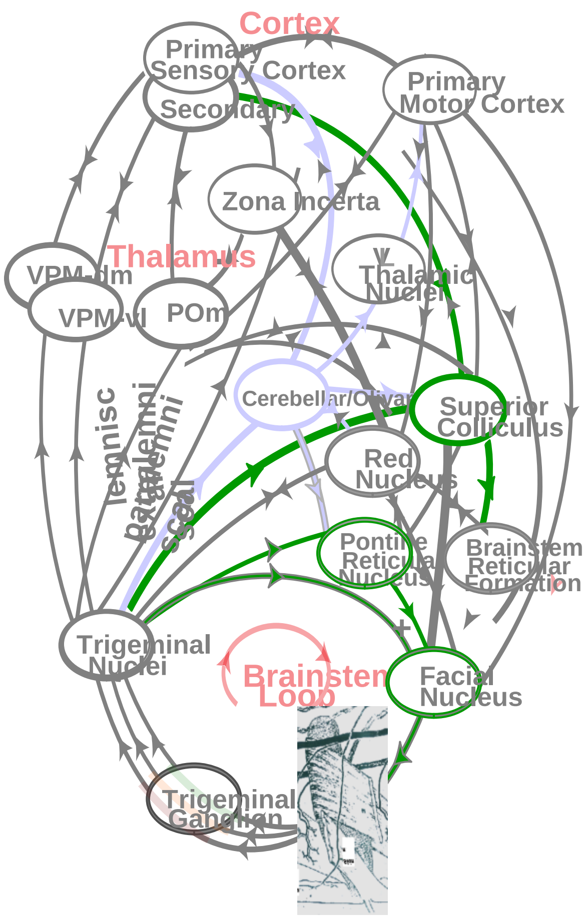
# ACTIVE SENSING

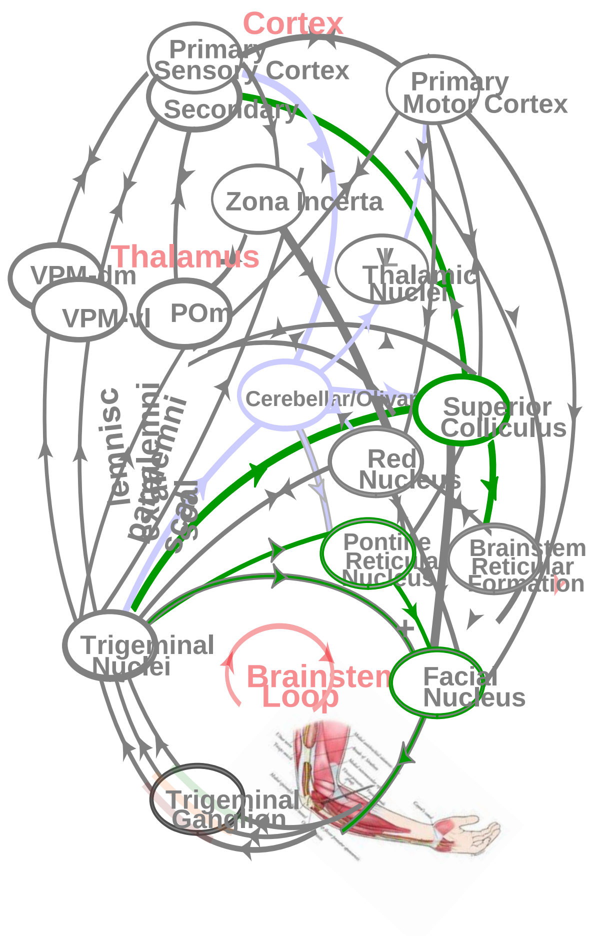
## Lecture 4:
## sensory coding

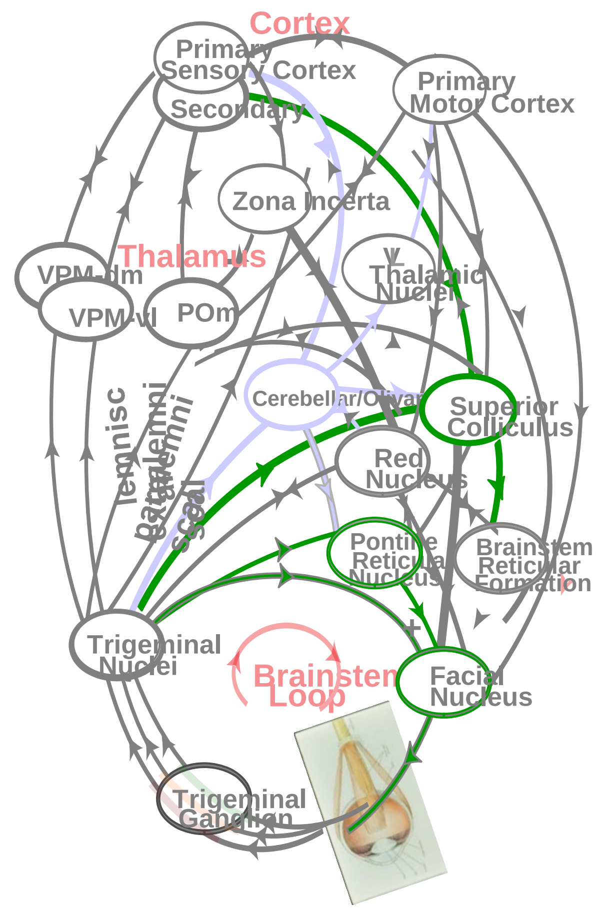
*"There is nothing in the intellect that was not previously in the senses."*

Aristotle (384 - 322 BC)

How can one (experimenter or a neuronal circuit) **read out** what's going on in each of the stations?

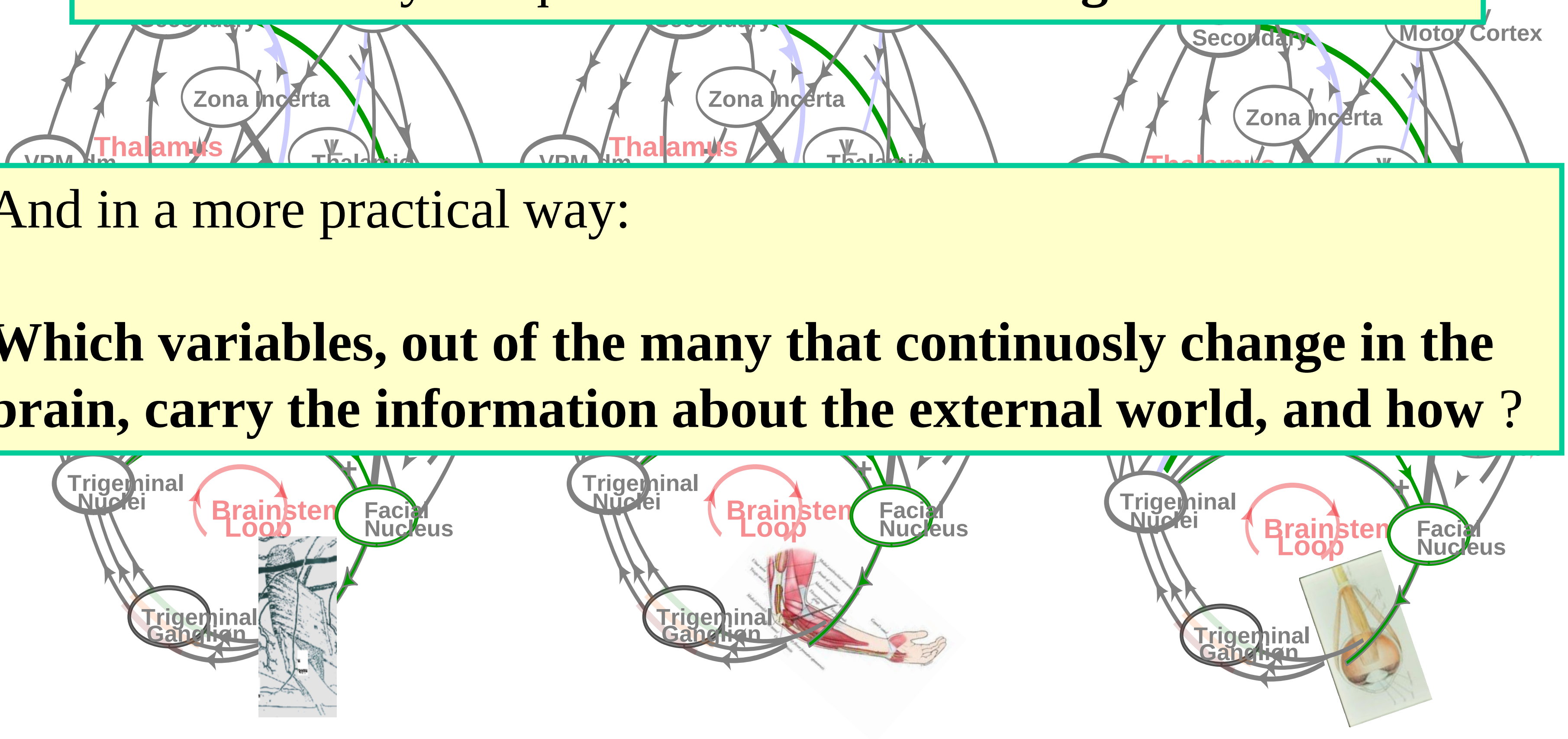


How can one (experimenter or a neuronal circuit) **read out** what's going on in each of the stations?

This is actually the question of **neural coding**




And in a more practical way:

**Which variables, out of the many that continuosly change in the brain, carry the information about the external world, and how** ?

# Transformations

## Sensory

Physical transformations (conductance, filtering, distortions)

Physical -> neuronal transformations (transduction)

## Brain

Neuronal transformations (conductance, filtering, coding)

