Foundations of Computational Neuroscience (2): Networks of Neurons

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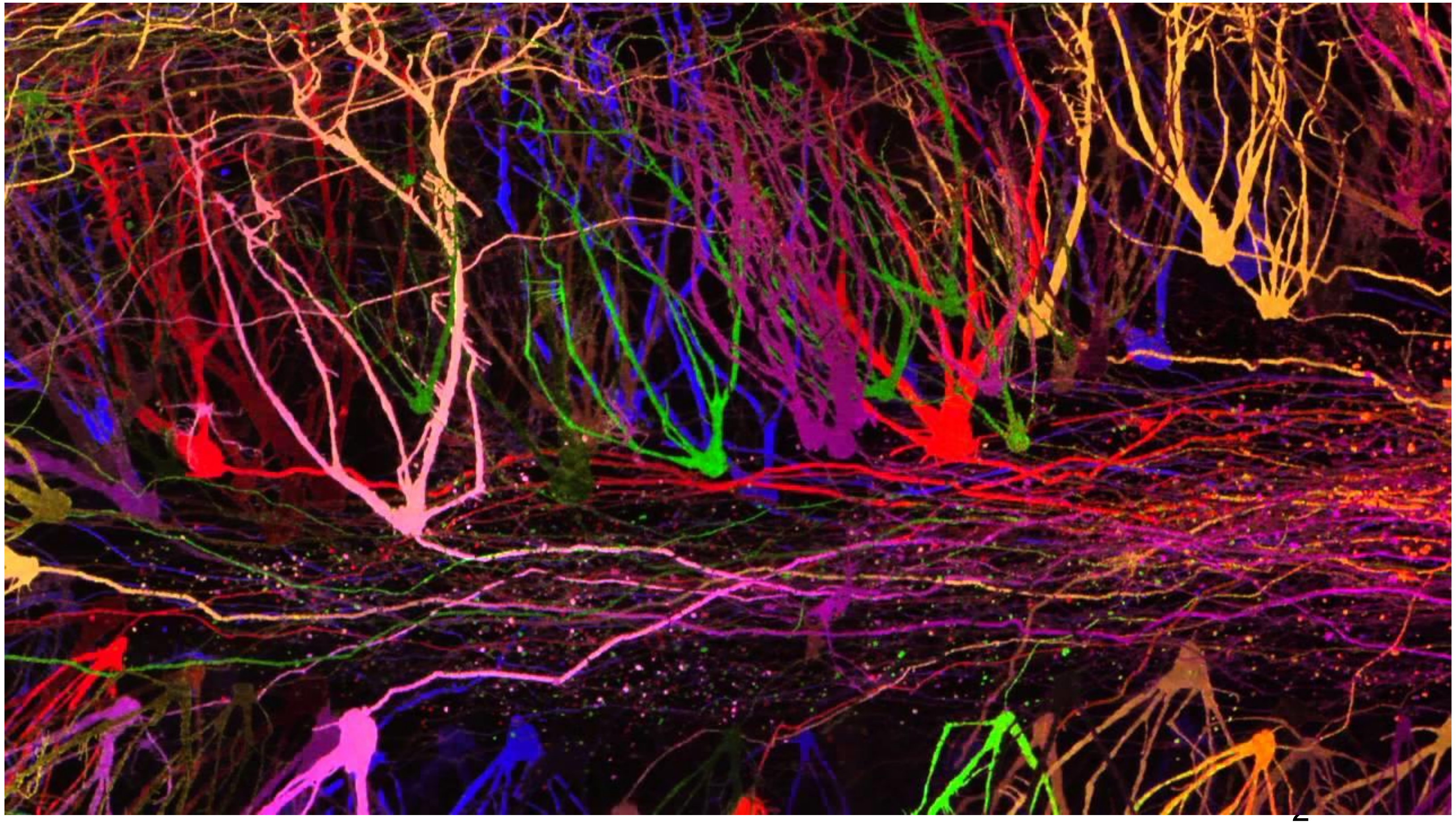
CCN lecture 4

- Neurons are organized in large networks. A typical neuron in cortex receives thousands of inputs.
- “Brainbow”: genetic engineering technique (in mice) which makes neighbouring neurons glow in different colours through fluorescent proteins.



Networks of Neurons

Aim of modelling networks: explore the computational potential of such connectivity.

- What properties?
- What dynamics and how are those generated ? (e.g. spontaneous activity, variability, oscillations)
- Why are networks the way they are? What are they problems they solve, what constraints? What computations? (e.g. learning, integration, gain modulation or selective amplification of some signal , memory etc..)
- What changes in properties can be related to ageing or disease?

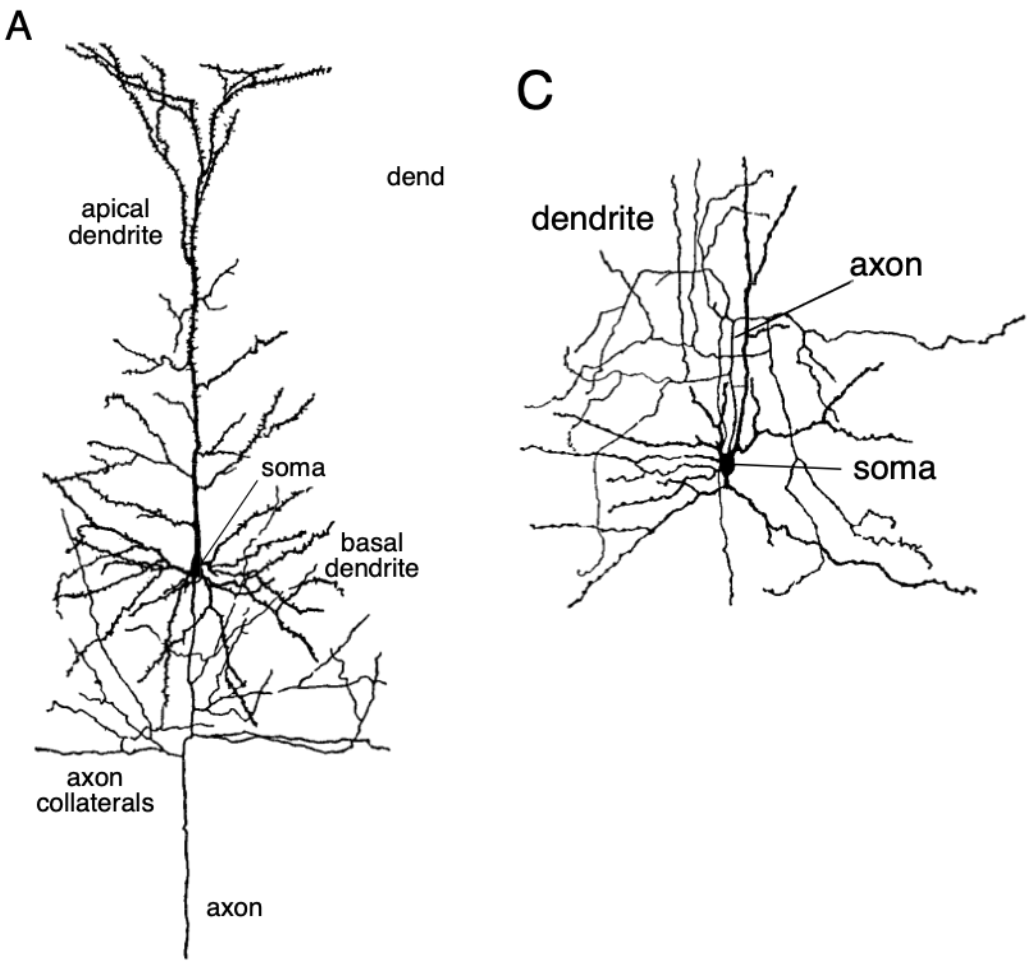
• Tools:

- models of neurons and synapses : spiking neurons (IAF) or firing rate
- analytical solutions (dynamical systems, mean field theory), numerical integration

The tools we choose depend on the question, the data we compare our model to and the scale of the problem.

What’s in a network of neurons ?

• In cortex, ~80% excitatory cells (pyramidal neurons), ~20% inhibitory neurons (smooth stellate + large variety of other types)/ a.k.a interneurons.

