first-spike

C2) Phase of an oscillation: Phase code

C3) Other spikes: Correlation and synchrony.

We will also discuss a method to read out information from spike times

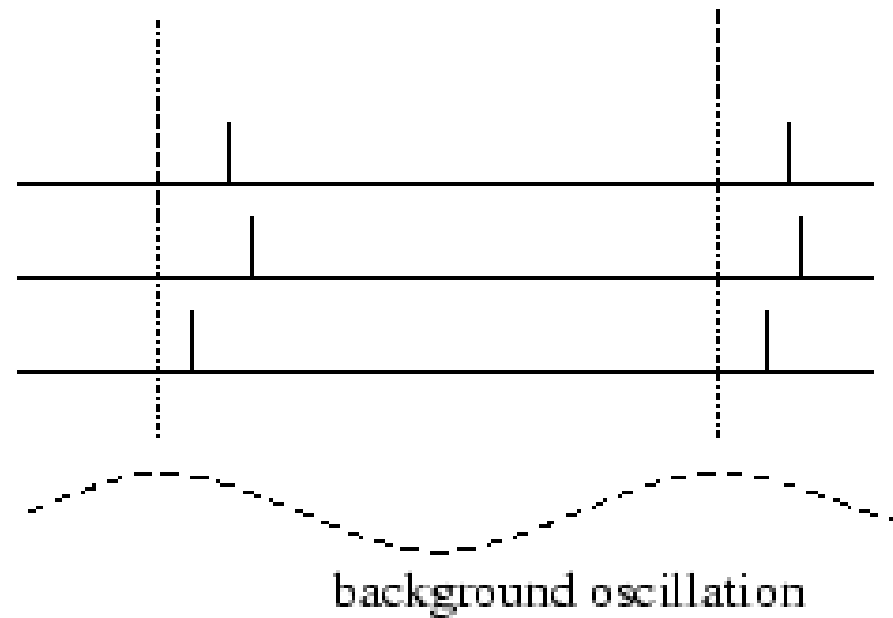
C4) Reverse Correlation



We assume some reference signal at time t_0 .

The time between the reference signal and the first spike of the neuron can code some real number.

Because of the speed of brain computations, most information about a stimulus has to be coded by the first spike (Thorpe, 1996).

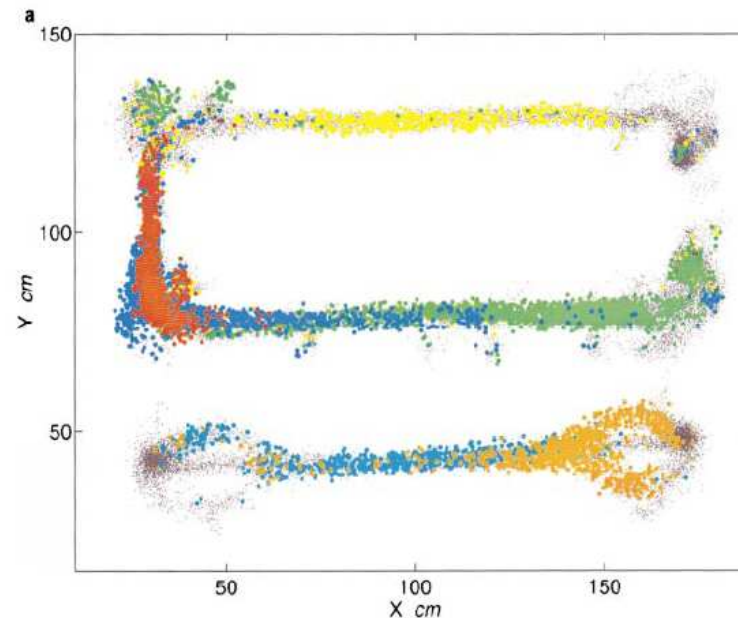


The reference signal can also be periodic.