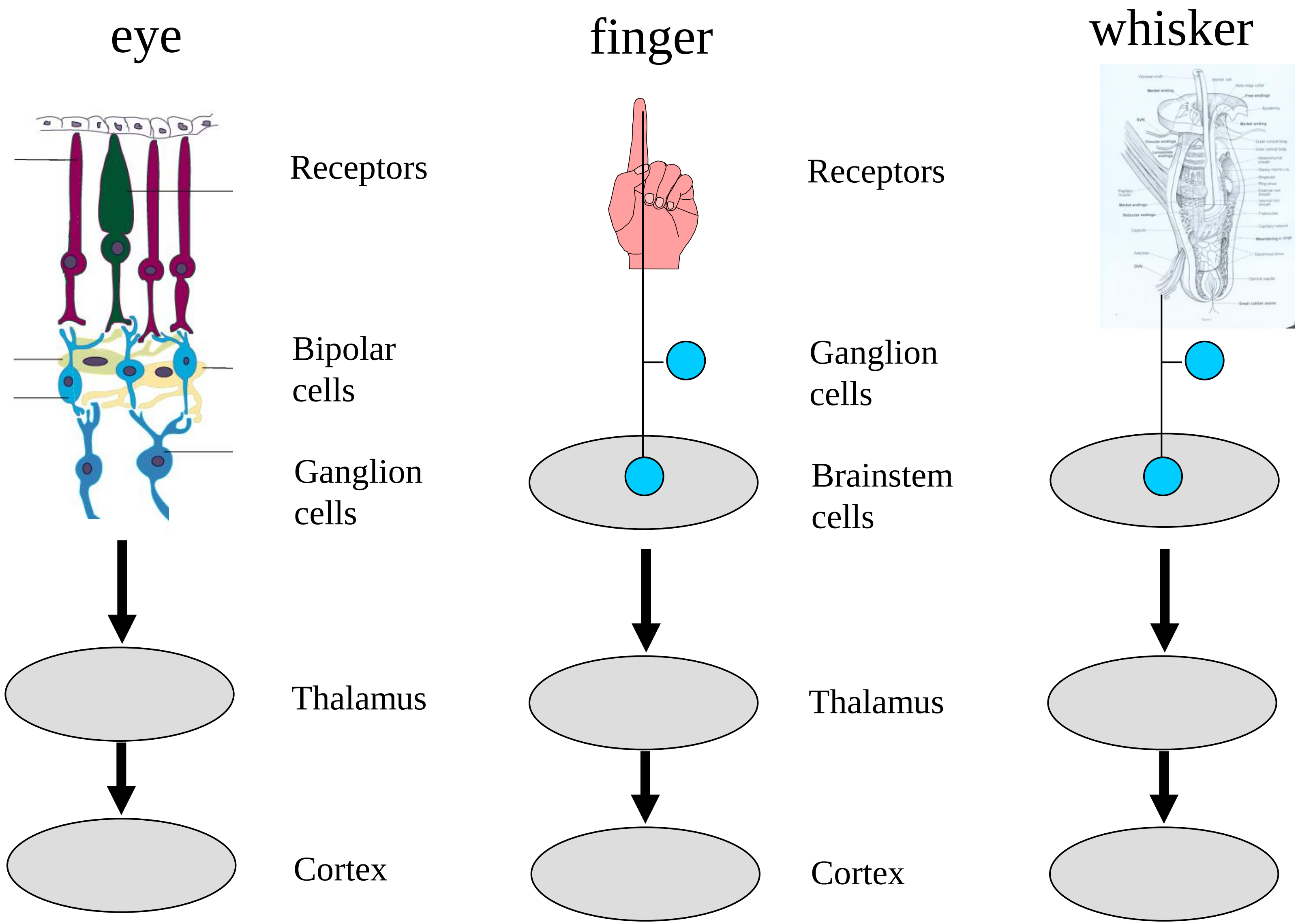
## Motor

neuronal -> physical transformations

Physical transformations (conductance, filtering, distortions)

Neuronal transformations (conductance, filtering, coding)

# Processing stations



# High-pass filtering – a common motif

Focus on changes

in time:

- Intrinsic in individual neurons
- Starting at the receptor level

in space:

- Circuits of neurons
- Starting after lateral inhibition

# Band-pass filtering – channels of information

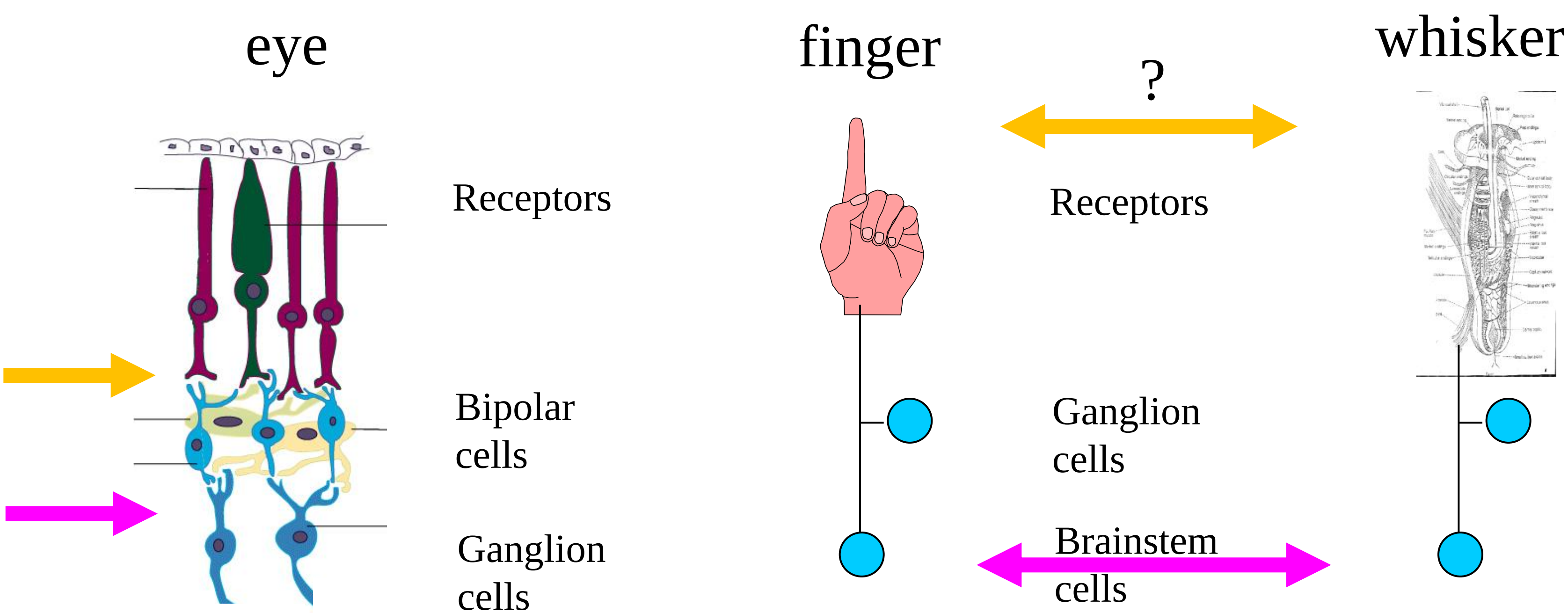
in time:

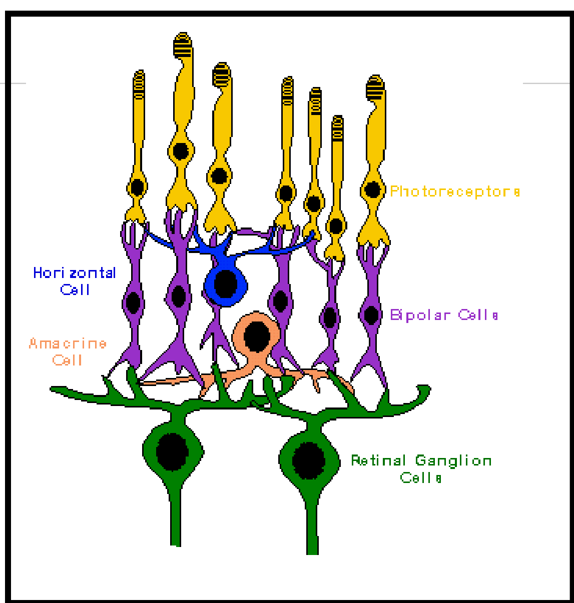
- SA/RA, x/y, parvo/magno, aud tuning

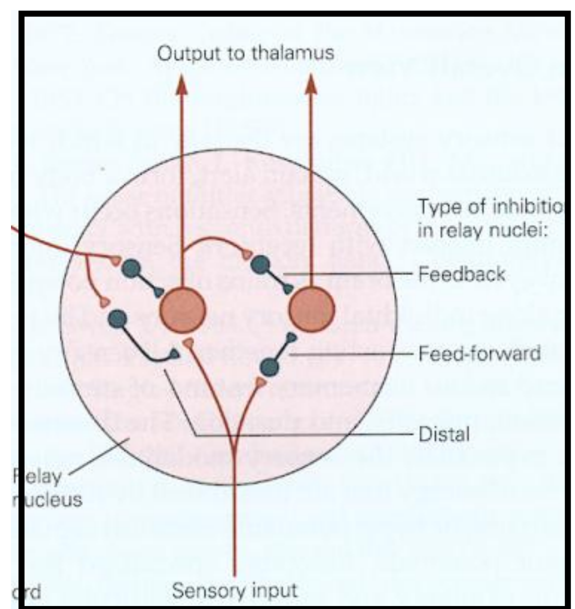
in space:

- spatial frequency channels

# **Spatial processing** (by Lateral inhibition)



Neuronal transformations (conductance, filtering, coding)

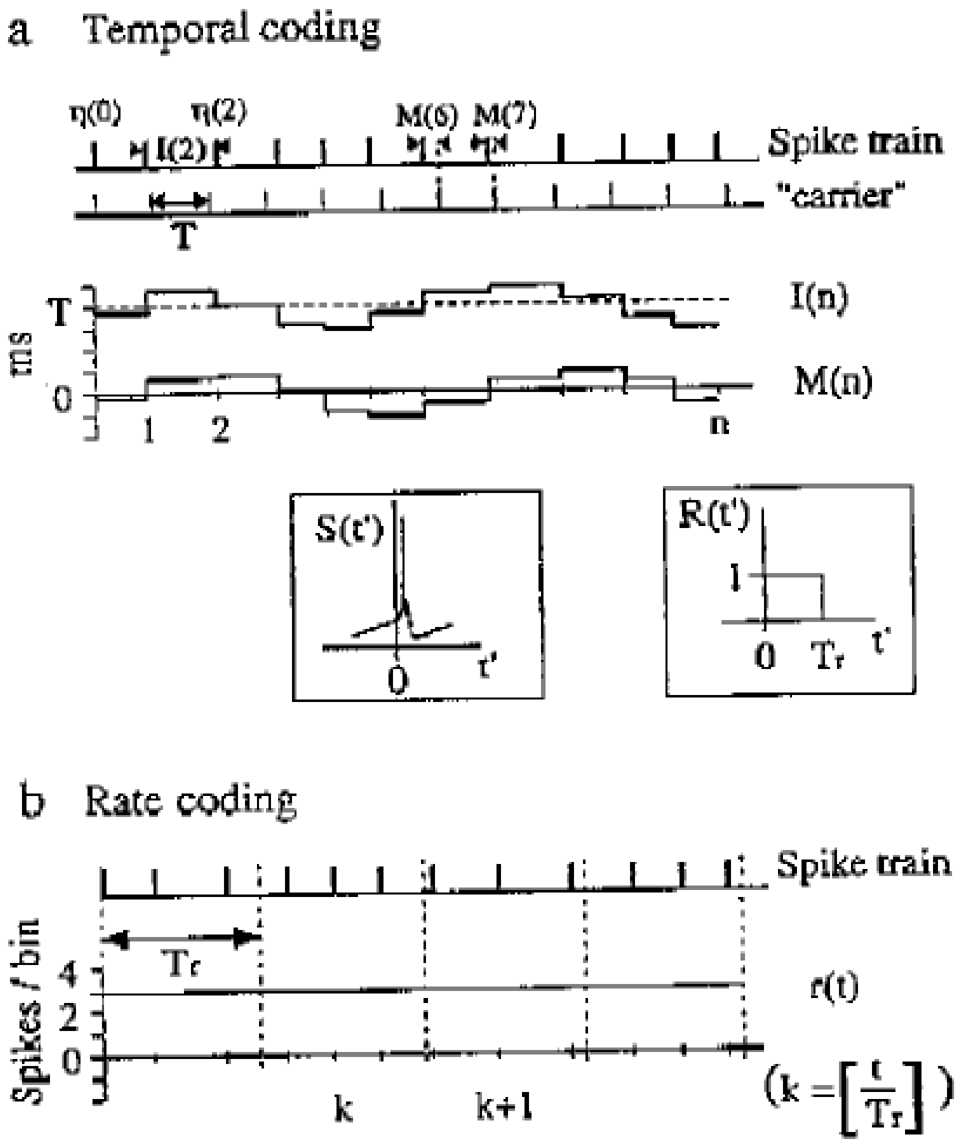
**Possible variable categories:**

- molecular profile
- chemical profile
- membrane-voltage profile
- spiking profile
- field-potential profile (EEG)
- hemodynamic profile