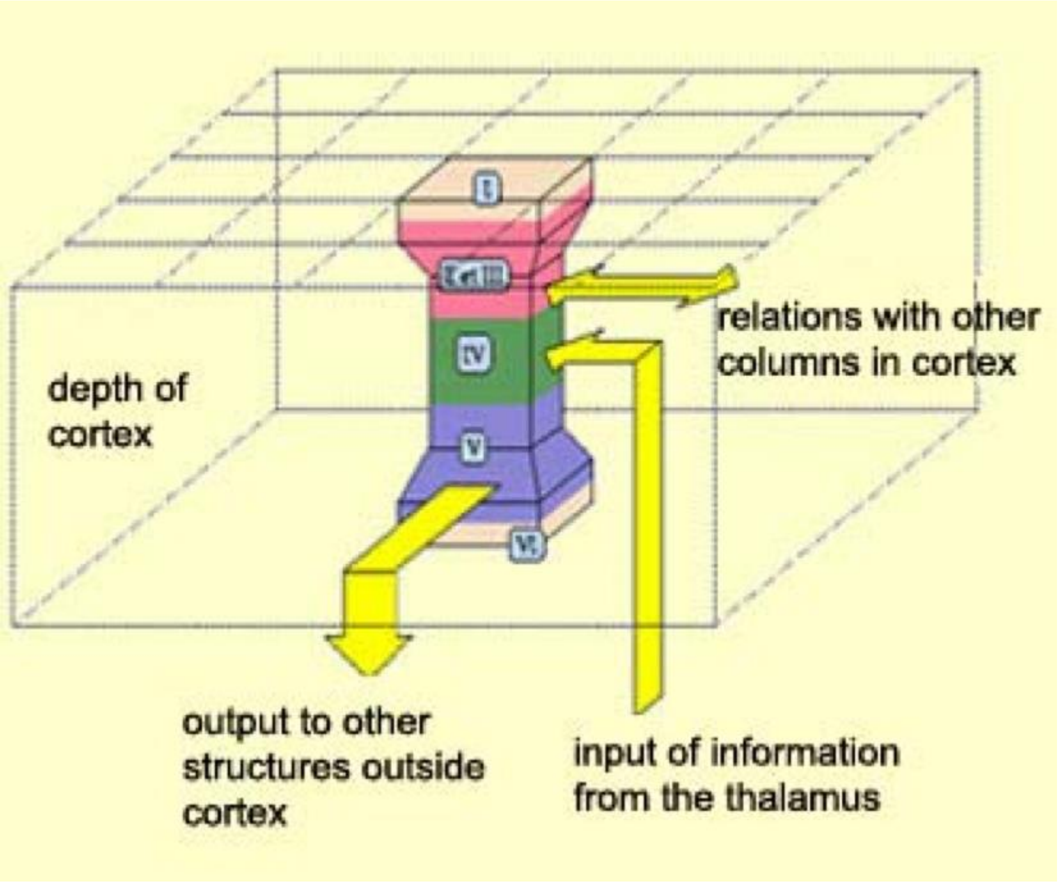


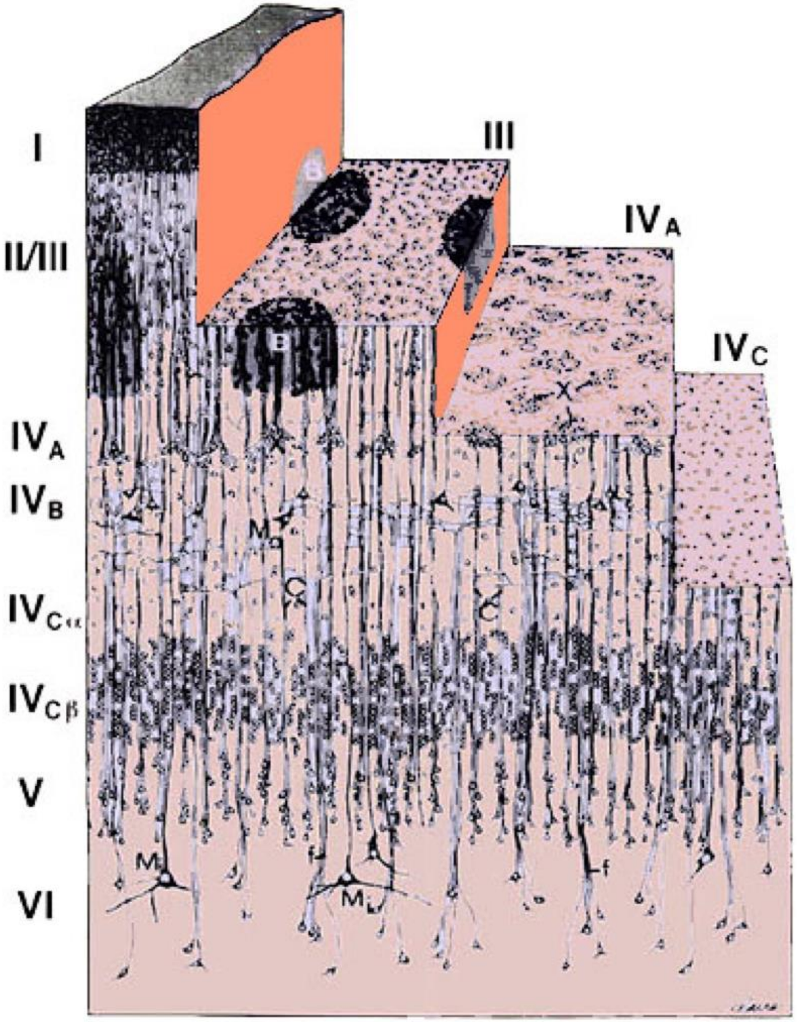
What's in a network of neurons ?

- Laminar Organization.

Cortex is divided into 6 layers.

Models usually pool all layers together.

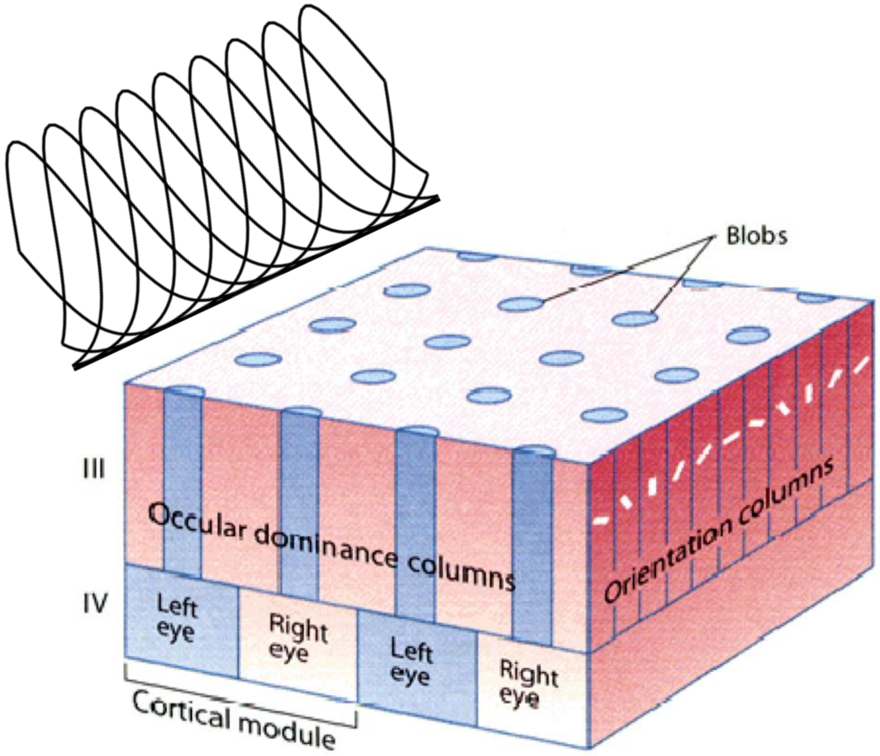




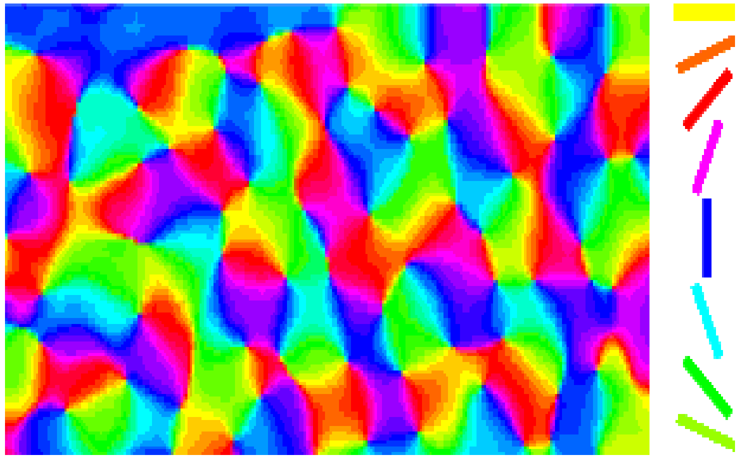
What's in a network of neurons ?

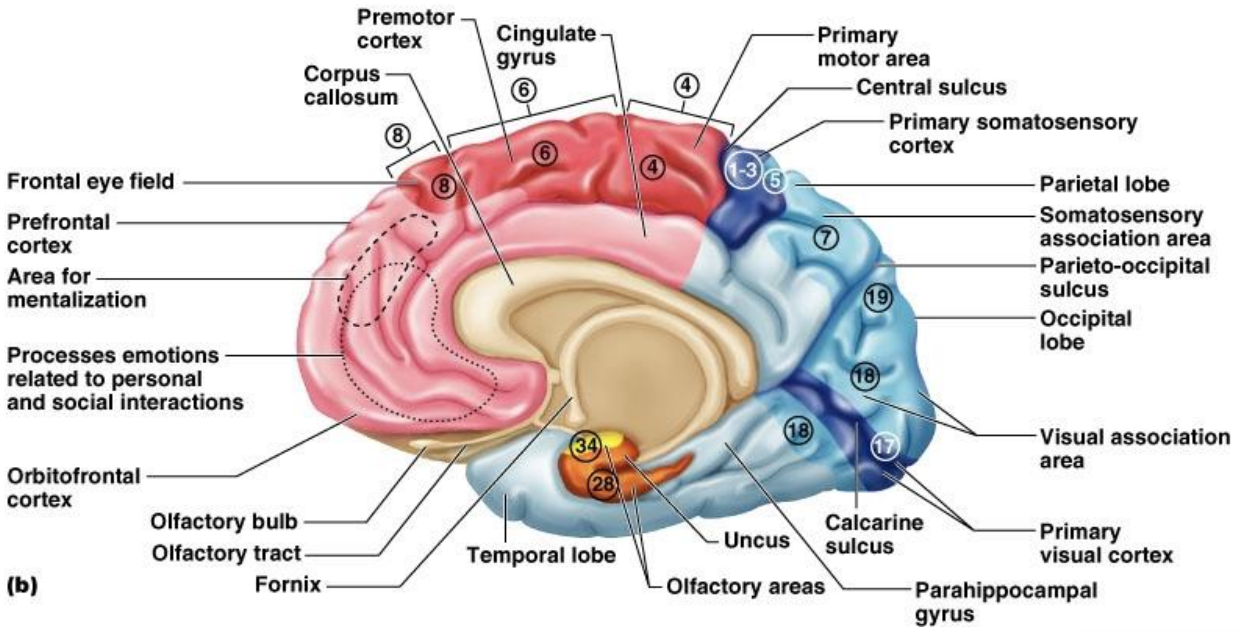
• Columnar Organization.

Neurons in small (30-100 micrometers) columns perpendicular to the layers (across all layers) respond to similar stimulus features.