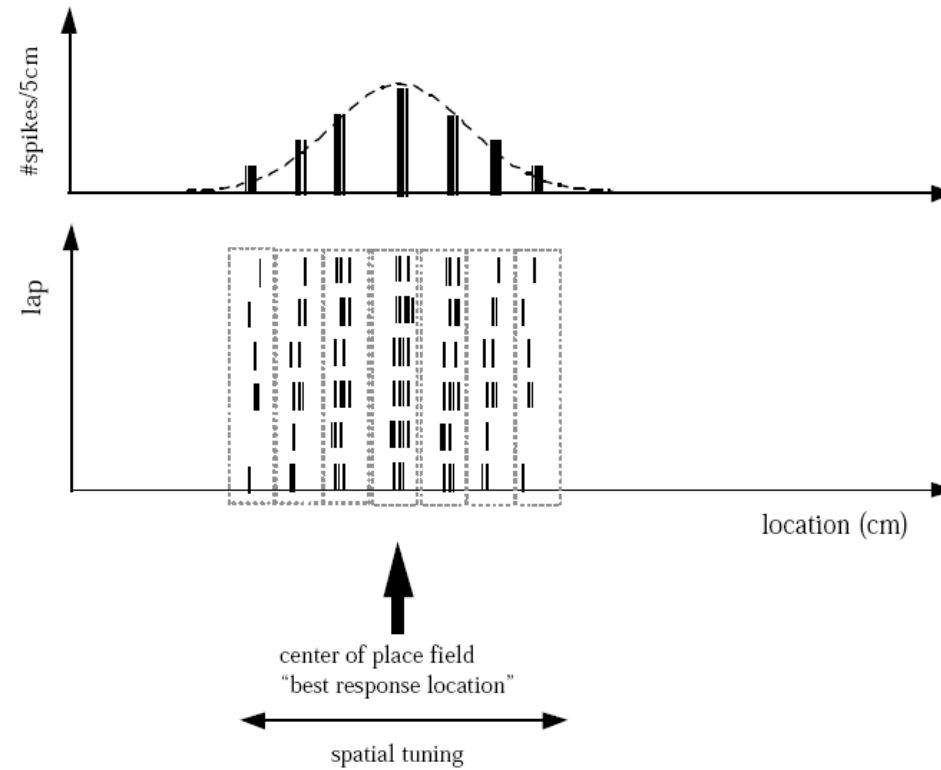
Oscillations are abundant in the brain (e.g. in the hippocampus).

The hippocampus is important for spatial memory.

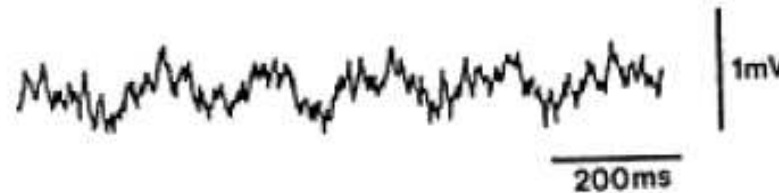
In rodents (mouse, rat), one can find cells in the hippocampus which are sensitive to the position of the animal in space (independent of its orientation).

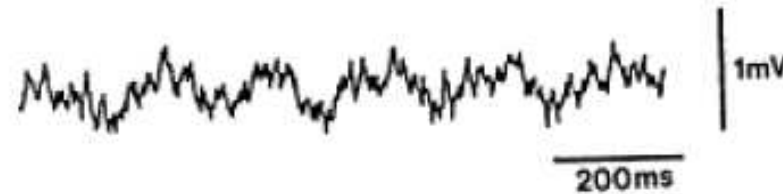


Different cells are marked with different colors in this plot. Each point corresponds to a spike which was emitted by the cell at the given location (Mehta et al 2000).

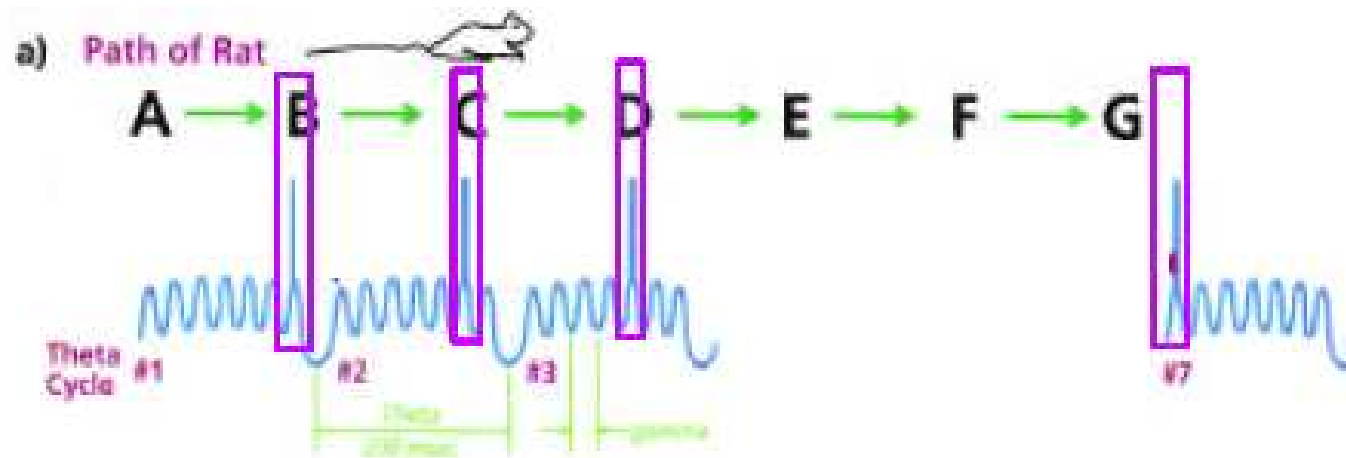


This looks like a rate code. However, one can also compare the spikes to the phase of local oscillations (theta and gamma):