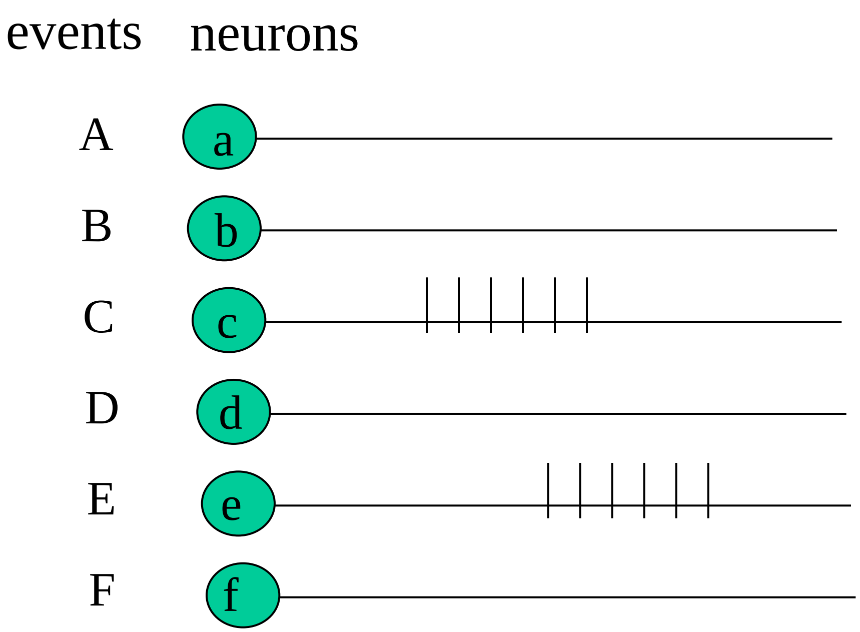
**spiking profile** is probably the best candidate for coding perceptual and motor events because:

- millisecond time scale
- communication over distance
- other?

# Spike patterns can be read in different ways



The simplest spike-based code would probably be the **“labeled-line code”**. This is a binary code: reporting **yes/no** about the occurrence of a given event.




Every neuron has a “label”

# Where is labeled-line coding used?

Coding modality

punch the eye -> see stars

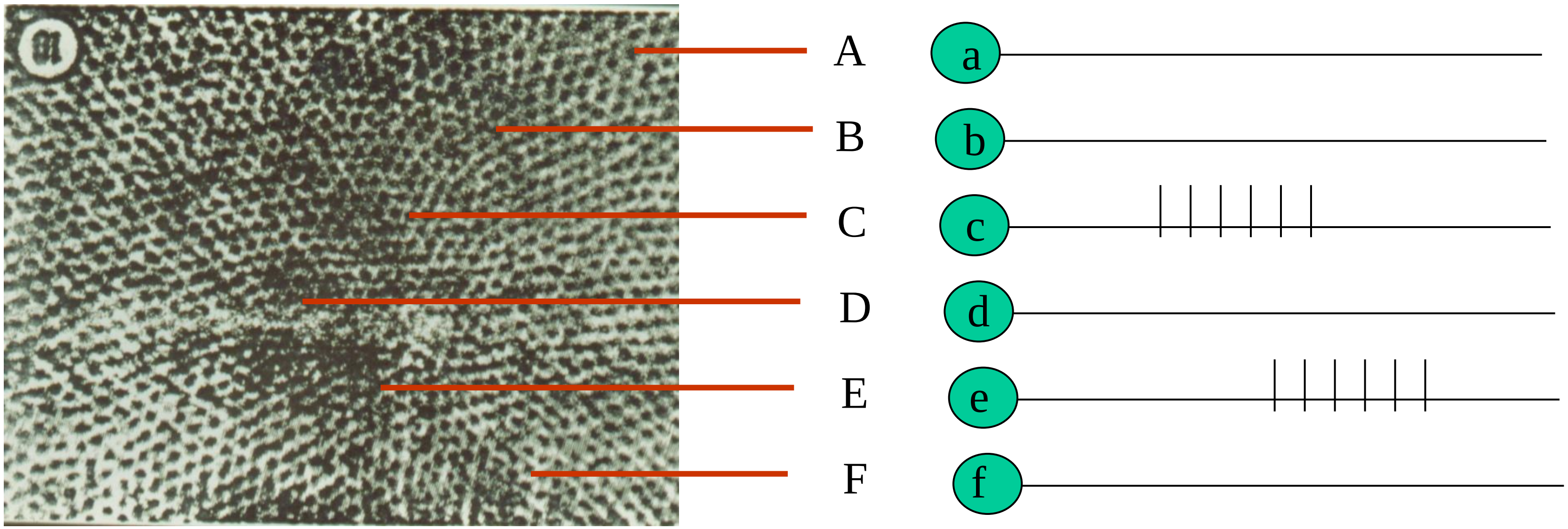
paradoxical cold: 45$^o$ to a cold spot on the skin -> cold sensation

Coding space

maps (phantom limb)

local sign

# The "local sign"




Reading the labeled-line code:

How would an **experimenter** read a labeled-line code ?

How would a **neural circuit** read a labeled-line code ?

Neuronal circuits do not *read* codes, they *translate* them

To what?

To other codes

Why?

For:

- Integration with other sensory inputs
- Interaction with memory
- Controlling motor activity
- ...

=> abstraction: distancing from the physical features

For practical benefit, we divide neuronal translation to two processes:

*translation* = *reading* + *re-coding*

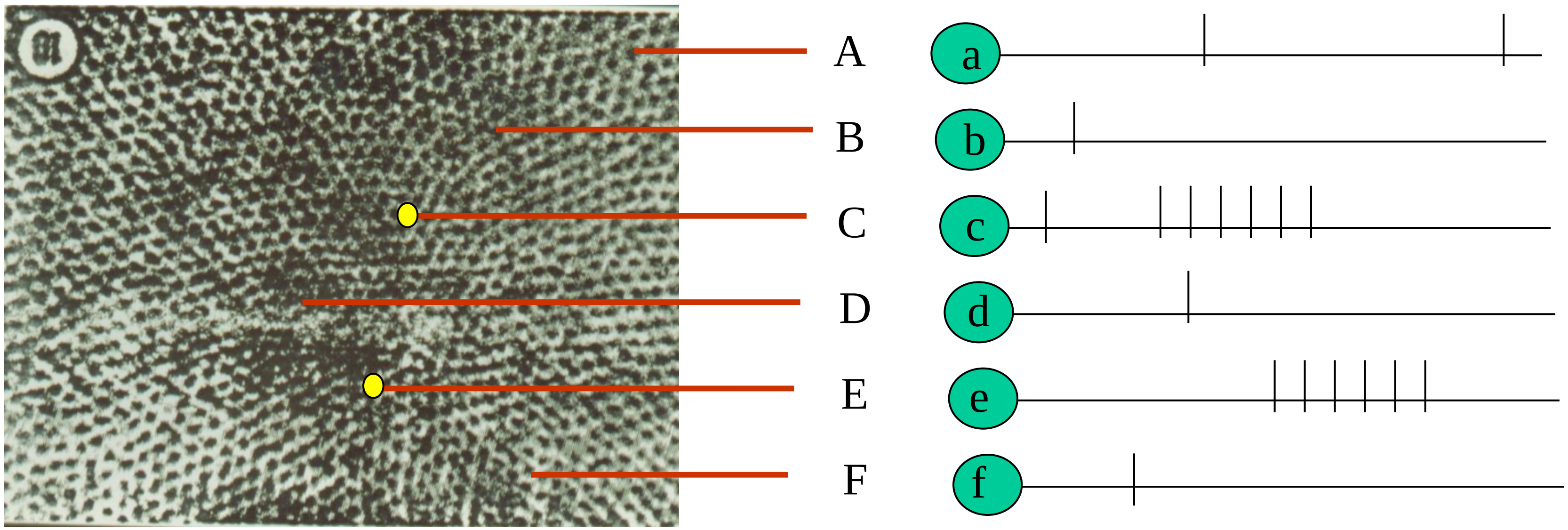
This allows us to talk about *reading a code* in neuronal terms, and to analyze this process by our cognitive reasoning.

*Reading* = *extracting the information* from the spiking profile

*Reading algorithm* = the process by which the information is extracted

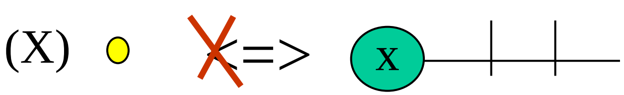
*The reading* circuit = *"readout circuit"*

# What would be the *reading algorithm* for the retina?




*reading algorithm:* a location X is illuminated if neuron x fires spikes

On what condition will this algorithm be valid?




Neuron x fires ~~*if and only if*~~ X is illuminated

Is this assumption valid?

The problem of **background activity**

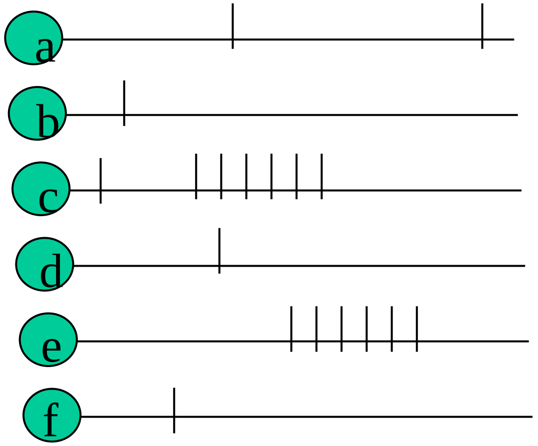
The “problem” of **sensor motion**

This means that:

a. The visual (and nervous) system does not use the straight-forward labeled-line code

b. the nervous system has to extract the signal from its background

The information allowing separating a signal from its background lies in the **spiking pattern**



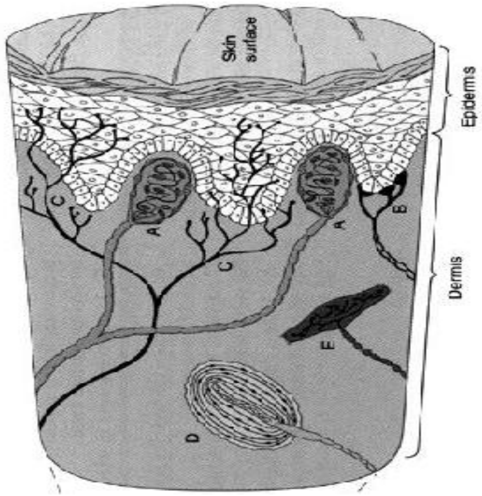

The information in the spiking pattern is conveyed by **spike timing**, because spike amplitude is constant.