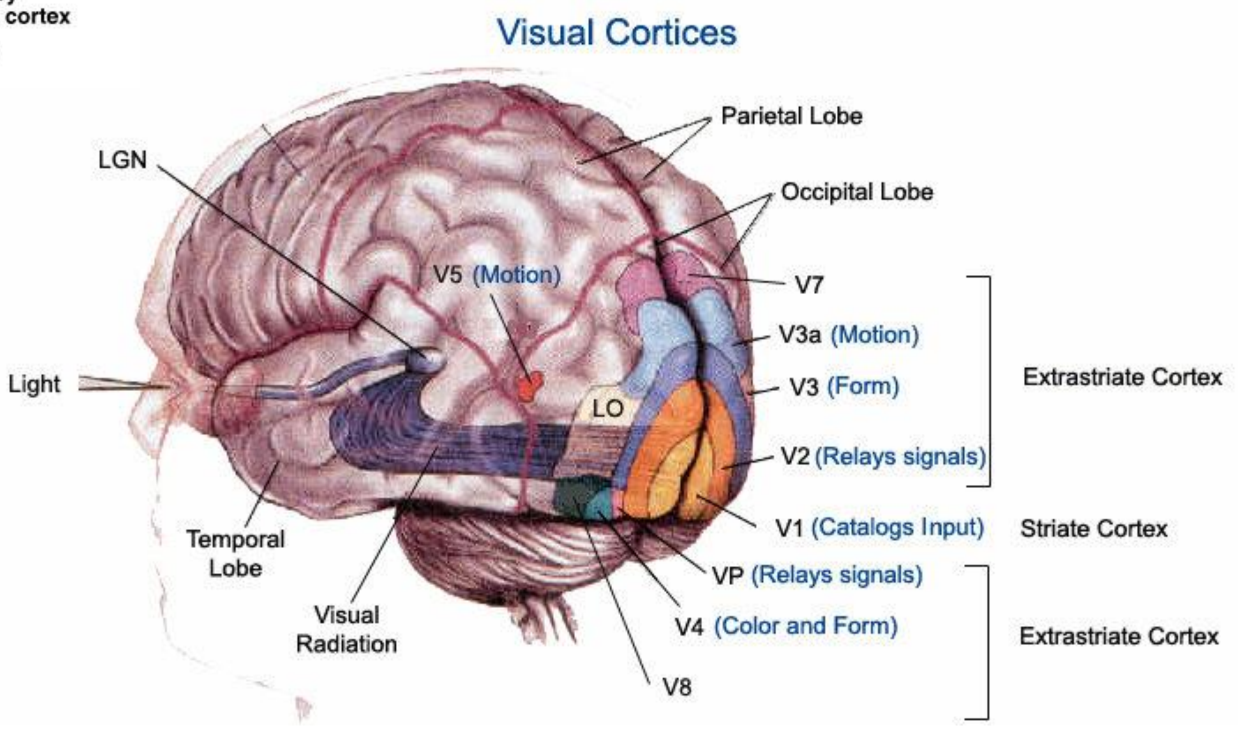


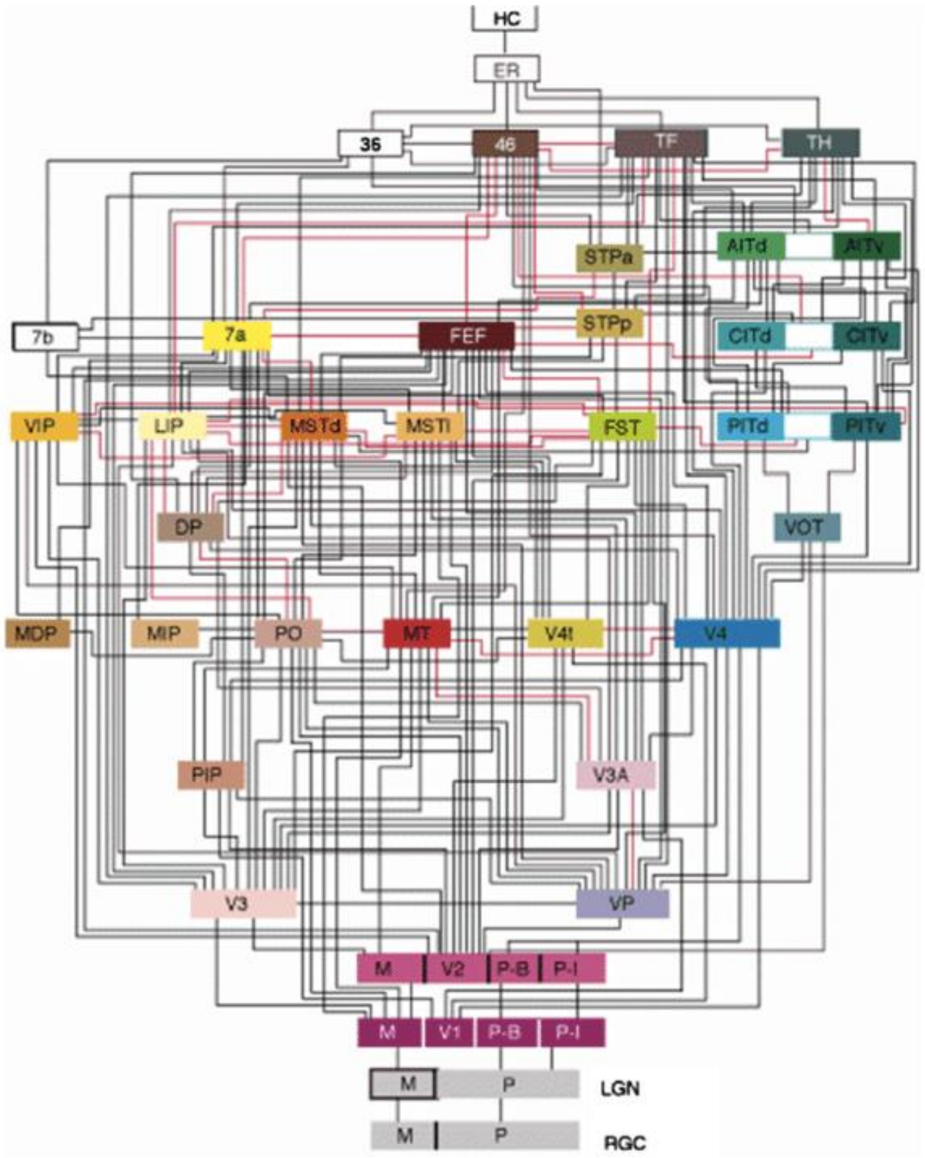
(Aus Gazzaniga et al., 1998)





Many interconnected areas. A very large fraction of the cortex (often quoted around ~20–30%+, depending on definition) is involved in visual processing.





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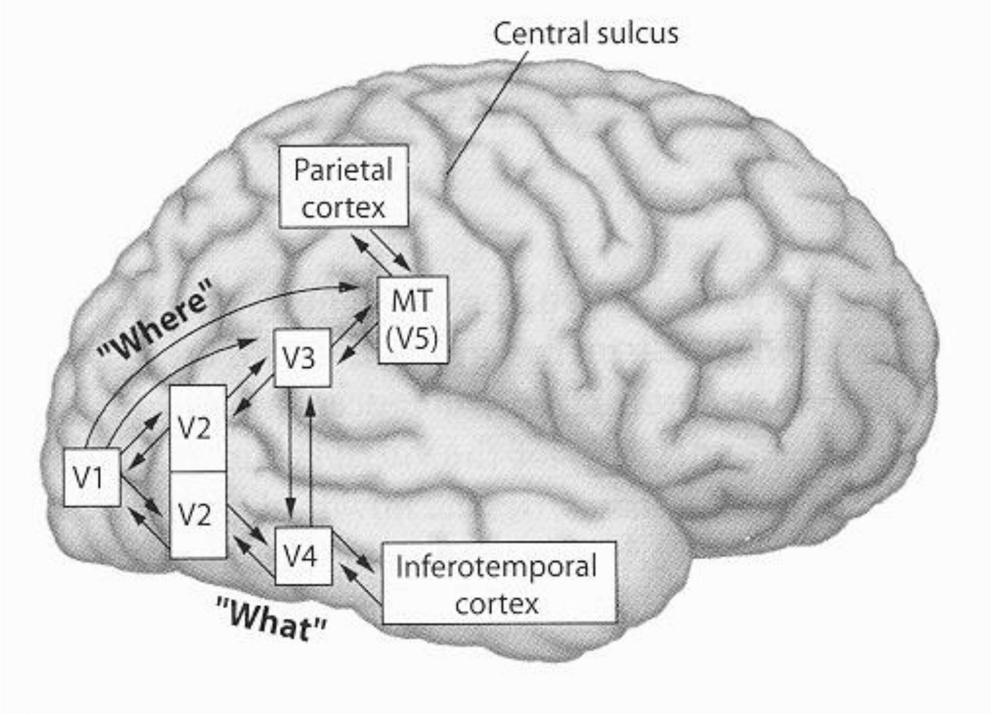
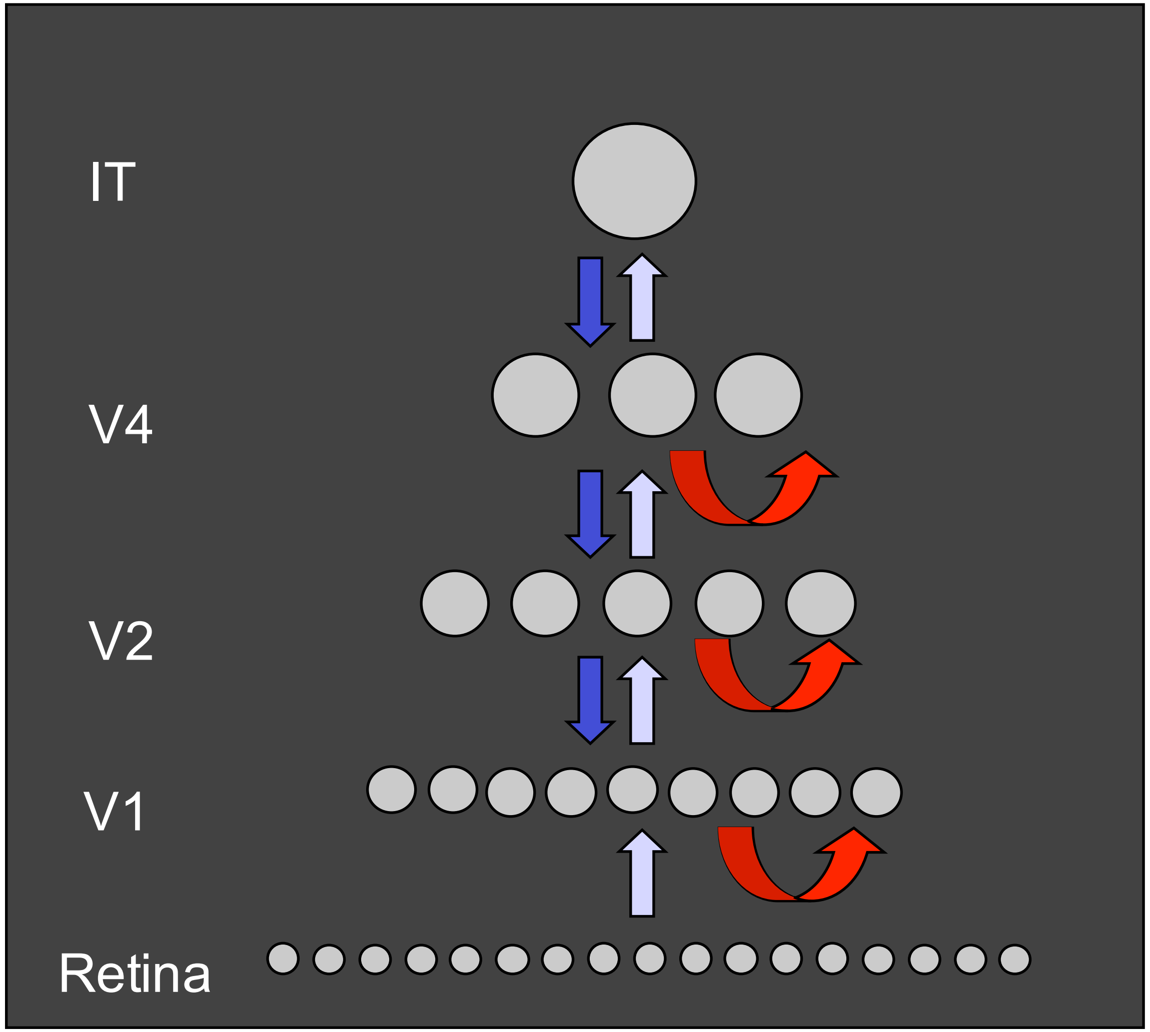
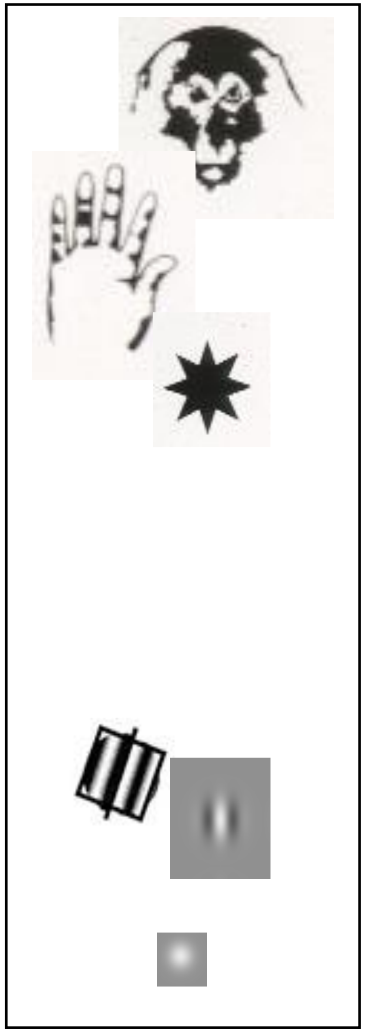


Connectivity

- 3 types of connections: feed-forward, recurrent (lateral), feedback.