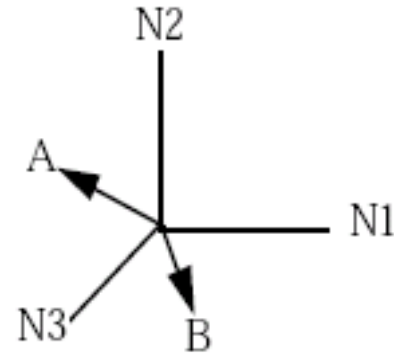
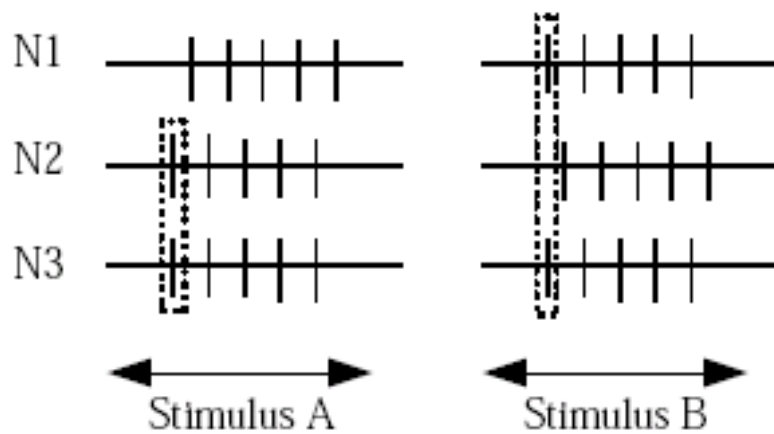


It turns out that spikes are consistently timed with respect to the theta oscillation. They are emitted earlier in the theta period the closer the animal is to the center of the neurons receptive field. (phase precession).



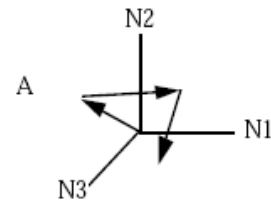
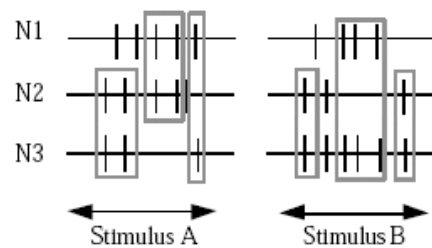
The additional gamma oscillations are sharpening the timing of the spikes (ca. 5-7 gamma oscillations per theta periode). Accuracy ca. 10ms.

The reference signal is given by spike times of other neurons



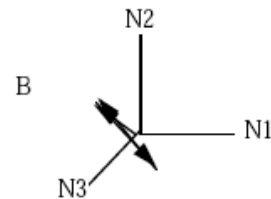
*Synchrony code:
Not rate, or numbers of
spikes count,
but the degree of synchrony
between neurons*