Thus we are basically left with two variables:
*Who* is firing and *when*

# *sensory encoding:* *What receptors tell the brain*

Sensory organs consist of **receptor arrays**:

**somatosensation** **audition** **vision**

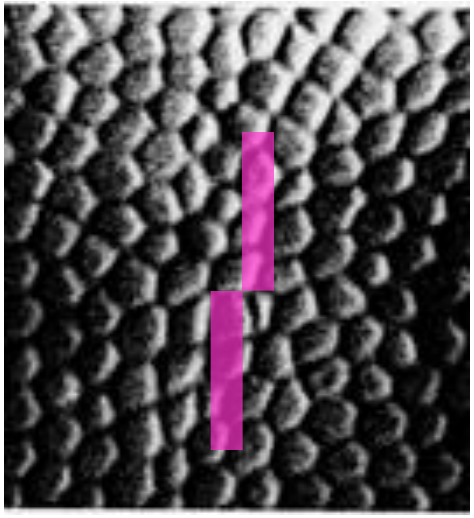



~200 μm

*Finger pad*


10 μm

*cochlea*



10 μm

*retina*

Spatial organization => Spatial coding (“*which* receptors are activated”)

Movements => Temporal coding (“*when* are receptors activated”)

# Spatial Encoding

(Assuming no sensor movement)

**spatial encoding:** the information is carried by the **identity of active (firing) receptors**

**Retina** – patterns of active GC **replicate** the external image. Something like Cartesian vision, but with neuronal space instead of optic space. This code is associated with a **rate-code** in which the firing rate of the neuron represents the intensity of the external signal. Thus, higher illuminations will lead to larger firing rates.

*Identity* codes pattern (shape)
*Firing rate* codes intensity (of light)

# Spatial Encoding

**Cochlea** – here *temporal frequency* is mapped onto the cohlear space.
*Identity* codes frequency ("place code")
*firing rate* codes intensity

**Skin -** as in vision:
*Identity* codes pattern (shape)
*firing rate* codes intensity (of pressure)

**Whisker** –
(1) as skin and eye:
*Whisker Identity* codes 2D pattern (shape)
(2)
*Receptor identity* codes radial pattern (depth)

# Tactile Spatial encoding Primate finger tip:

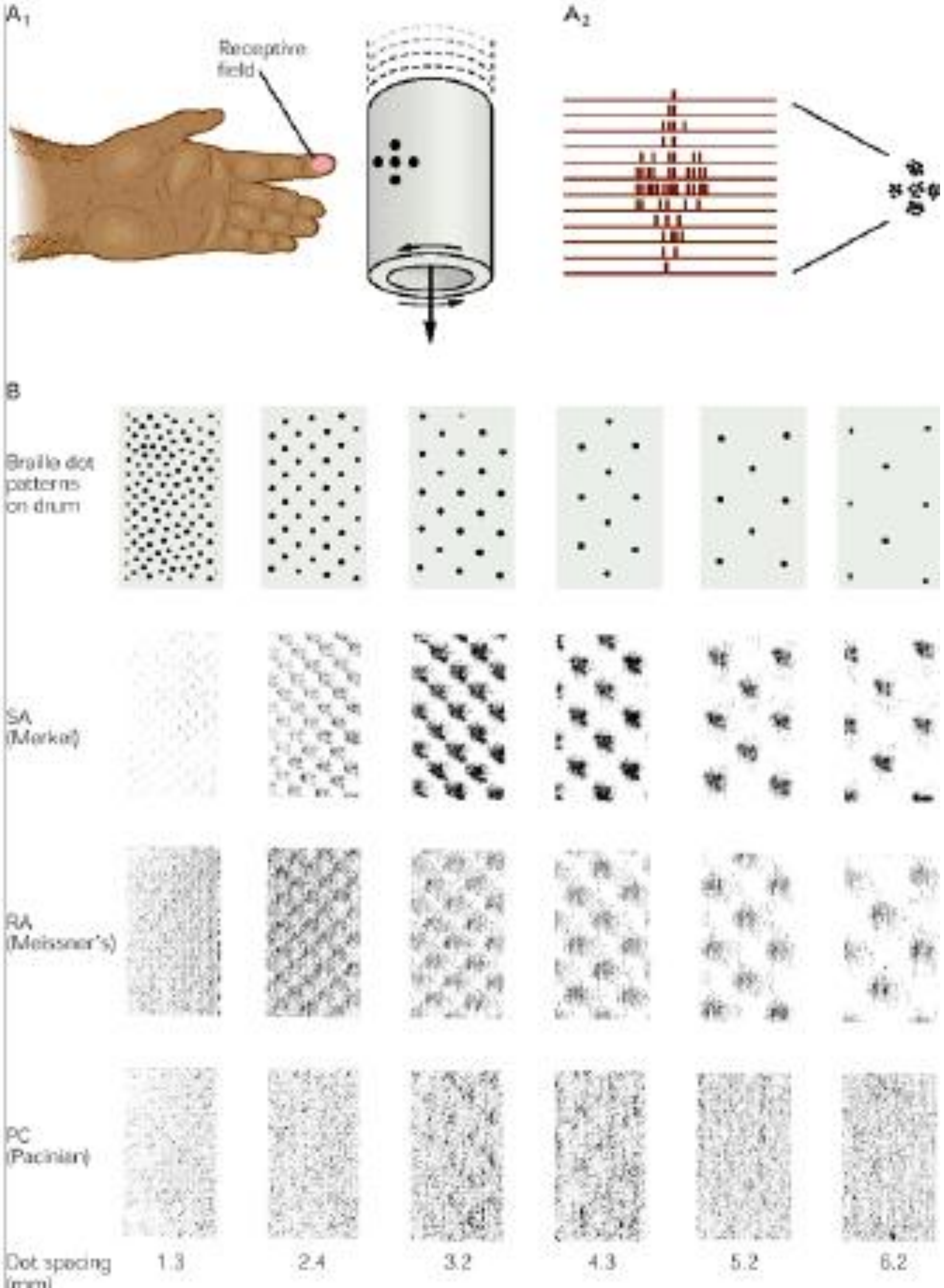



**Figure 22-8 The firing patterns of mechanoreceptors in the superficial layers of the skin encode the texture of objects rubbed across the skin.**
**A. 1. The nerve responses to textures are measured with the hand immobilized. The receptive field of a single receptor on a monkey's finger is stimulated with an embossed array of raised dots on a rotating drum. The pattern moves horizontally over the receptive field as the drum rotates. The experimenter thus controls the speed of movement and the location of the dot pattern in the receptive field. The pattern is moved laterally on successive rotations to allow the dots to cross the medial, central, and lateral portions of the receptive field on successive rotations. The composite response of an individual nerve fiber to successive views of the raised dots simulates the distribution of active and inactive nerve fibers in the population. 2. Sequential action potentials discharged by individual receptors during each revolution of the drum are represented in spatial event plots in which each action potential is a small dot, and each horizontal row of dots represents a scan with the pattern shifted laterally on the finger.**
**B. Spatial event plots of three types of mechanoreceptors to dot patterns with different spacing. Slowly adapting Merkel disk receptors and rapidly adapting Meissner's corpuscles differentiate between dots and blank space when the spacing of the dots exceeds the receptive field diameter. A receptor fires bursts of action potentials for each dot, spaced by silent intervals. As the dots are brought closer together, the resolution of individual dots blurs. Pacinian corpuscles do not distinguish texture patterns because their receptive fields are larger than the dot spacing. (Reproduced from Connor et al. 1990.)**

# Tactile Spatial encoding

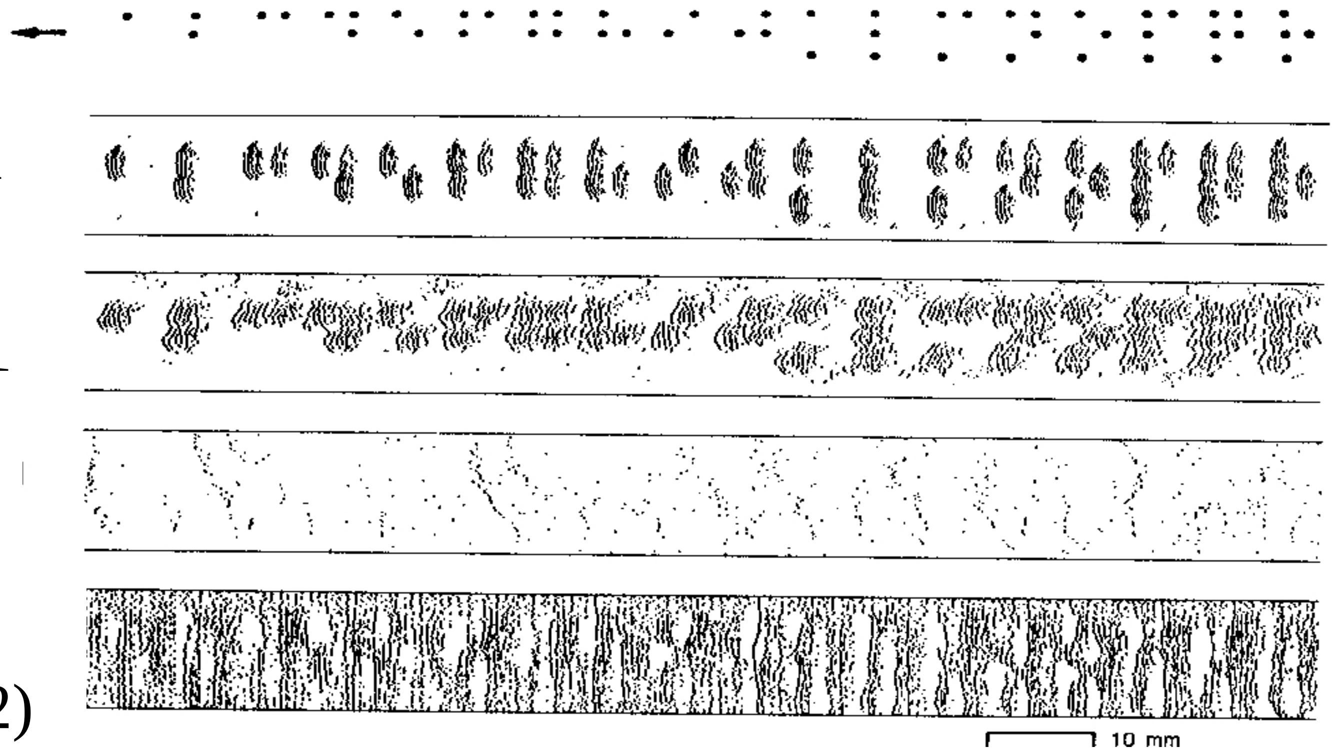
Primate finger tip:

SA1

RA1

SA2

PC (RA2)




Rat whisker array:

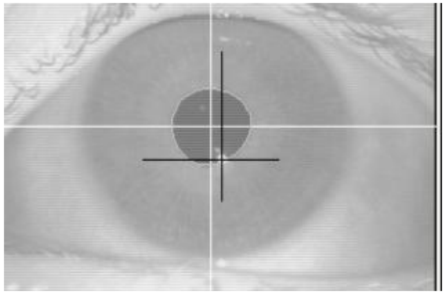
# Temporal encoding

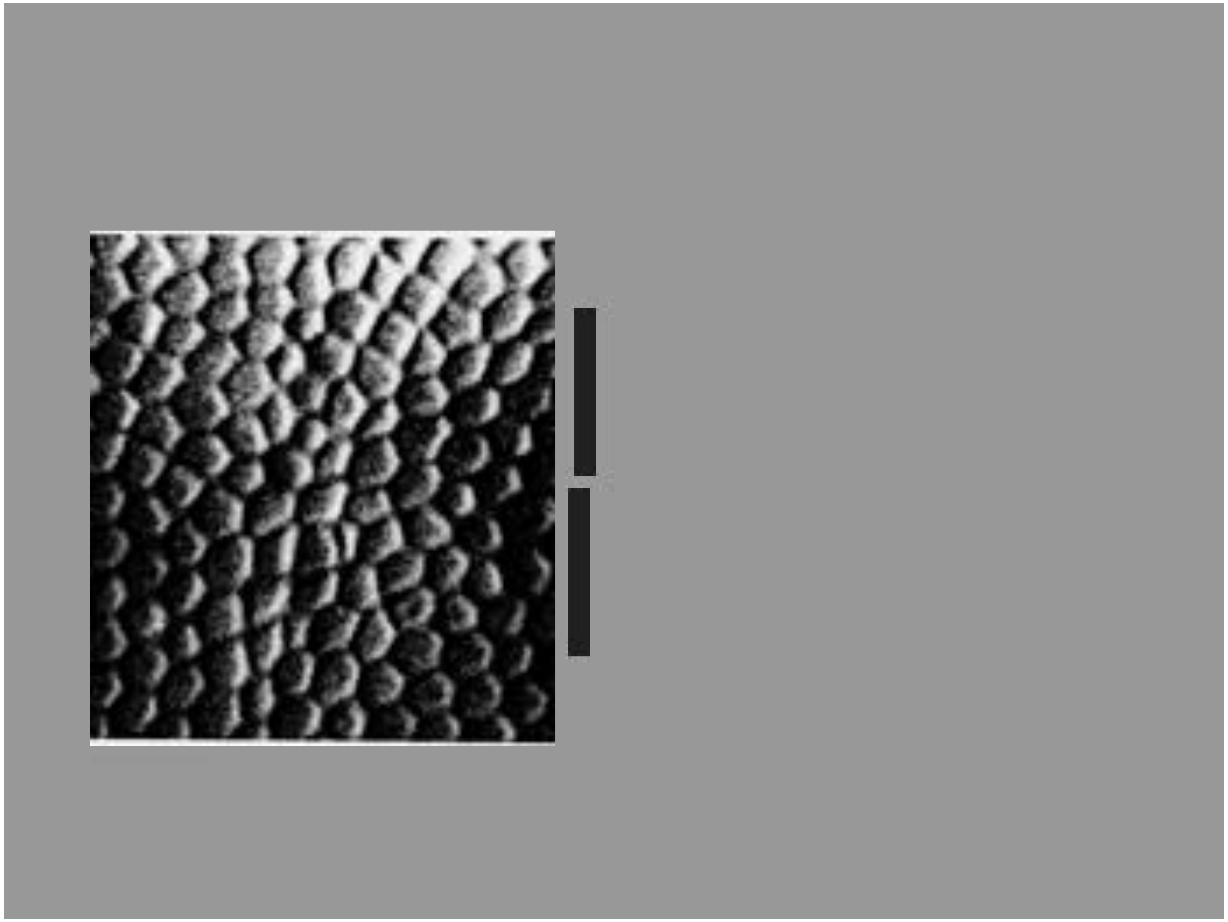
With temporal coding the information is carried by the **times** of neuronal firings.

**Audition:**

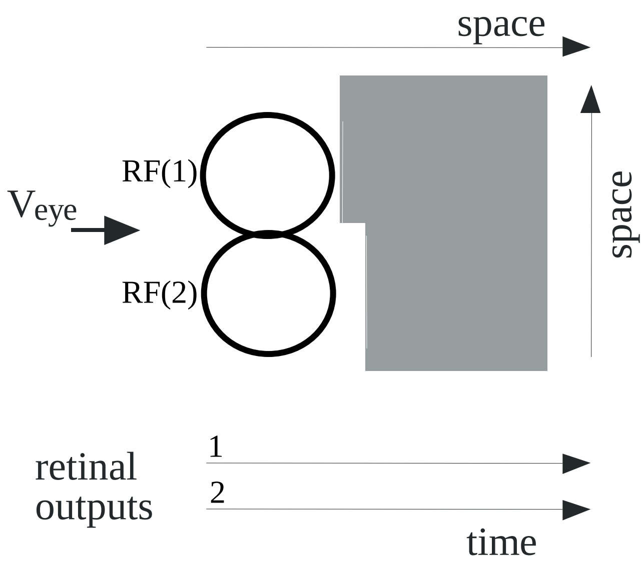
- the natural stimulus, sound, contains temporal information: the period of the sound wave (1/frequency). Cochlear hair cells follow the temporal structure of the stimulus.  They can follow the frequency up to 500 Hz and the phase up to 5000 Hz.
- Location of sound source is encoded by amplitude difference and temporal delay between the two ears. Humans are sensitive to 10 us delays)
- With Echo-location by bats, spatial distance is encoded by temporal delay (between sound to echo).

# Eye movements during fixation





# Vision: Temporal encoding due to eye movement



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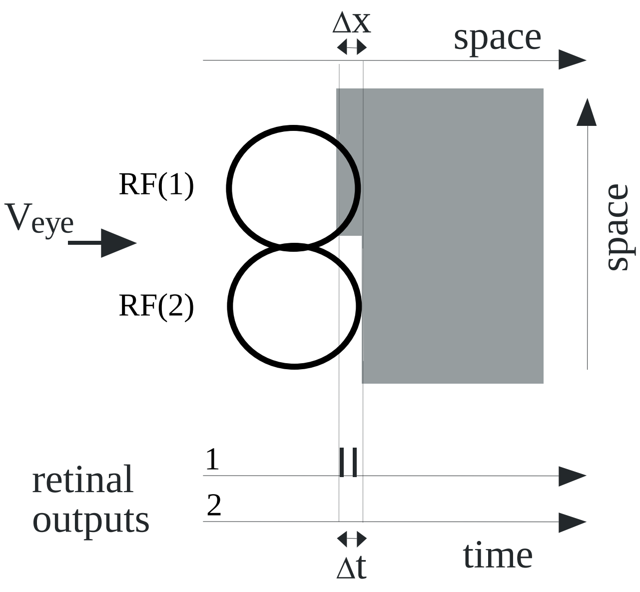

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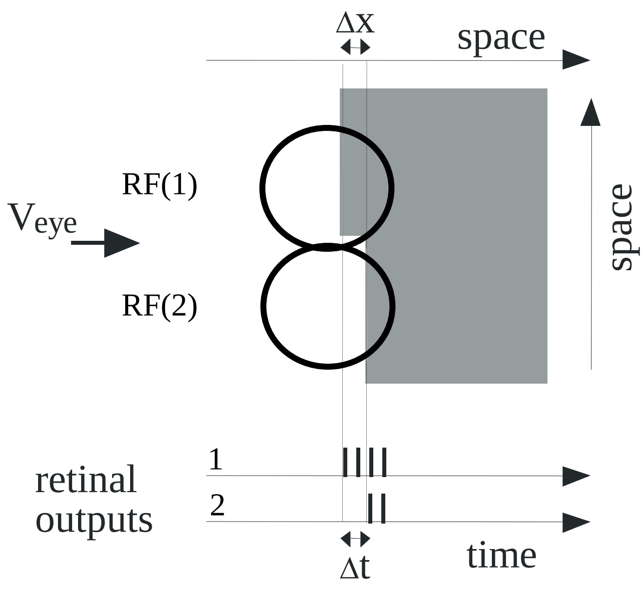

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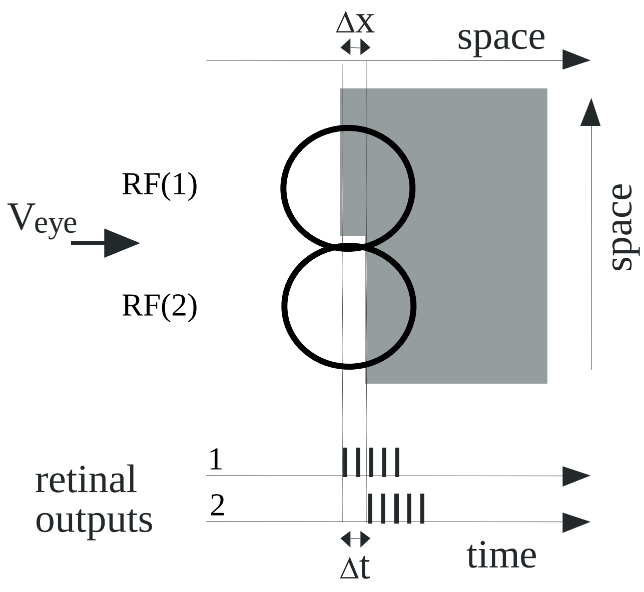

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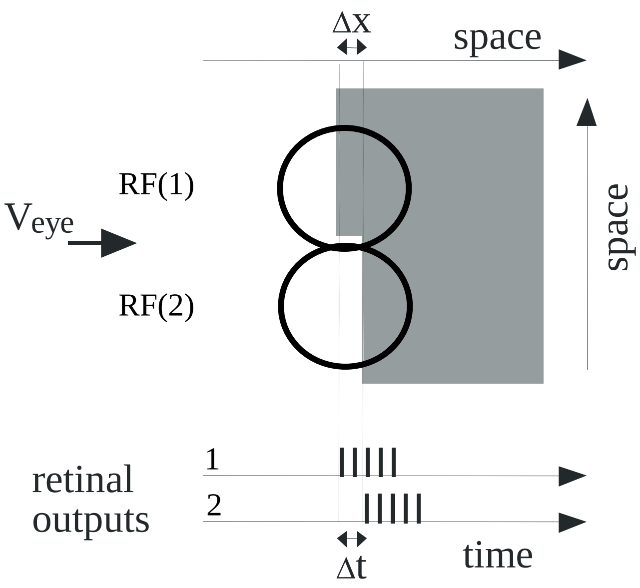


# Touch: Temporal encoding due to finger movement

# Touch: Temporal encoding due to finger movement

Darian-Smith & Oke,
J Physiol, 1980

anesth. monkey,
MR fibers

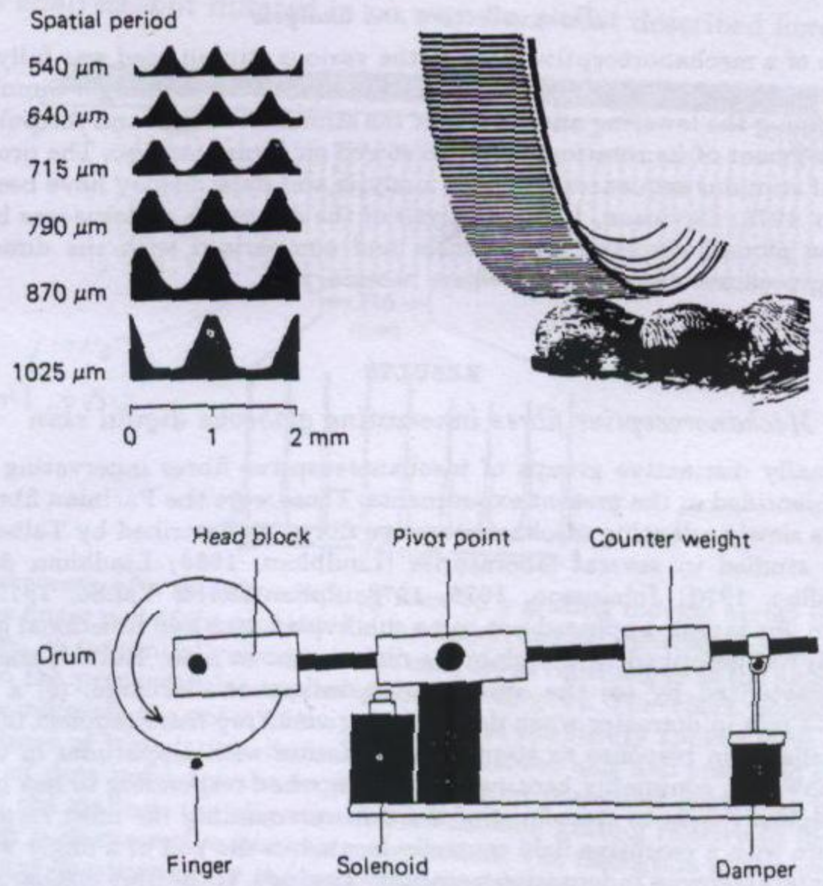



*Fig. 1. Details of the* stimulator used for presenting gratings to finger pad skin. The grating was mounted on a rotating drum 100 mm in diameter (upper right). The profile of each of the six gratings used is shown (upper left), along with its spatial period. The lower diagram illustrates the mechanisms for controlling the period of contact of the grating moving across the finger pad skin. The drum was mounted at one end of a counter-poised lever and rotated at a preset velocity. This drum was positioned *1 mm above the skin surface*: an actuated solenoid held the drum off the skin except for the required contact period. The perpendicular force at which the moving grating was applied to the skin during this contact period was determined by the counter-weight: this could be set in the range 20–100 g wt.