Network modeling strategies (1)

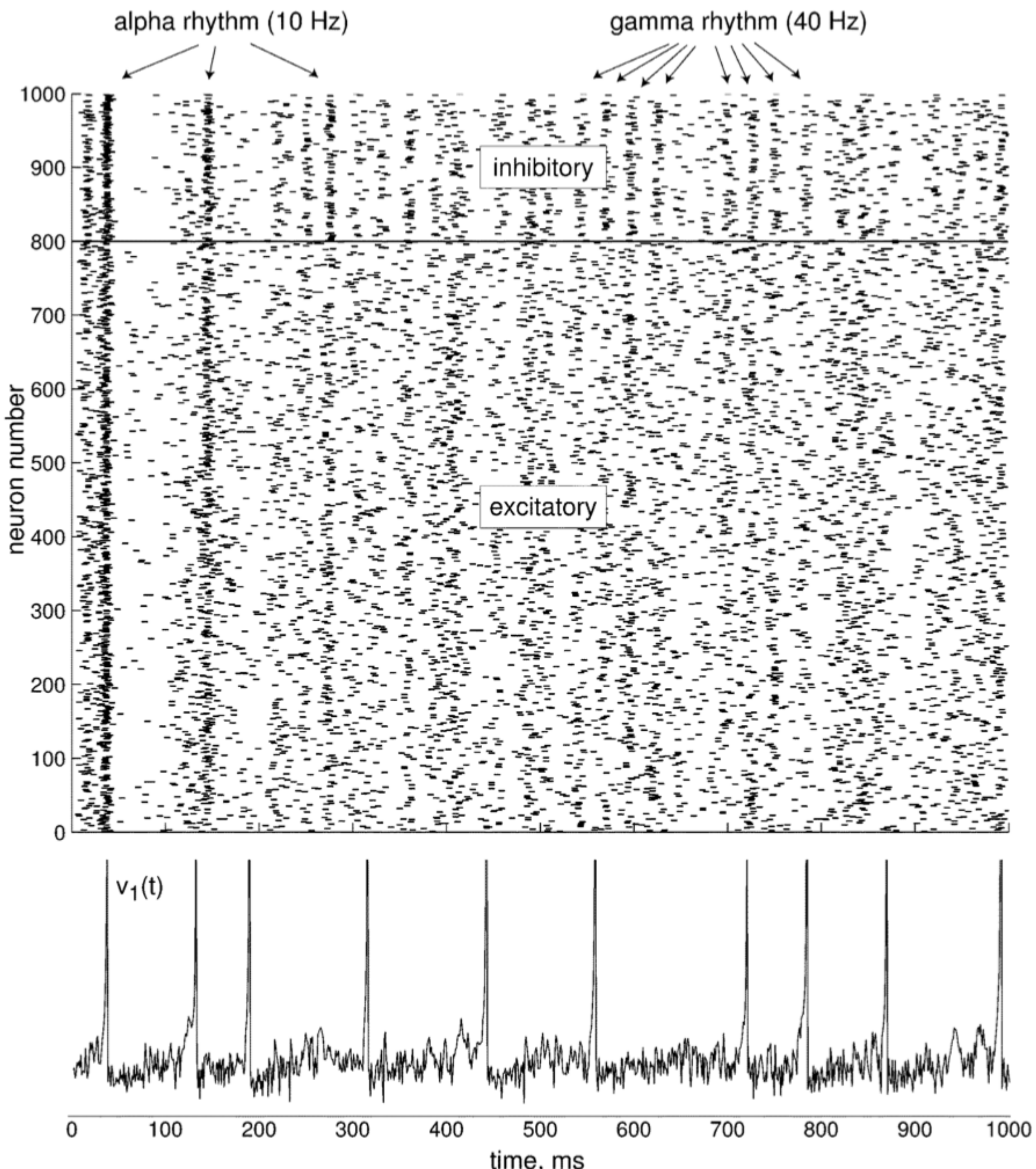
- method 1: spiking neurons, e.g. integrate and fire neurons

$$C_m \frac{dV_i(t)}{dt} = -\sum_j g_{ij}\left(t-\tau_{ij}\right)\left(V_i(t)-E_{\mathrm{EXCIT}}\right) - \sum_j g_{ij}\left(t-\tau_{ij}\right)\left(V_i(t)-E_{\mathrm{INHIB}}\right)$$
$$-g_{\mathrm{LEAK}}\left(V_i(t)-E_{\mathrm{LEAK}}\right) - g_{\mathrm{AHP}}\left(t\right)\left(V_i(t)-E_{\mathrm{AHP}}\right).$$

$$g_{ij}\left(t\right) = \bar{g}_{ij}\sum_l \left[t-t_j^l\right]^+ \left(\frac{e}{\tau_{\mathrm{peak}}}\right)\exp\left(-\frac{t-t_j^l}{\tau_{\mathrm{peak}}}\right).$$

- up to 10,000 neurons+.
- advantage: comparison with electrophysiology, a system where all neurons can be ‘recorded’ at all times.
- difficulties: lots of parameters/assumptions, long simulations, analysis difficult.

Network modeling strategies (2)



spike raster

neuron trace

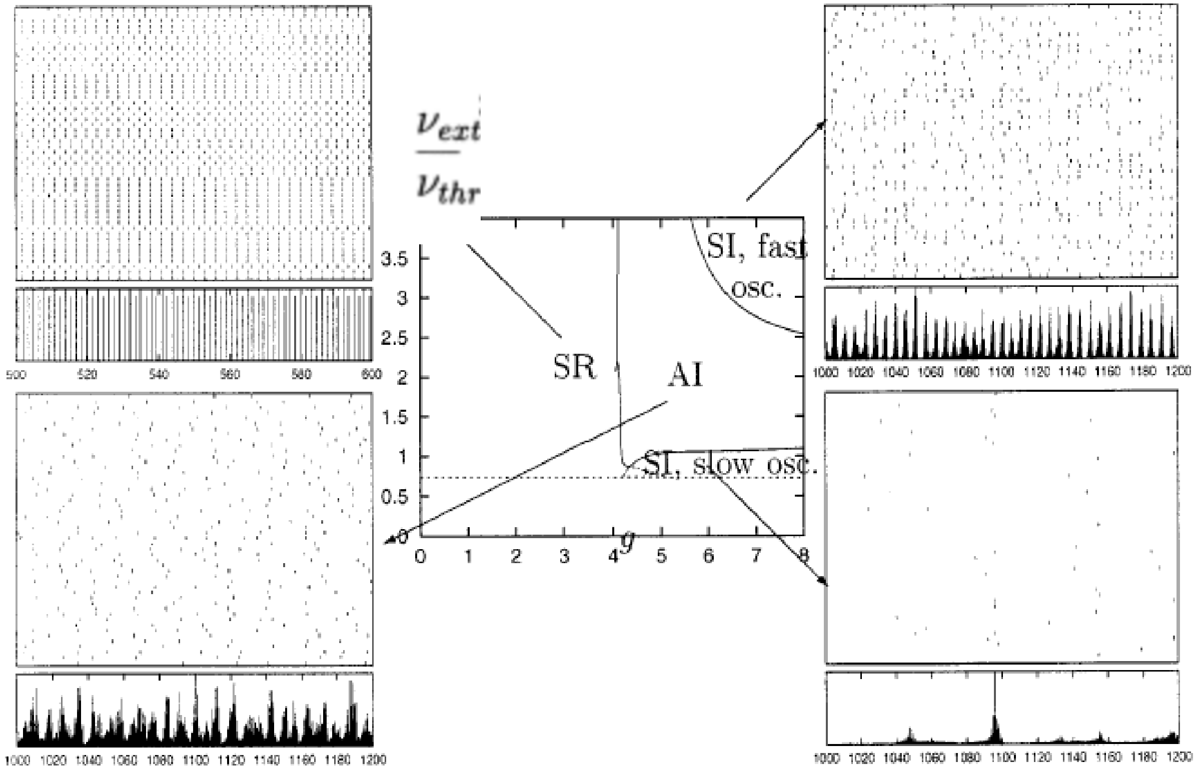
[Izhikevitch, 2003]

Dynamics of Recurrent Networks

Recurrent Networks can show rich dynamics, oscillations, chaotic / asynchronous states depending on Excitation/Inhibition (E/I) balance.

synchronous,
regular, high rates

asynchronous irregular



Synchronous
fast oscillations

Synchronous
slow oscillations

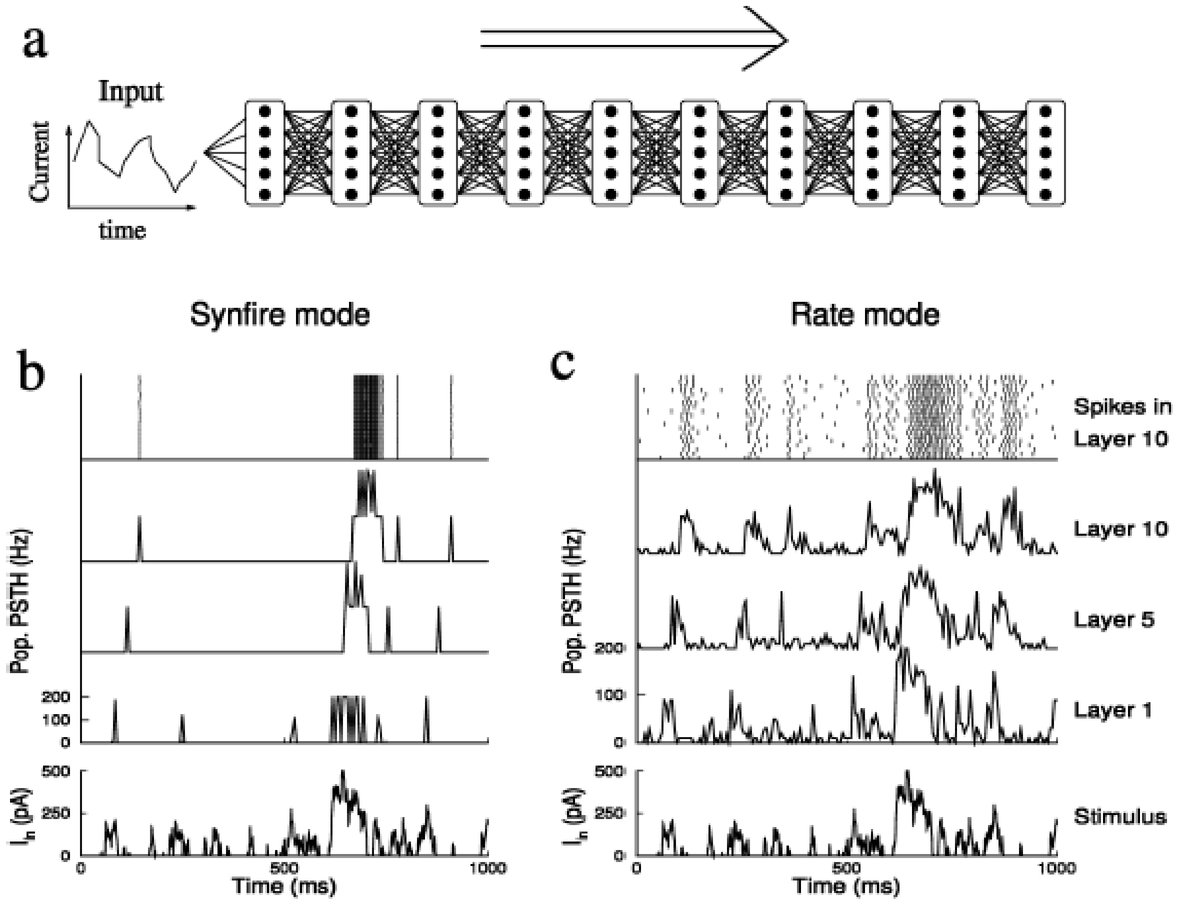
Figure 11. Simulations of a network of 10 000 pyramidal cells and 2 500 interneurones illustrate the different types of collective states, or 'phases' of the system. For each of the four examples are indicated the temporal evolution of the global activity of the system (instantaneous firing frequency computed in bins of 0.1 ms), together with the firing times (rasters) of fifty randomly chosen neurones. In the SR state, the network is almost fully synchronized and neurones fire regularly at high rates. In the fast oscillatory SI state, there is a fast oscillation of the global activity, and neurones fire irregularly at a rate which is lower than the global frequency. In the AI state, the global activity is stationary (fluctuations seen in the graph are a finite size effect, see Section 3.3.4), neurones fire irregularly. In the slow oscillatory SI state, there is a slow oscillation of the global activity, and neurones firing irregularly at very low rates.