Also possible: Temporal patterns of synchrony

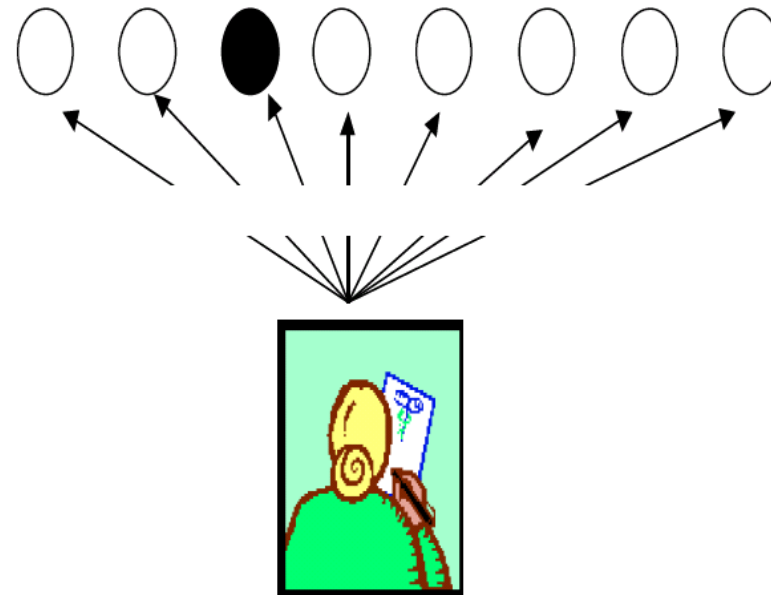


Synchronization trajectory

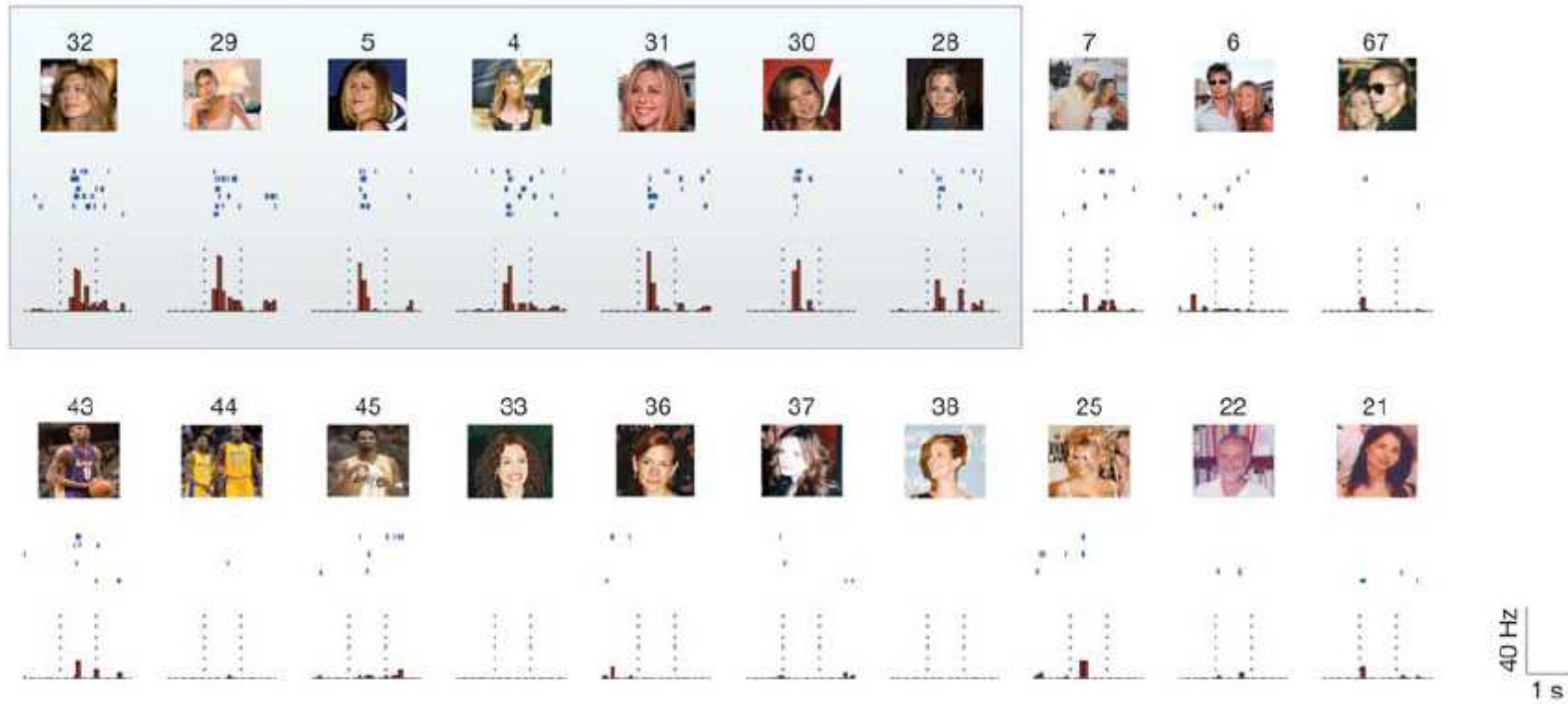
*Synchrony code:
Not rate, or numbers of
spikes count,
but the temporal arrangement
of synchronization patterns*