# RA fiber

Vel - constant

$f = SF * V$

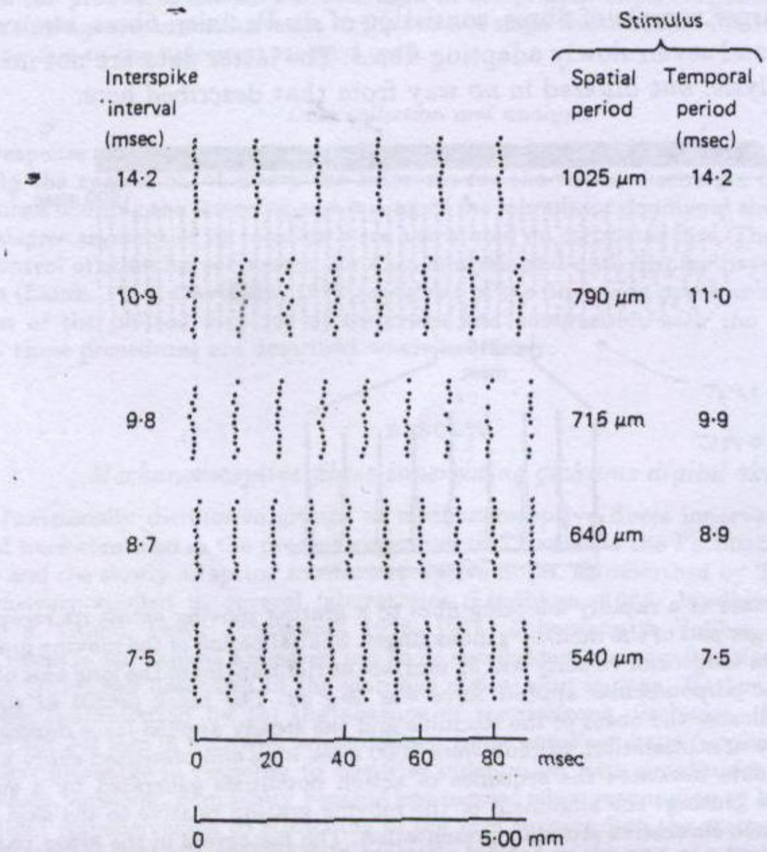



Fig. 3. Responses of a rapidly adapting fibre to different gratings moving across its receptive field on the ridged glabrous skin of terminal phalanx of thumb. The tangential velocity was 72 mm/sec in a direction at right angles to the long axis of the finger and the applied force was 60 g wt. for all records; successive stimuli were presented every 3 sec. Each row of dots indicates the occurrence of action potentials in response to a single passage of the grating across the skin; twelve successive responses are illustrated for each grating; spatial periods of these gratings are indicated on the right. The 80 msec response segment illustrated had its onset at approximately 500 msec after the beginning of stimulation, as is shown in Fig. 2. With these records there was both precise alignment of the time of occurrence of action potentials after the onset of stimulation, and also alignment relative to the instantaneous position of the grating on the skin. The stimulus spatial and temporal periods are indicated for each data block on right side of Figure. The mean interspike interval is to the left of each data block.

# Working ranges

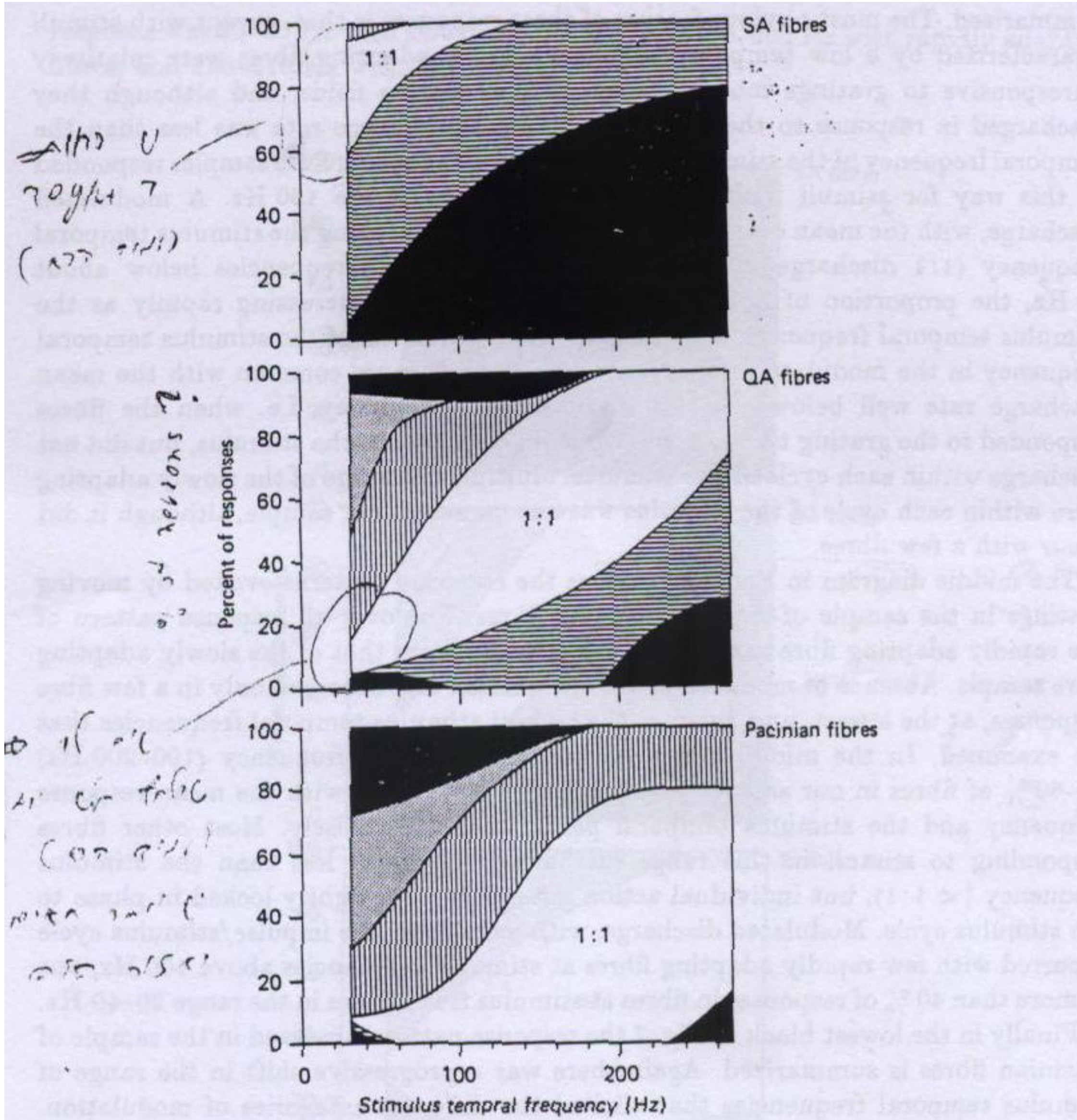



Fig. 7. Relationship of response modulation pattern to the stimulus temporal frequency

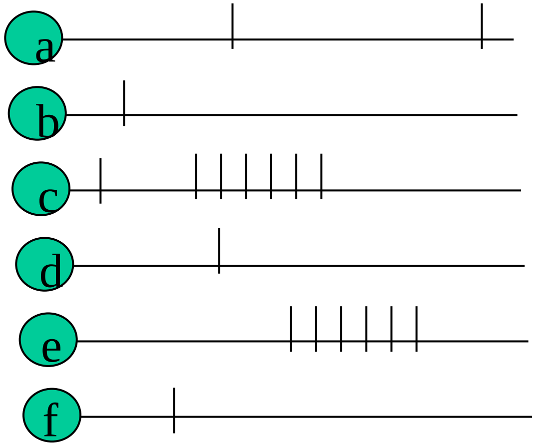
This means that:

a. The visual (and nervous) system does not use the straight-forward labeled-line code

b. the nervous system has to extract the signal from its background

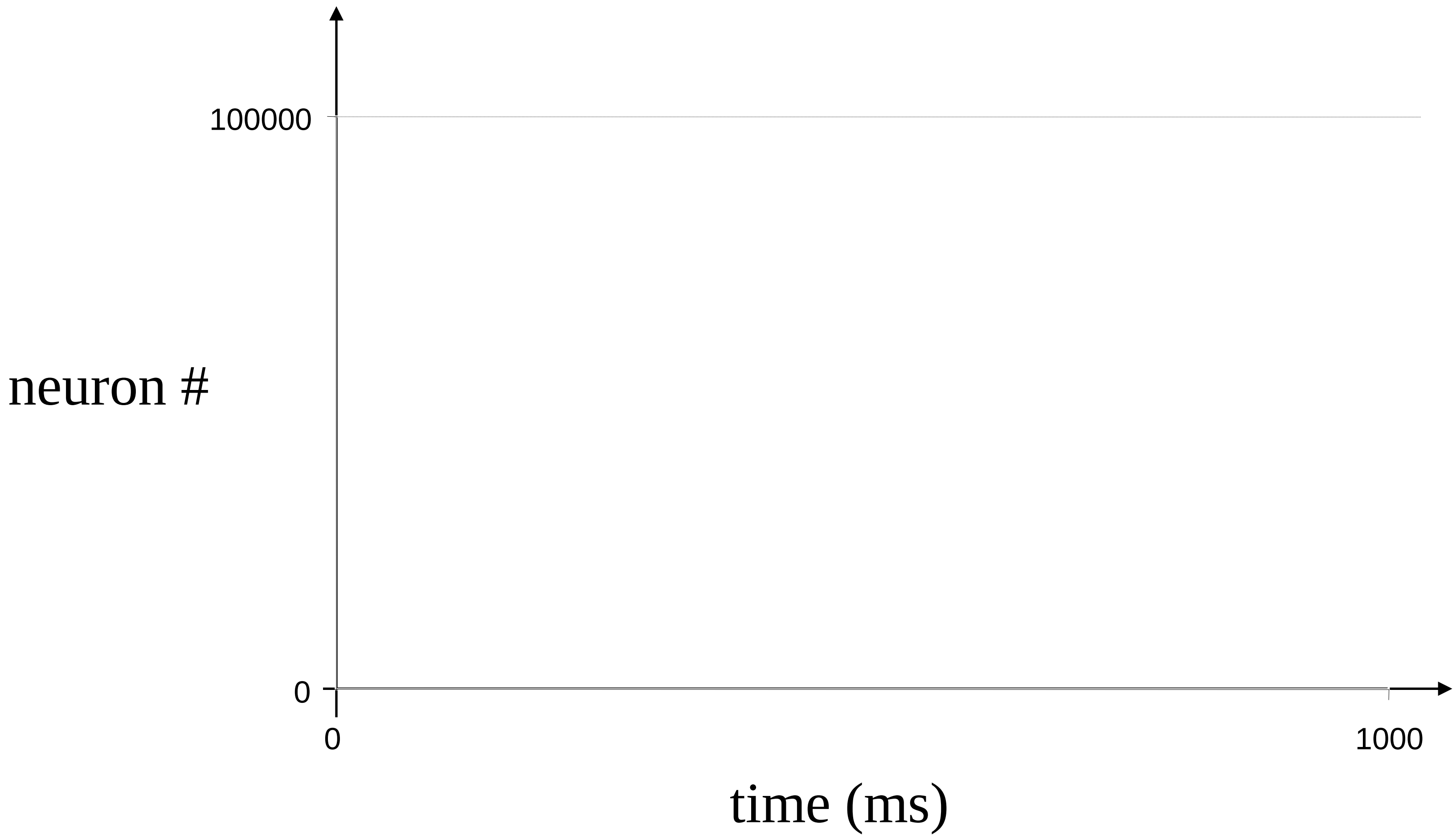
The information allowing separating a signal from its background lies in the **spiking pattern**

The information in the spiking pattern is conveyed by **spike timing**, because spike amplitude is constant.