Here g on x-axis is the relative strength of inhibitory synapses compared to excitatory synapses.

[Brunel, 2000]

Dynamics of Feedforward Networks

How do inputs propagate across Feedforward networks ?
(How fast? What's the role of synchrony?)



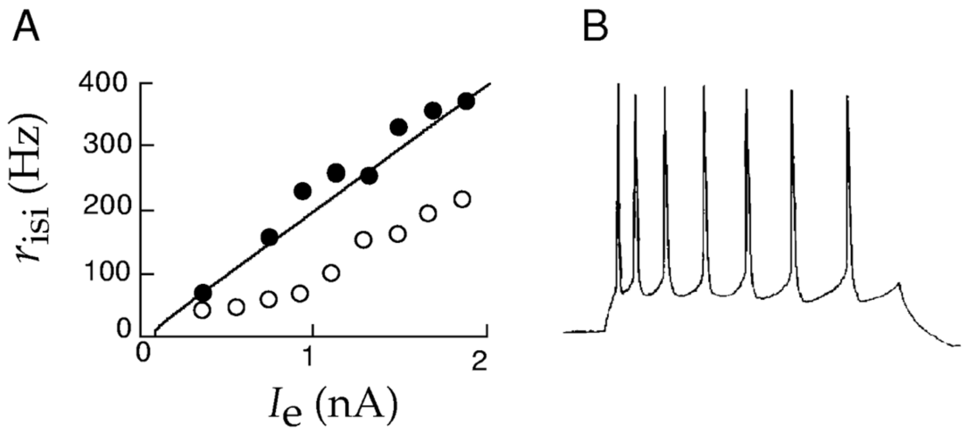
Low noise regime

High noise regime

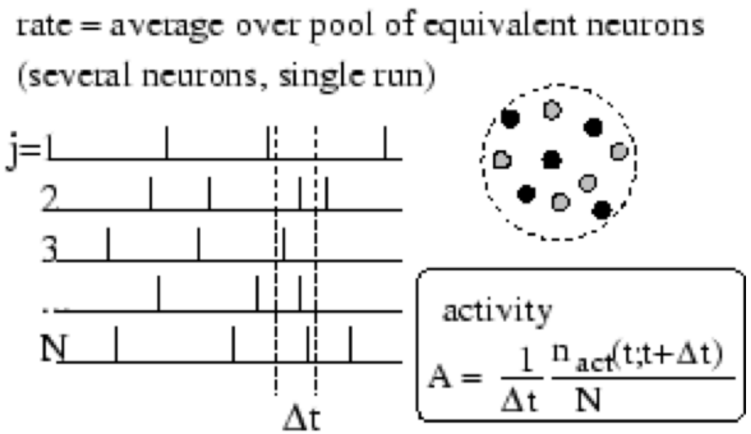
Network modeling strategies (3)

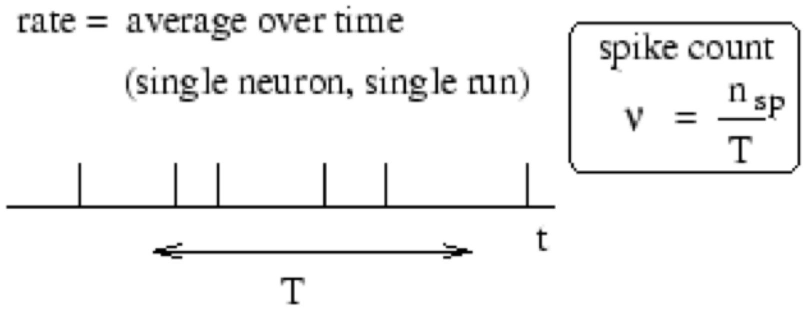
- Method 2: reduce the description to describe only rate of spiking r(t) (also confusingly sometimes denoted v(t)), instead of Vm(t).

$$\tau_r \frac{dr_i(t)}{dt} = -r_i(t) + \mathrm{input}(t)$$



- Interpretation: average over equivalent neurons or over time

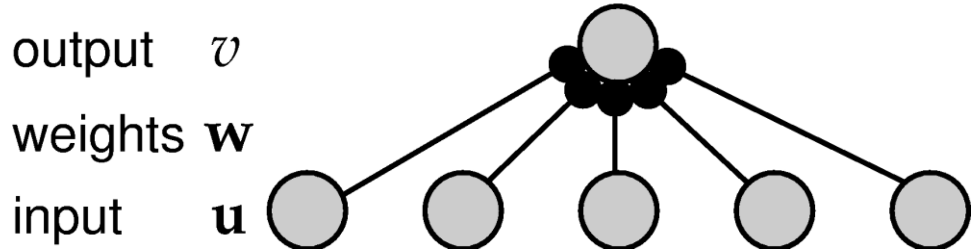




Firing rate model (1)

- Each neuron is described at time t by a firing rate v(t).

$$\tau_r \frac{dv_i(t)}{dt} = -v_i(t) + F\left(\sum_{j=1}^{j=N} w_{ij} u_j\right)$$



- In absence of input, the firing rate relaxes to 0 with a time constant τ_r - which also determines how quickly the neuron responds to input.
- The input from a presynaptic neuron is proportional to its firing rate *u*
- The weight w_{ij} determines the strength of connection of neuron j to neuron i
- The total input current is the sum of the input from all external sources.

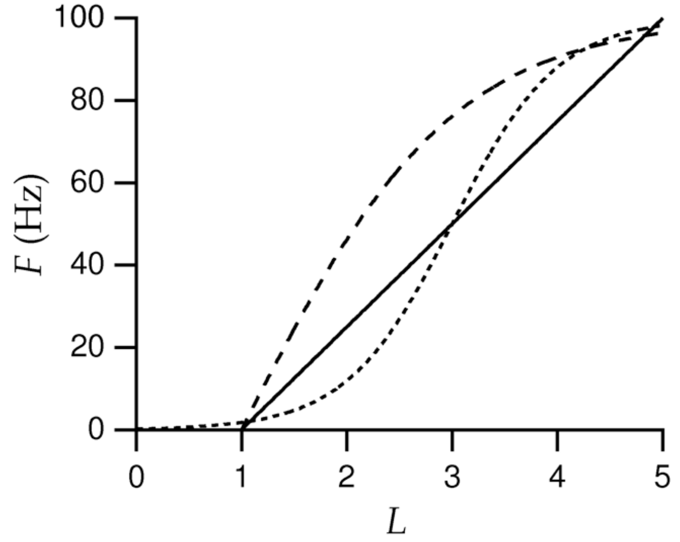
Firing rate model (2)

- Each neuron is described at time t by a firing rate v(t).

$$\tau_r \frac{dv_i(t)}{dt} = -v_i(t) + F(\sum_{j=1}^{j=N} w_{ij}u_j) = -v_i(t) + F(\mathbf{w.u})$$

dot-product

- F determines the steady state r as a function of input
- F is called the activation function
- F can be taken as a saturating function, e.g. sigmoid
- F is often chosen to be threshold linear



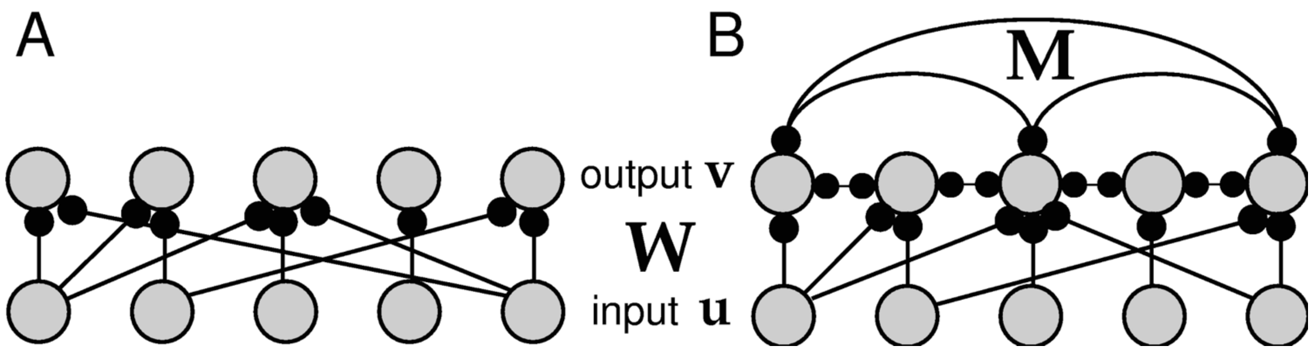
Network Architectures

- A: Feedforward

$$\tau_r \frac{dv_i(t)}{dt} = -v_i(t) + F(\sum_{j=1}^{N} W_{ij} u_j(t))$$

- B: Recurrent

$$\tau_r \frac{dv_i(t)}{dt} = -v_i(t) + F(\sum_{j=1}^{N} W_{ij} u_j(t) + \sum_{k=1}^{N} M_{ik} v_k(t))$$



Excitatory - Inhibitory Network

- Some models have a single population of neurons and the weights are allowed to be positive and negative.
- Other models represent the excitatory and inhibitory population separately (more 'biological' + richer dynamics).
- 4 weight matrices, M_{EE}, M_{IE}, M_{II}, M_{EI}

$$\tau_{\mathrm{E}} \frac{d\mathbf{v}_{\mathrm{E}}}{dt} = -\mathbf{v}_{\mathrm{E}} + \mathbf{F}_{\mathrm{E}} \left(\mathbf{h}_{\mathrm{E}} + \mathbf{M}_{\mathrm{EE}} \cdot \mathbf{v}_{\mathrm{E}} + \mathbf{M}_{\mathrm{EI}} \cdot \mathbf{v}_{\mathrm{I}} \right)$$

and

$$\tau_{\mathrm{I}} \frac{d\mathbf{v}_{\mathrm{I}}}{dt} = -\mathbf{v}_{\mathrm{I}} + \mathbf{F}_{\mathrm{I}} \left(\mathbf{h}_{\mathrm{I}} + \mathbf{M}_{\mathrm{IE}} \cdot \mathbf{v}_{\mathrm{E}} + \mathbf{M}_{\mathrm{II}} \cdot \mathbf{v}_{\mathrm{I}} \right) .$$

Example:

Orientation selectivity as a model computation

Neurons in V1 are selective to orientation

J. Physiol. (1959) 148, 574–591

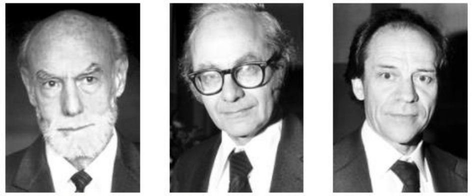
RECEPTIVE FIELDS OF SINGLE NEURONES IN THE CAT'S STRIATE CORTEX

By D. H. HUBEL* and T. N. WIESEL*
From the Wilmer Institute, The Johns Hopkins Hospital and University, Baltimore, Maryland, U.S.A.