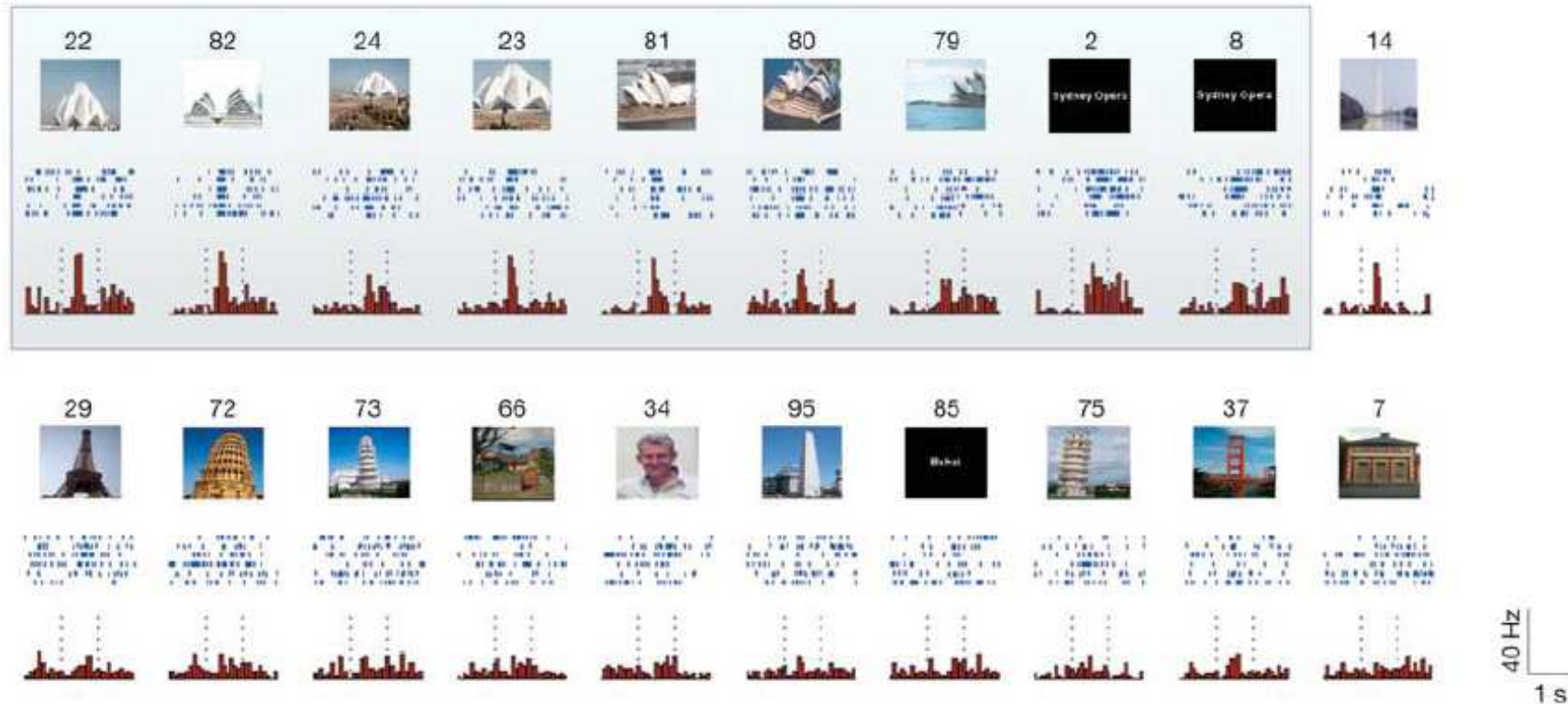
In higher cortical areas, objects are coded by small groups (?) of neurons. This led to the concept of “grandmother cells”: A neuron that fires selectively whenever one sees, smells, hears, (etc.) his grandmother.



Example: Jennifer Aniston neuron (Quiroga et. al., Nature 2005):

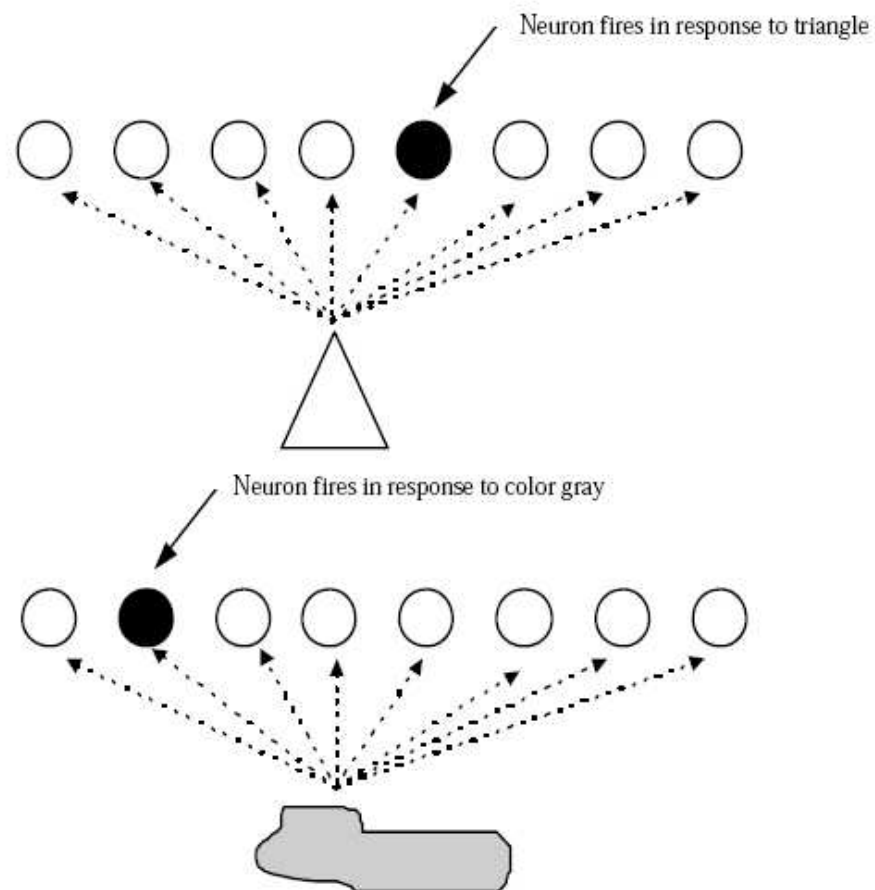


Sydney Oper and Baha'i Tempel (Quiroga et. al., Nature 2005):