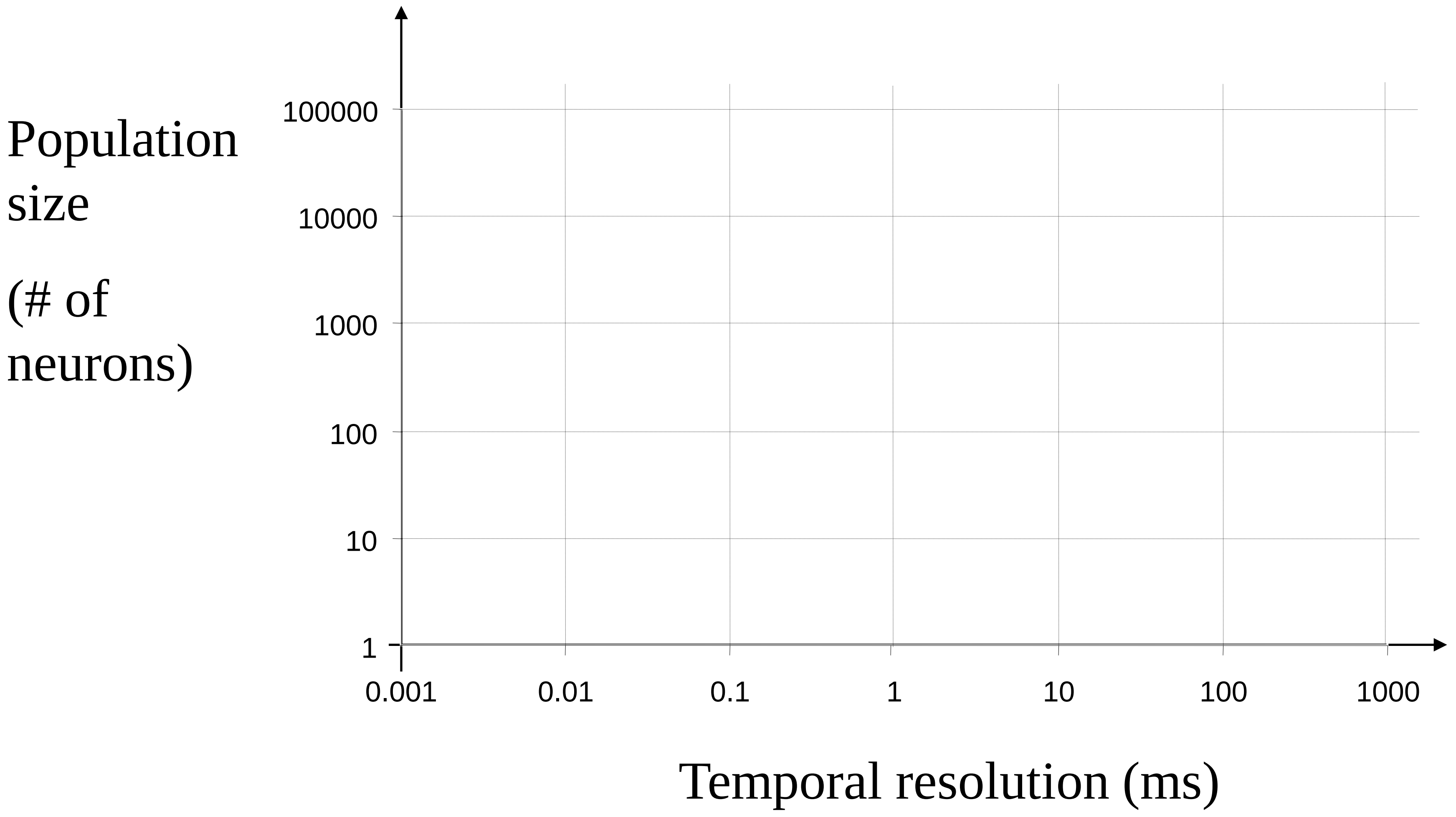



Thus we are basically left with two variables:
*Who* is firing and *when*

# Spikogram – who fires when



# Spatio-temporal coding space



**Spiking profiles** that are currently considered as candidates for coding:

Single neurons

- exact timing (1 ms) (*"temporal code"*)
- number of spikes in a time bin (*"spike count"*)
- peak rate of spikes (*"rate code"*)