(*Received 22 April* 1959)

In the central nervous system the visual pathway from retina to striate cortex provides an opportunity to observe and compare single unit responses at several distinct levels. Patterns of light stimuli most effective in influencing units at one level may no longer be the most effective at the next. From differences in responses at successive stages in the pathway one may hope to gain some understanding of the part each stage plays in visual perception.

The Nobel Prize in Physiology or Medicine 1981

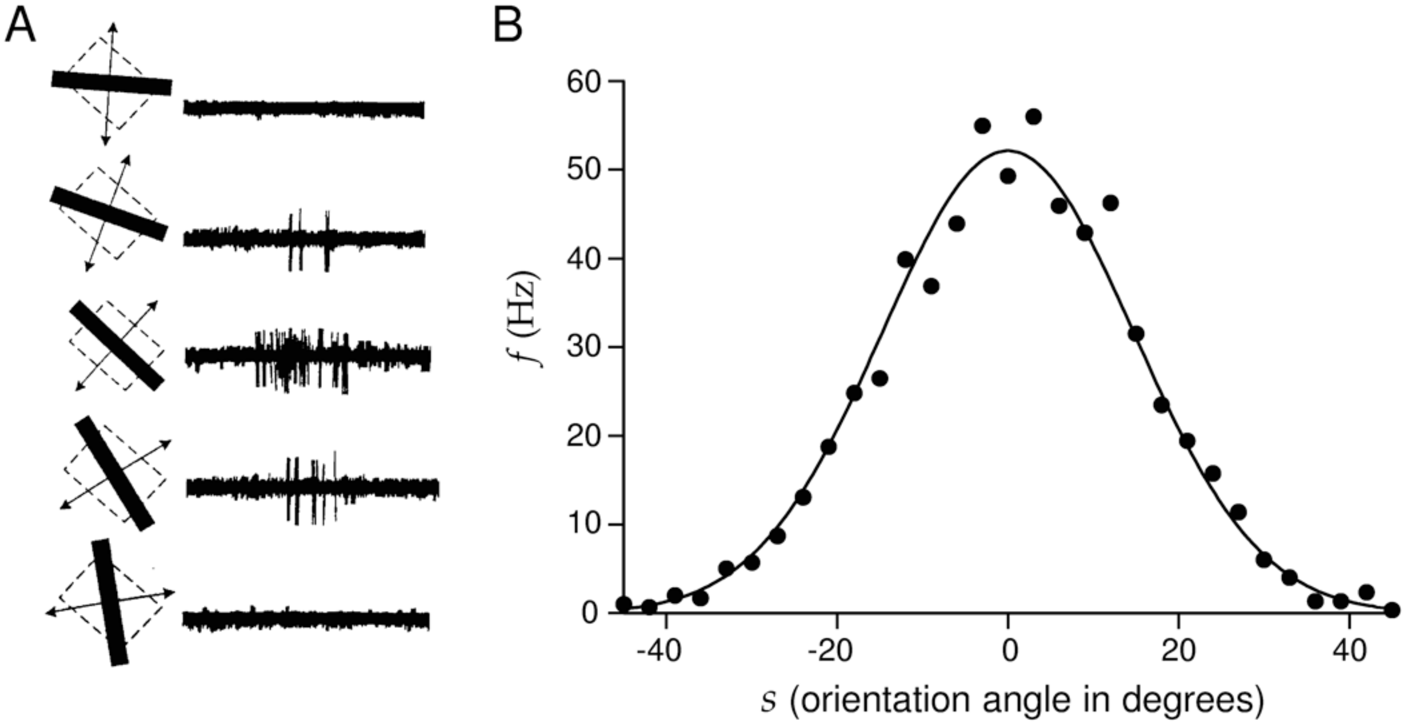


Roger W. Sperry
Prize share: 1/2

David H. Hubel
Prize share: 1/4

Torsten N. Wiesel
Prize share: 1/4

The Nobel Prize in Physiology or Medicine 1981 was divided, one half awarded to Roger W. Sperry *"for his discoveries concerning the functional specialization of the cerebral hemispheres"*, the other half jointly to David H. Hubel and Torsten N. Wiesel *"for their discoveries concerning information processing in the visual system"*.



Origin of Orientation selectivity ?

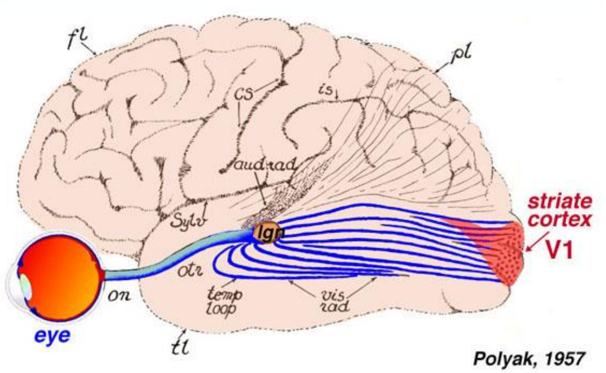
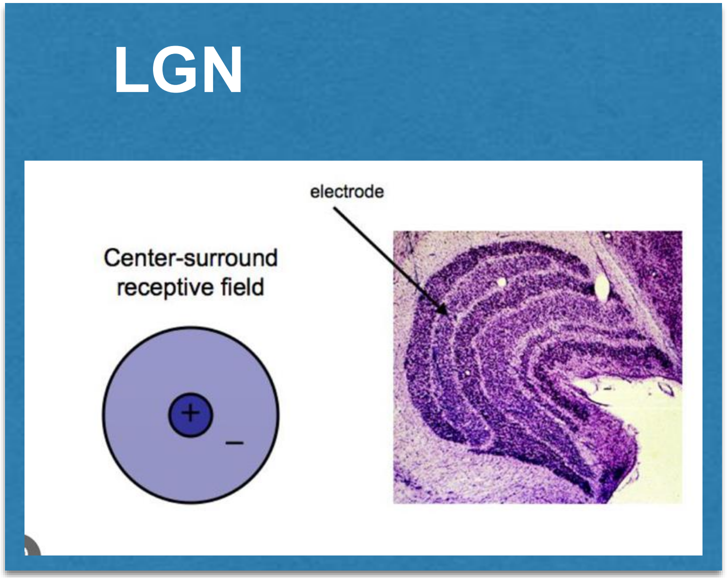
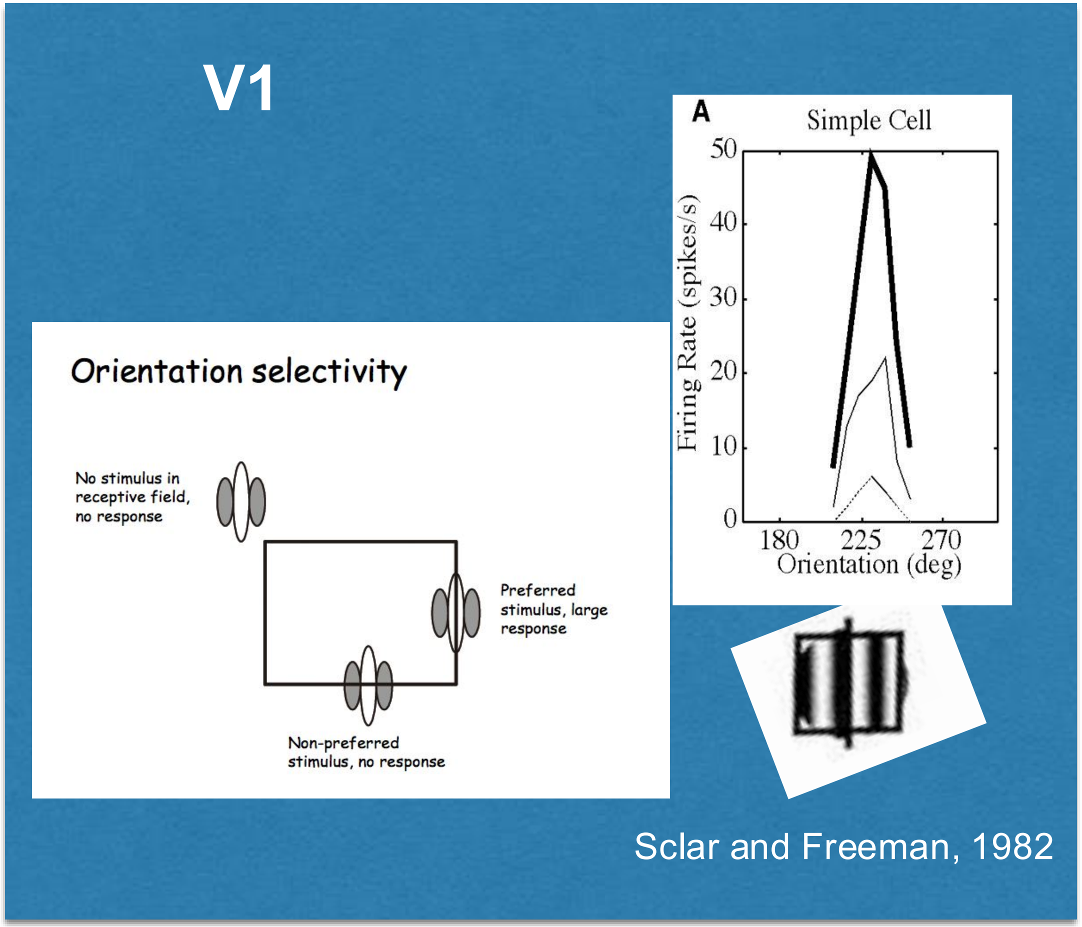


Figure 8. Visual input to the brain goes from eye to LGN and then to primary visual cortex, or area V1, which is located in the posterior of the occipital lobe. Adapted from Polyak (1957).