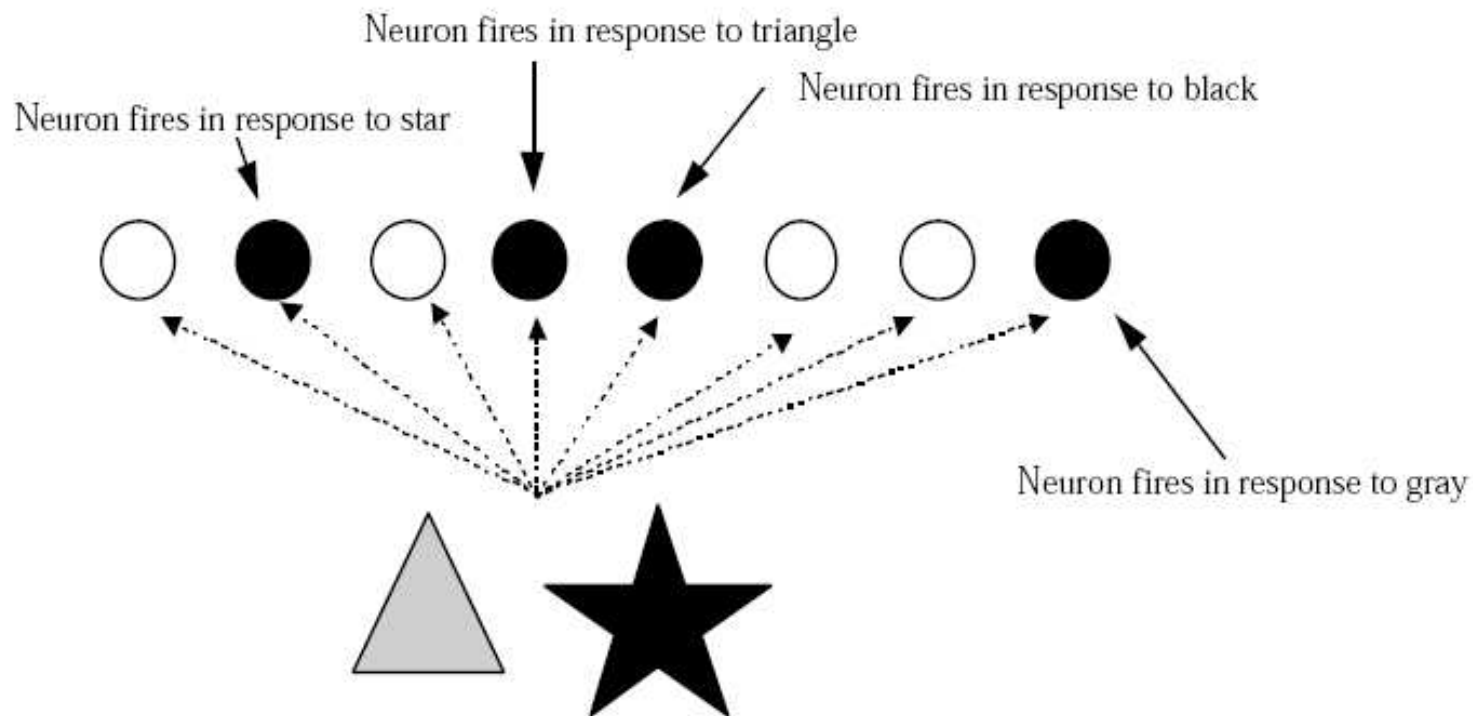


The generalization of these findings is controversial. Do we have a neuron for every combination of features? Example: Yellow Volkswagen.