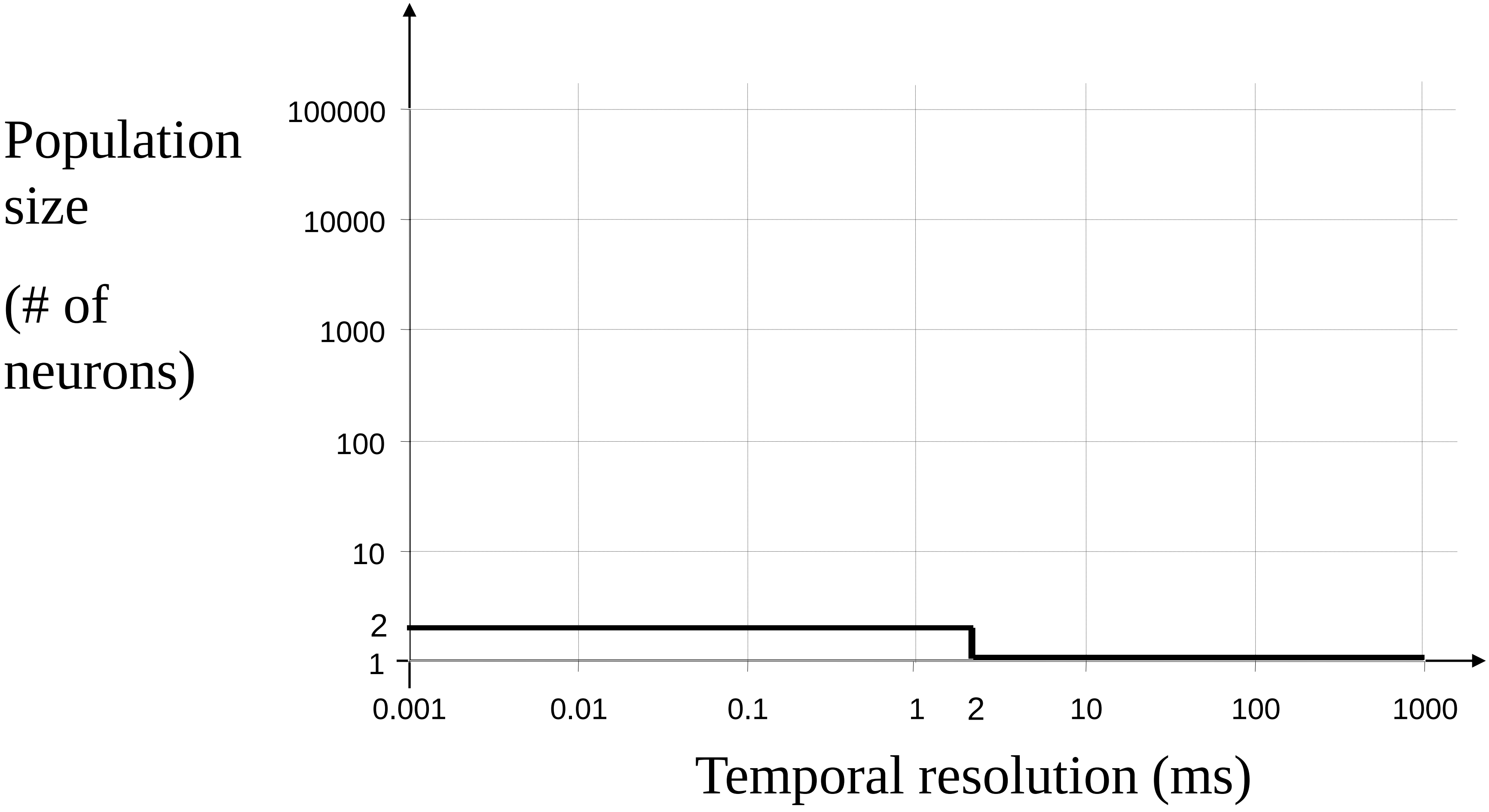
*"Intensity codes"*

Populations of neurons

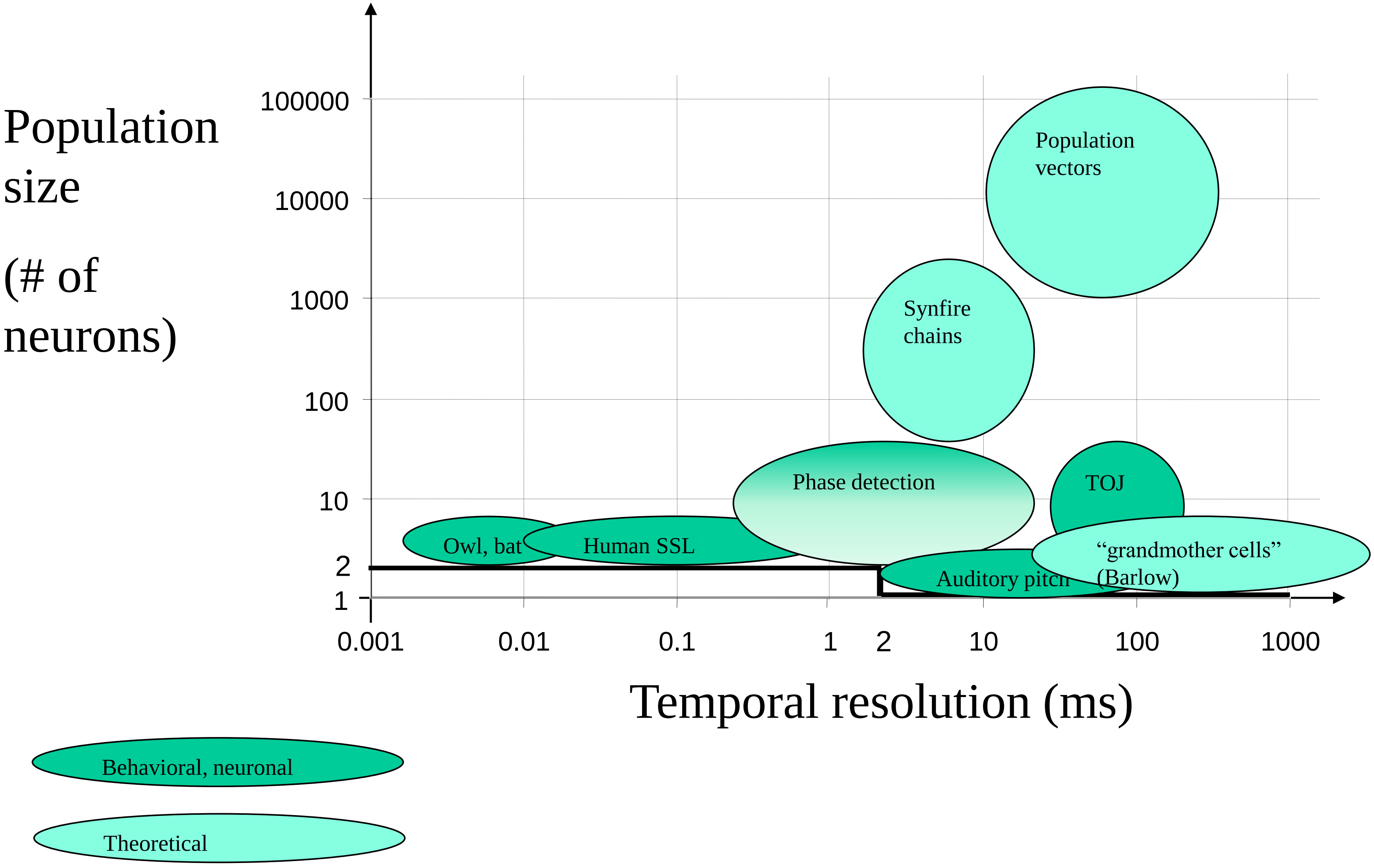
- spatial profile of spike-counts/ rates (*"population code": "population vector", "place code", "labeled-line code"*)
- synchronous firing among neurons (*"synchrony code"*)
- delayed firing among neurons (*"delay code"*)

Other codes: Perkel & Bullock 1968

# Can we constrain the coding space by a-priori knowledge?



# Can we constrain the coding space by a-priori knowledge?



# Is there a unique code across the entire brain?

Probably not

Every processing stage performs a **transformation** which sometimes cause **code translation.**

Examples of possible code conversions:

labeled line -> population vector

...

intensity code -> labeled line

...

delay code -> labeled line

...

delay code -> population vector

...

# Examples of code translations

| code | Can be transformed from |
|---|---|
| **Spatial codes (neuronal space)** | |
| <u>Intensity</u> | |
| Labeled line | Temporal delay + coincidence detector (CD)<br>Weighted sums + threshold |
| Population vector | Weighted sums of labeled lines<br>Weighted sums of populations<br>Temporal delays + phase detectors (PD) |
| **Temporal codes** | |
| <u>Delay</u> | |
| Single-neuron latency | Stimulus intensity |
| Inter-neuronal delay | Intensity differences<br>stimulus pattern + movement |
| Single-neuron inter-spike interval (ISI) | Input intensity |
| Population vector of latencies/ISIs | Population intensity |
| Chain of ISIs ("synfire") | Population vector + wiring |
| | |
| <u>Frequency</u> | |
| Single neuron frequency | Input intensity |
| Population coherence ("binding") | Population vector + wiring |

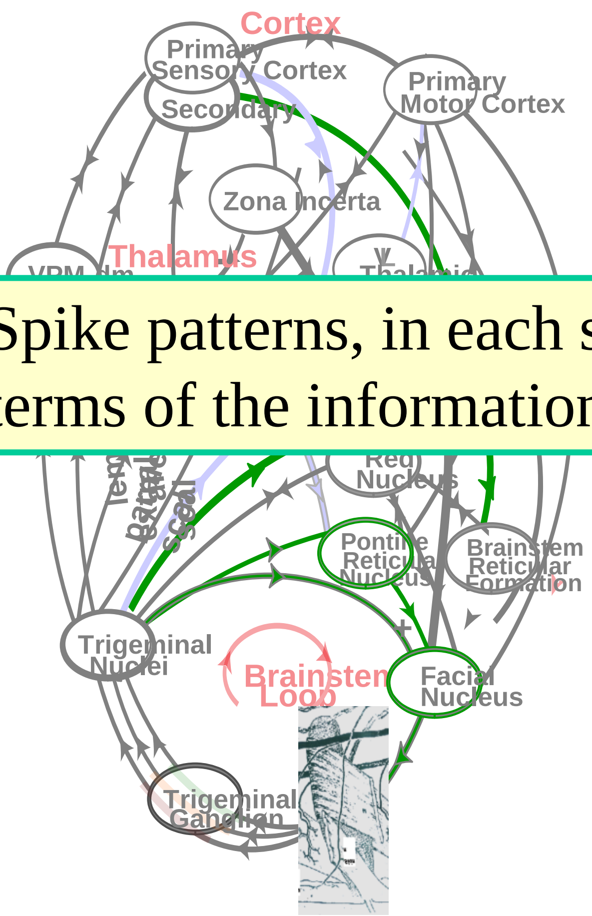
Thus, coding depends on the processing level.

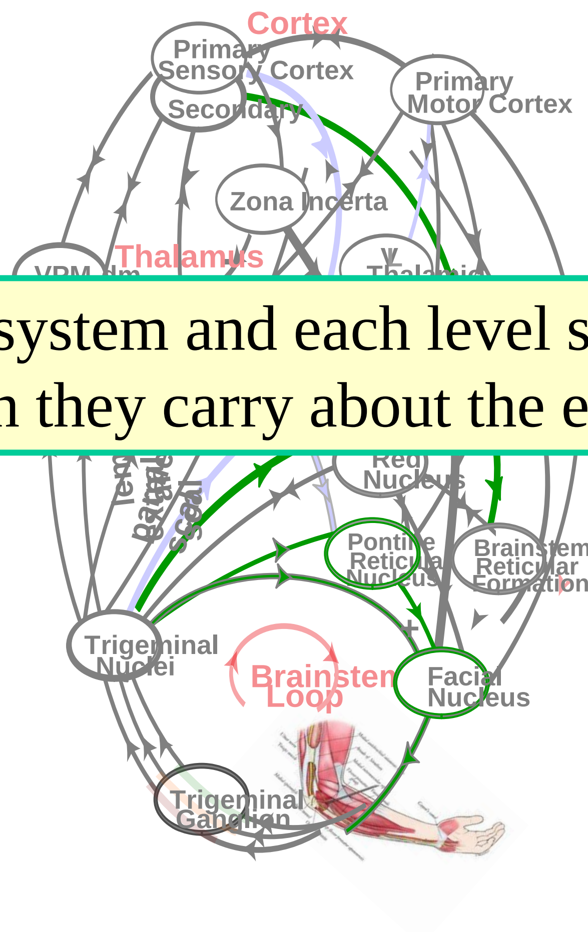
we cannot ask: what is the neural code?

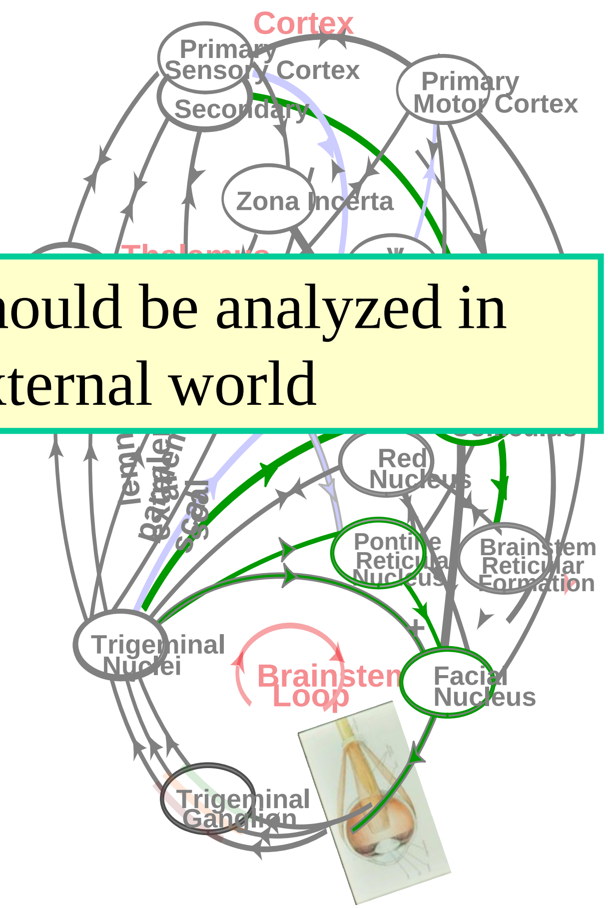
we should ask

**what is the code(s) in a specific processing level.**

How can one (experimenter or a neuronal circuit) **read out** what's going on in each of the stations?



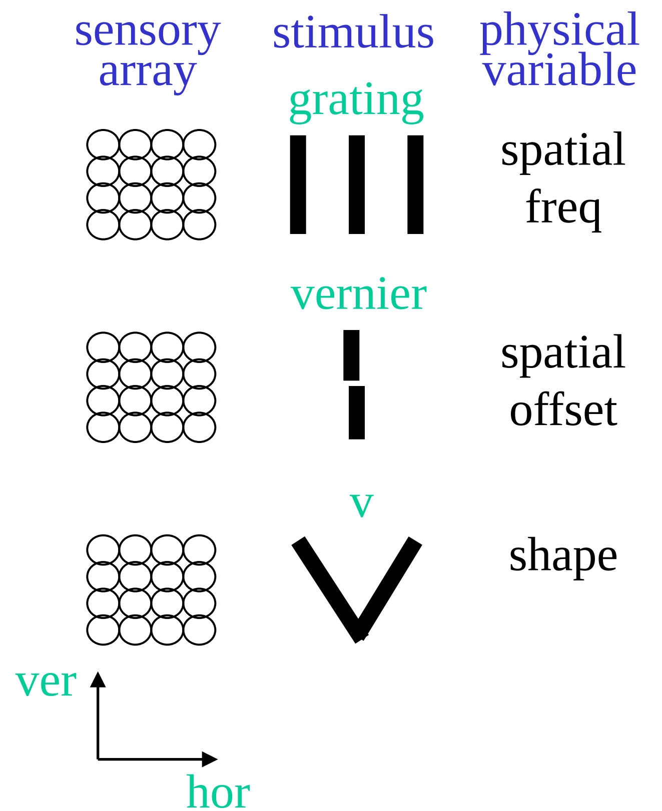




Spike patterns, in each system and each level should be analyzed in terms of the information they carry about the external world

# Exercise #1

- consider a matrix of 4x4 receptors (R)
- consider 3 stimuli: grating, vernier, V, and their associated physical variables
- describe the neuronal variables that encode the physical variables, and analyze their behavior, for each stimulus in 3 cases:
  - passive: stimuli flash on the array for 100 ms
  - active 1: the array moves in one direction; stimuli are stationary
  - active 2: the array oscillates (back and forth) at 10 Hz; stimuli are stationary




- assume the spatial relationships depicted in the figure
- assume a constant array velocity = 100 R/s
- analyze active 1 & 2 for both horizontal and vertical motion
- analyze the effect of stimulus size in relation to receptor size
- for each case, mark the coding regime in a spatio-temporal coding space