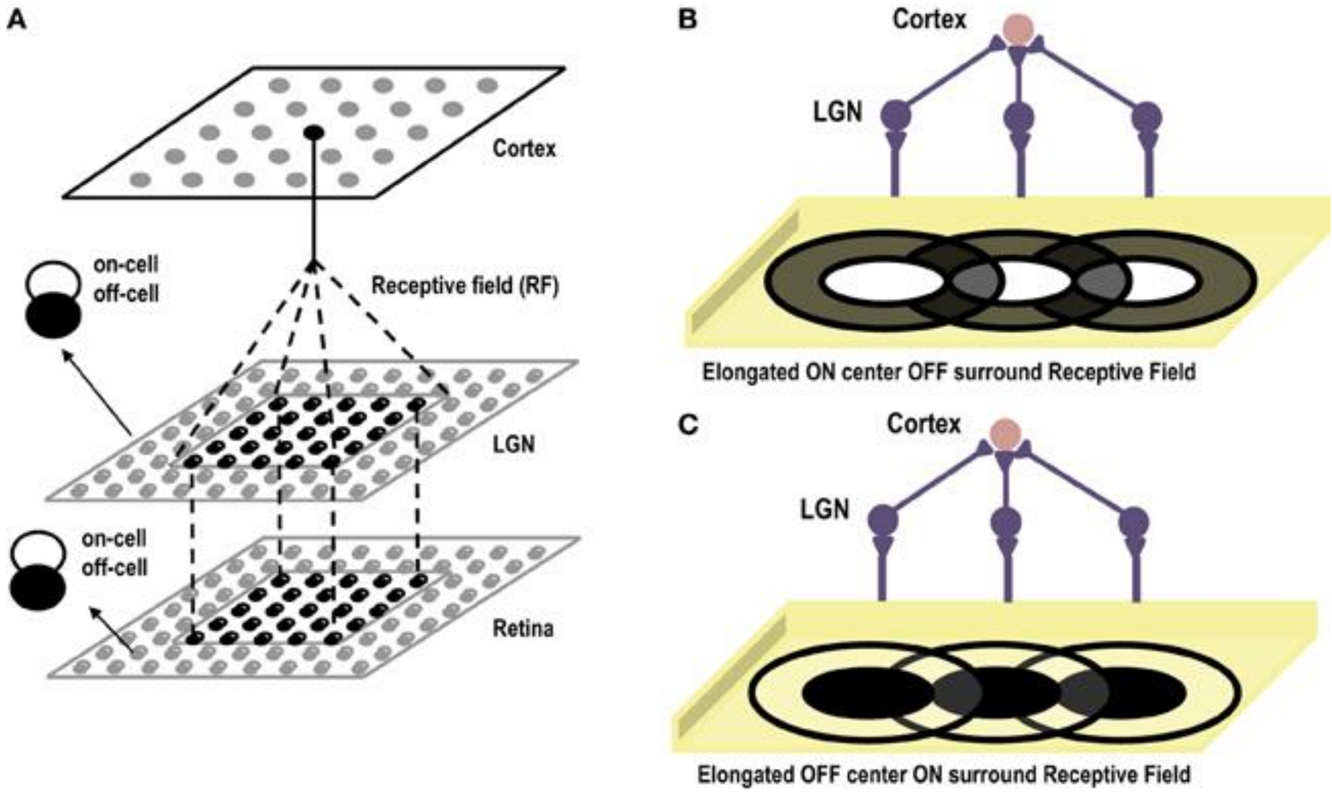




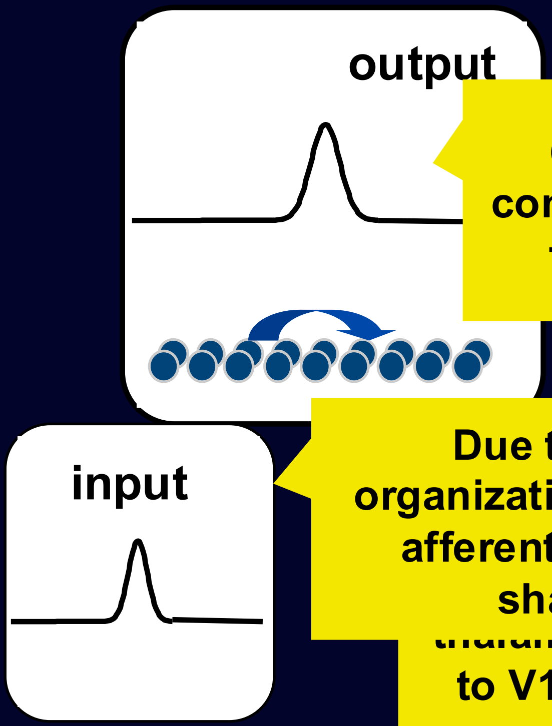
- Example of a computation, emergence of a new property.

Model of Hubel and Wiesel (1962)

- Hubel and Wiesel (1962) proposed that the oriented fields of V1 neurons could be generated by summing the input from appropriately selected LGN neurons.
- The model accounts for selectivity in V1 on the basis of a purely feedforward architecture.



Feedforward vs Recurrent models of Orientation Selectivity

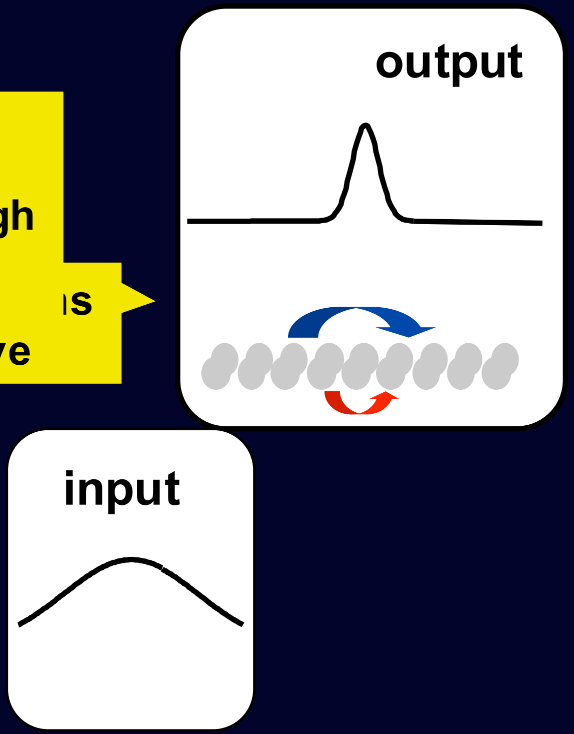


Connectivity achieves contrast invariance through feedforward inhibition

Due to the precise organization of the thalamic afferents, input to V1 is sharply tuned

Feedforward

Hubel and Wiesel, 1962; Troyer, Krukowski, Priebe and Miller, 1998



the tuning curve

to V1 is broadly tuned

Recurrent

Somers, Nelson and Sur 1995; Sompolinsky and Shapley, 1997

The Recurrent/ Ring Model of orientation selectivity (1)

• If the input from LGN is broadly tuned, can contrast-invariant orientation selectivity be achieved within V1**, through recurrent interactions** between neurons?

Proc. Natl. Acad. Sci. USA
Vol. 92, pp. 3844–3848, April 1995
Neurobiology

Theory of orientation tuning in visual cortex

(neural networks/cross-correlations/symmetry breaking)

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Communicated by Pierre C. Hohenberg, AT&T Bell Laboratories, Murray Hill, NJ, December 21, 1994 (received for review July 28, 1994)

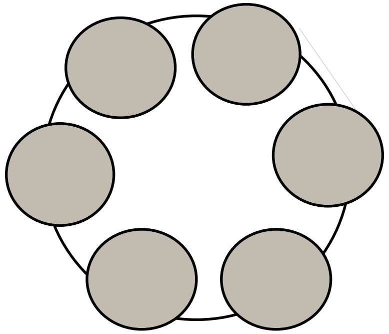
ABSTRACT The role of intrinsic cortical connections in processing sensory input and in generating behavioral output is poorly understood. We have examined this issue in the context of the tuning of neuronal responses in cortex to the orientation of a visual stimulus. We analytically study a simple network model that incorporates both orientation-selective input from the lateral geniculate nucleus and orientation-specific cortical interactions. Depending on the model parameters, the network exhibits orientation selectivity that originates from within the cortex, by a symmetry-breaking mechanism. In this case, the width of the orientation tuning can be sharp even if the lateral geniculate nucleus inputs are only weakly anisotropic. By using our model, several experimental consequences of this cortical mechanism of orientation tuning are derived. The tuning width is relatively independent of the contrast and angular anisotropy of the visual stimulus. The transient population response to changing of the stimulus orientation exhibits a slow "virtual rotation." Neuronal cross-correlations exhibit long time tails, the sign of which depends on the preferred

ivity among cortical neurons can be gained from measurements of the correlations between the responses of different neurons (10). Theoretical predictions regarding the magnitude and form of correlation functions in neuronal networks have been lacking.

Here we study mechanisms for orientation selectivity by using a simple neural network model that captures the gross architecture of primary visual cortex. By assuming simplified neuronal stochastic dynamics, the network properties have been solved analytically, thereby providing a useful framework for the study of the roles of the input and the intrinsic connections in the formation of orientation tuning in the cortex. Furthermore, by using a recently developed theory of neuronal correlation functions in large stochastic networks, we have calculated the cross-correlations (CCs) between the neurons in the network. We show that different models of orientation selectivity may give rise to qualitatively different spatiotemporal patterns of neuronal correlations. These predictions can be tested experimentally.

Model

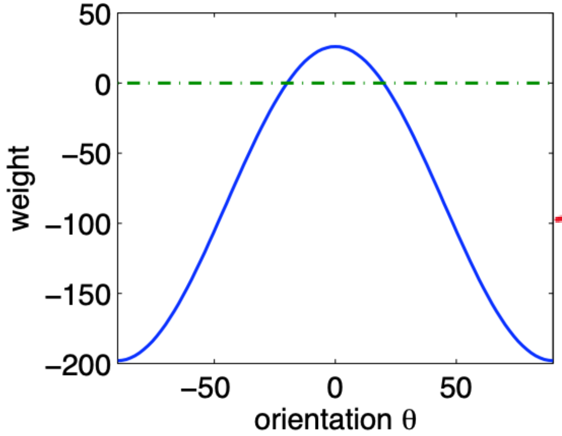
The Recurrent/ Ring Model of orientation selectivity (2)

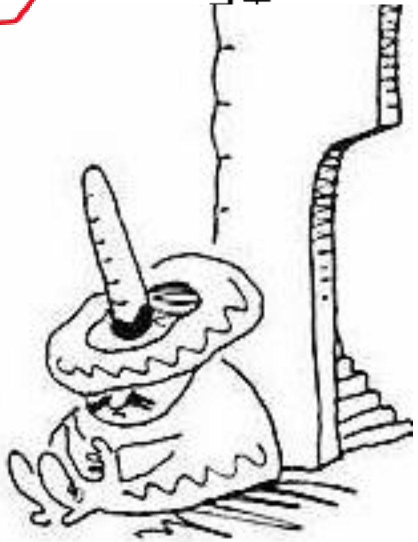


- N neurons, with preferred angle, θ_i, evenly distributed between $-\pi/2$ and $\pi/2$
- Neurons receive thalamic inputs *h*.

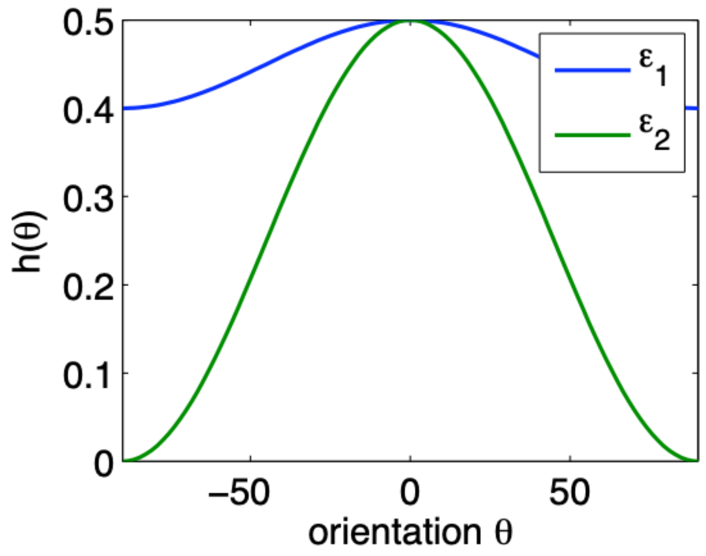
+ recurrent connections, with excitatory weights between nearby cells and inhibitory weights between cells that are further apart (mexican-hat profile)

$$\tau_r \frac{dv(\theta)}{dt} = -v(\theta) + \left[h(\theta) + \int_{-\pi/2}^{\pi/2} \frac{d\theta'}{\pi} \underbrace{\left(-\lambda_0 + \lambda_1 \cos(2(\theta - \theta'))\right)} v(\theta') \right]_+$$





The Recurrent/ Ring Model of orientation selectivity (3)



• h is input, can be tuned (Hubel Wiesel scenario) or very broadly tuned.

$$h(\theta) = c[1 - \epsilon + \epsilon * cos(2\theta)]$$

• The steady-state can be solved analytically. Model analyzed like a physical system.