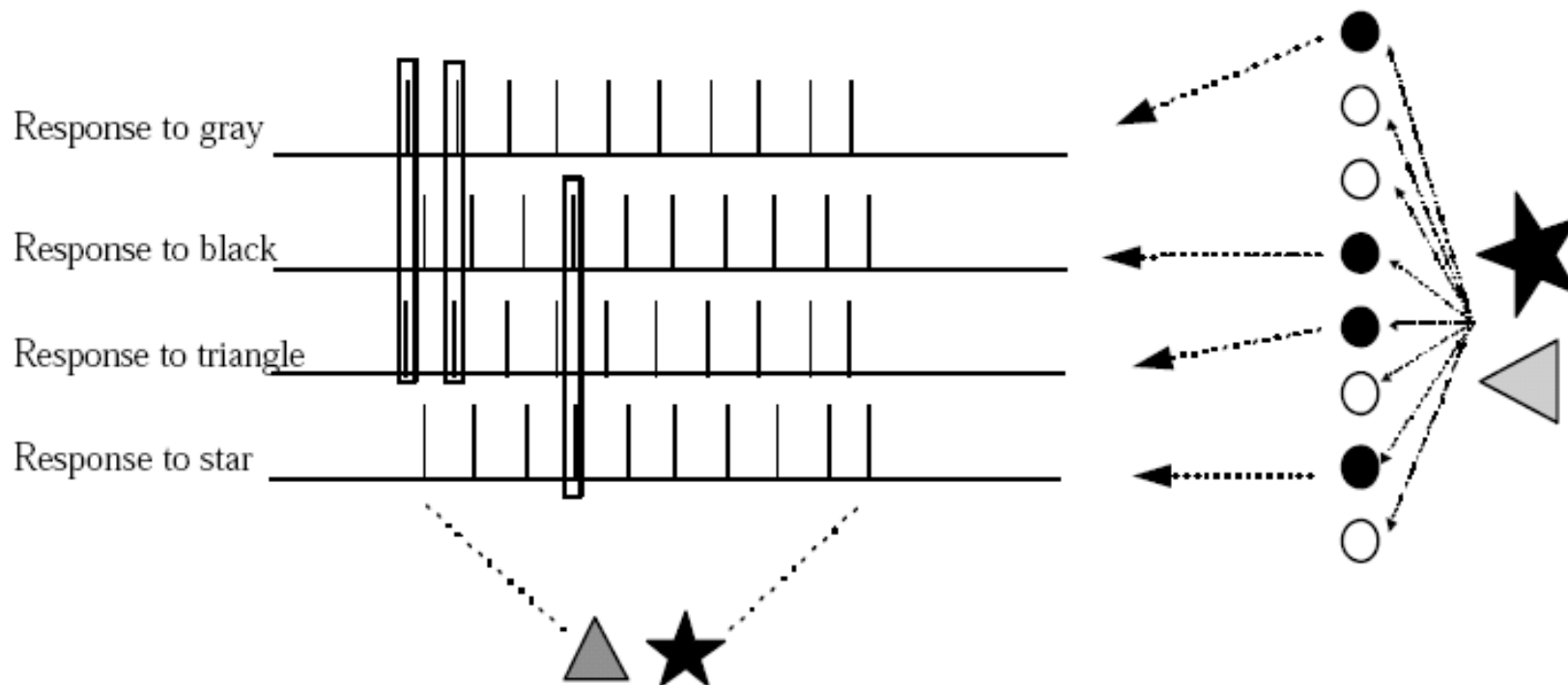
Alternative hypothesis: Features are combined.



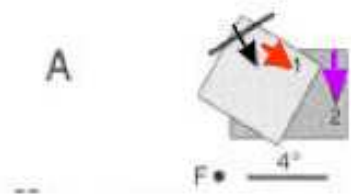
The binding problem appears when several objects are represented concurrently. How are the features bound to the corresponding objects?






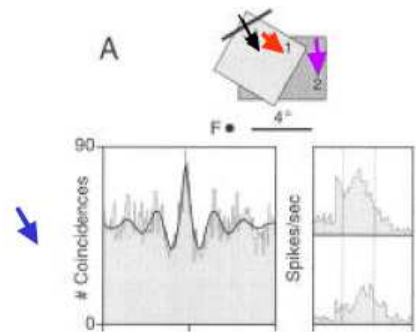
The problem could be solved by synchronous activity. Features which belong to one object are coded by synchronous groups of neurons.




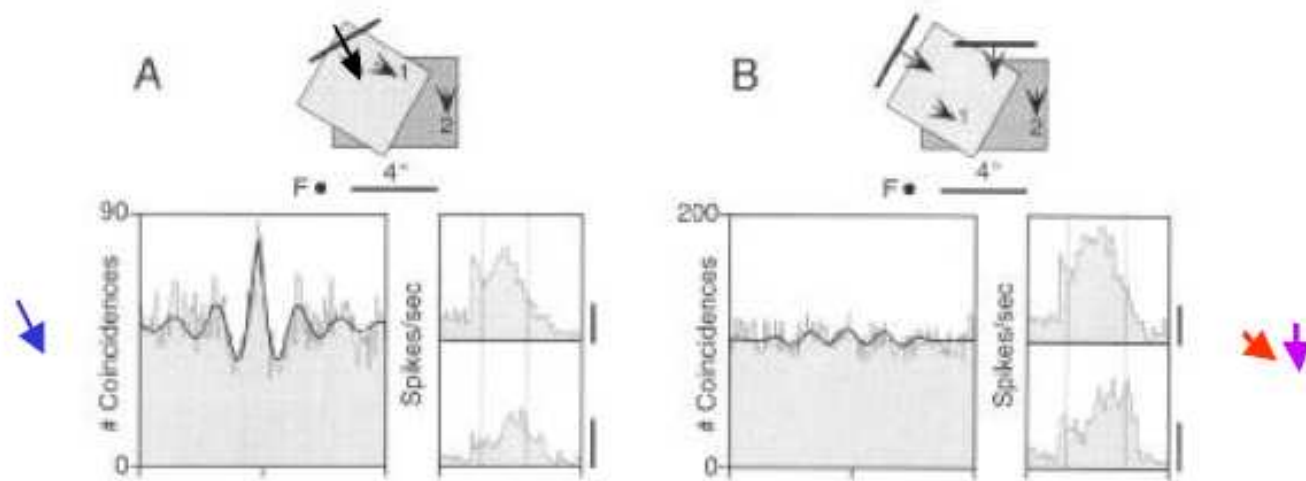
Example: Correlations in monkey MT



Recordings from two cell groups with different preferred stimulus directions (1  and 2 ). Both groups of cells will also respond to a stimulus moving in a direction intermediate to their preferred directions ()

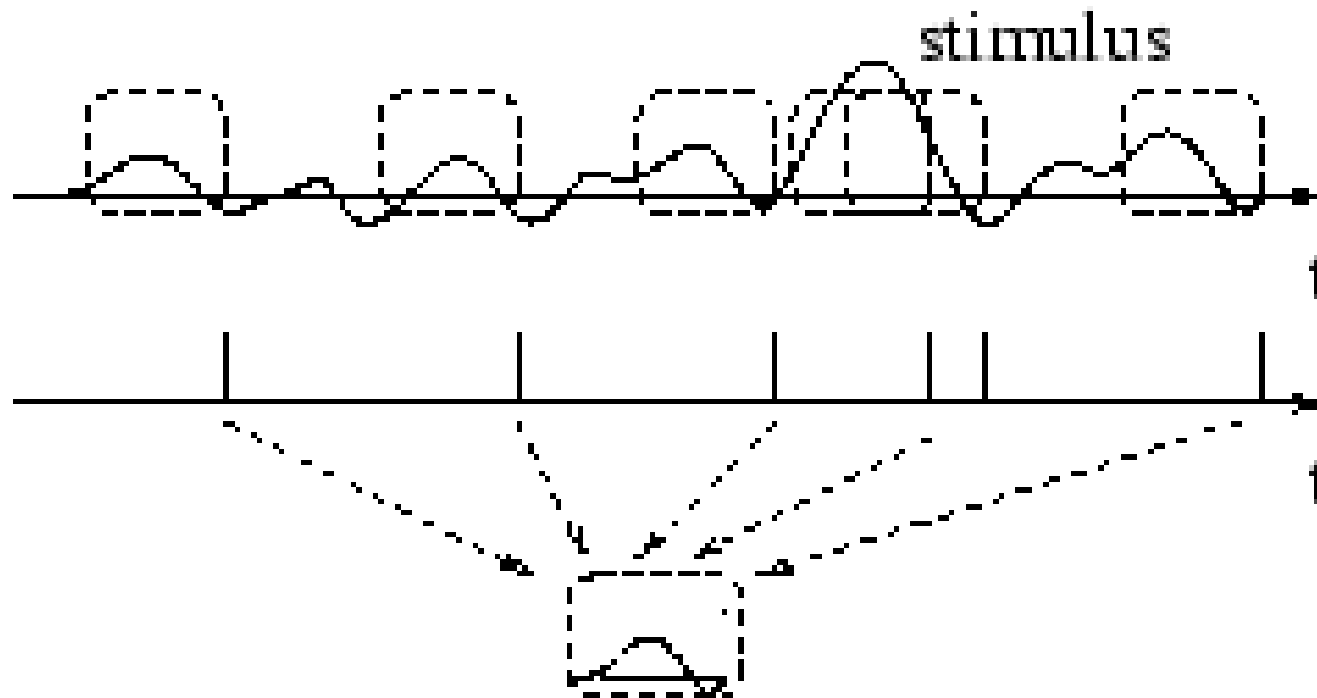


When a stimulus with intermediate direction () is presented, both cell groups fire and a high number of coincident spikes can be observed.



When a stimulus with intermediate direction (↙) is presented, both cell groups fire and a high number of coincident spikes can be observed.

When two stimuli with preferred directions of both cell groups (↘↙) are presented, both cell groups fire but very low number of coincident spikes can be observed.



Whenever the neuron spikes, we store the stimulus $s(t)$ in some small time interval before t (e.g., 100ms).

The mean of these temporal patterns describes the average stimulus that precedes a spike (reverse correlation).

That's how one can read the thoughts of a fly (Bialek et. al., 1991).