• Model achieves i) orientation selectivity; ii) contrast invariance of tuning, even if input is very broad.

• The width of orientation selectivity depends on the shape of the mexican-hat, but is independent of the width of the input.

• Symmetry breaking /Attractor dynamics.

The Recurrent/ Ring Model of orientation selectivity (4)

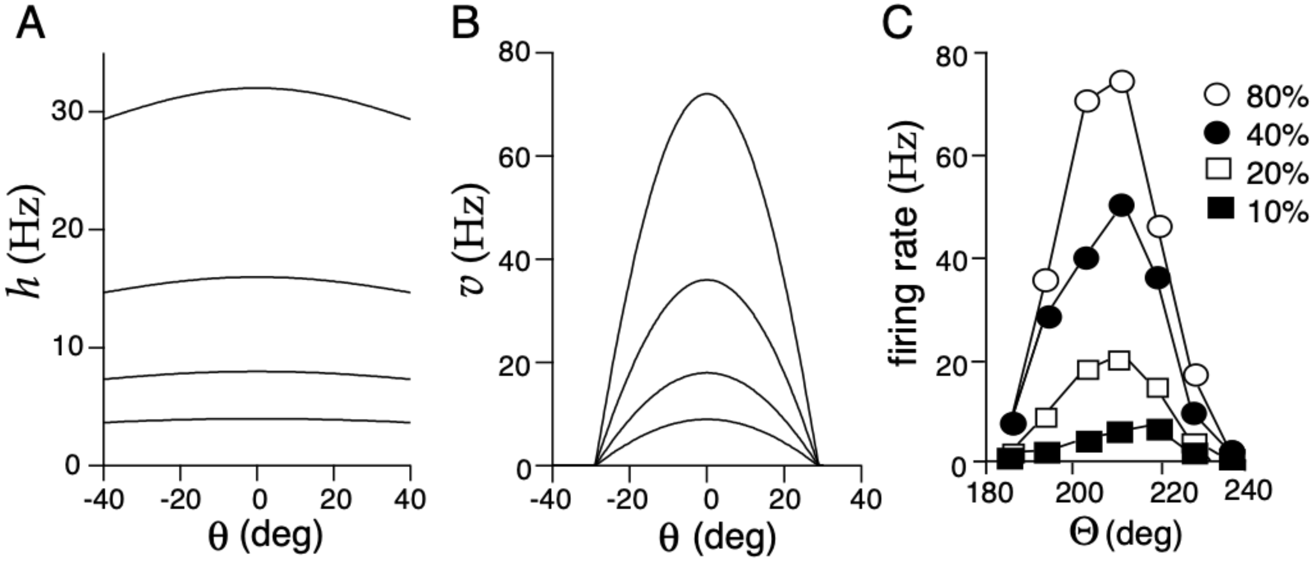


Figure 7.10: The effect of contrast on orientation tuning. A) The feedforward input as a function of preferred orientation. The four curves, from top to bottom, correspond to contrasts of 80%, 40%, 20%, and 10%. B) The output firing rates in response to different levels of contrast as a function of orientation preference. These are also the response tuning curves of a single neuron with preferred orientation zero. As in A, the four curves, from top to bottom, correspond to contrasts of 80%, 40%, 20%, and 10%. The recurrent model had $\lambda_0 = 7.3$, $\lambda_1 = 11$, $A = 40$ Hz, and $\epsilon = 0.1$. C) Tuning curves measure experimentally at four contrast levels as indicated in the legend. (C adapted from Sompolinsky and Shapley, 1997; based on data from Sclar and Freeman, 1982.)

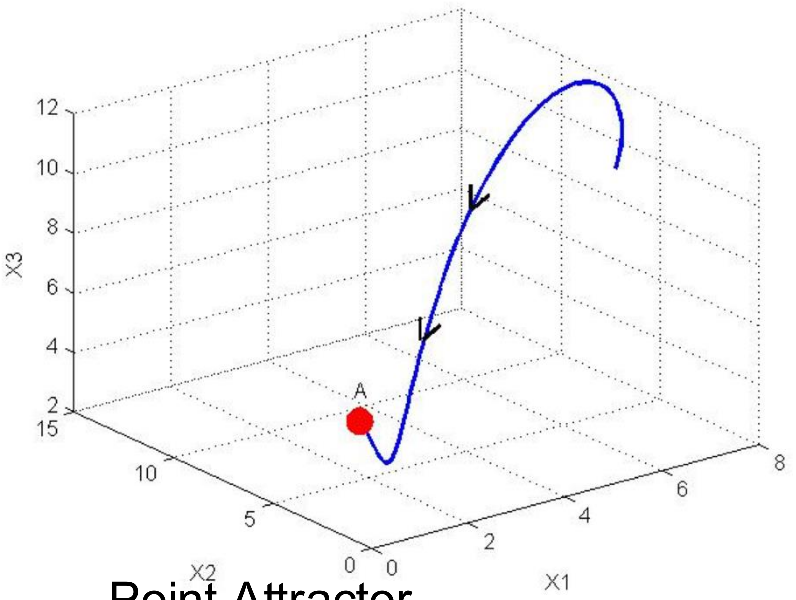
Attractor Networks

• Attractor network : a network of neurons, usually recurrently connected, whose time dynamics settle to a stable pattern.

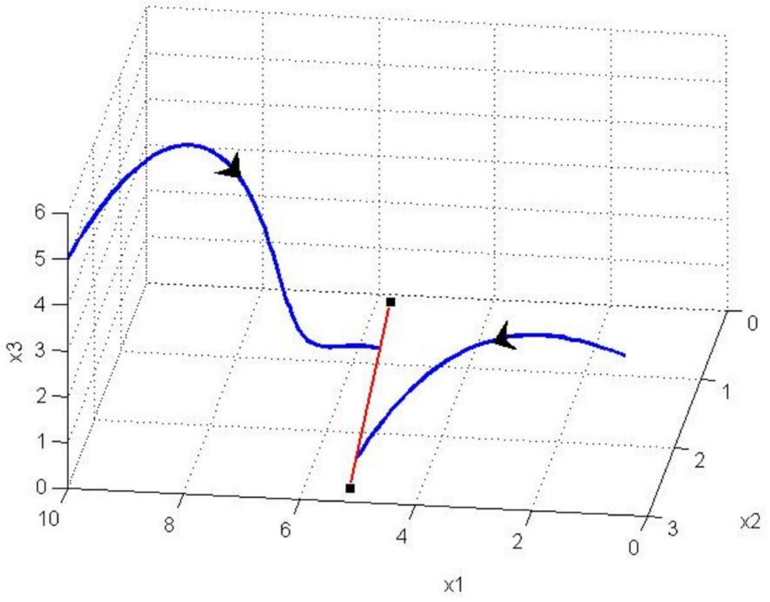
• That pattern may be stationary (fixed points), time-varying (e.g. cyclic), or even stochastic-looking (e.g., chaotic).

• The particular pattern a network settles to is called its ‘attractor’.

•The ring model is called a line (or ring or continuous) attractor network. Its stable states are also sometimes referred to as ‘bump attractors’.



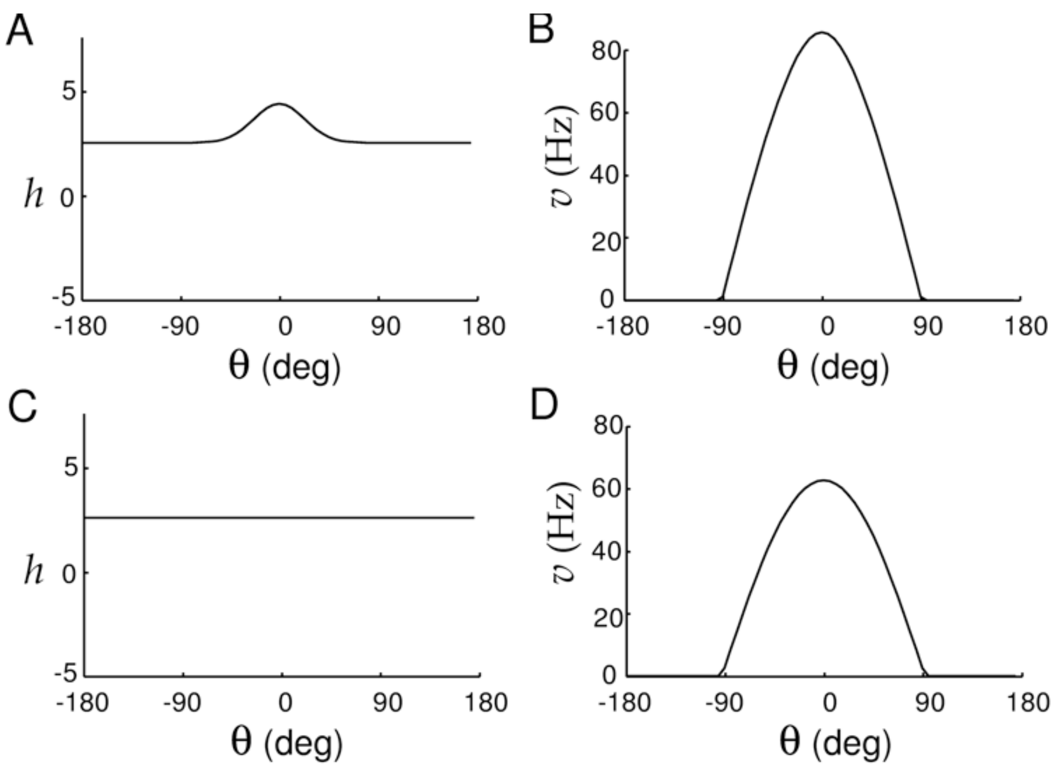
Point Attractor



Line Attractor

The Ring Model (5): Sustained Activity

- If recurrent connections are strong enough, the pattern of population activity once established can become independent of the structure of the input. It can persist when input is removed.
- A model of working memory ?



Recurrent model of orientation selectivity with spiking neurons

Using same recurrent principles, we can implement a spiking model of orientation selectivity

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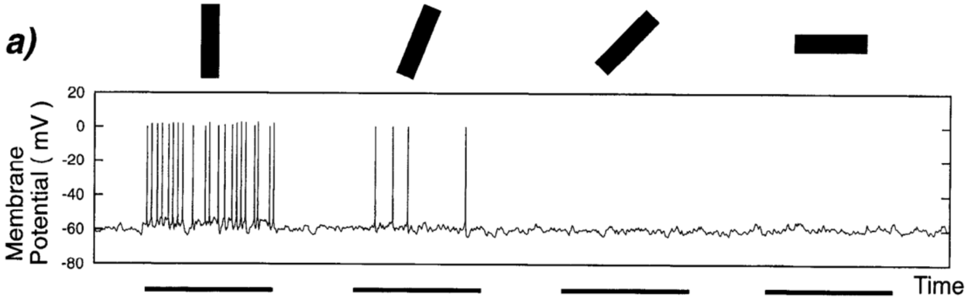
Different questions can be asked:

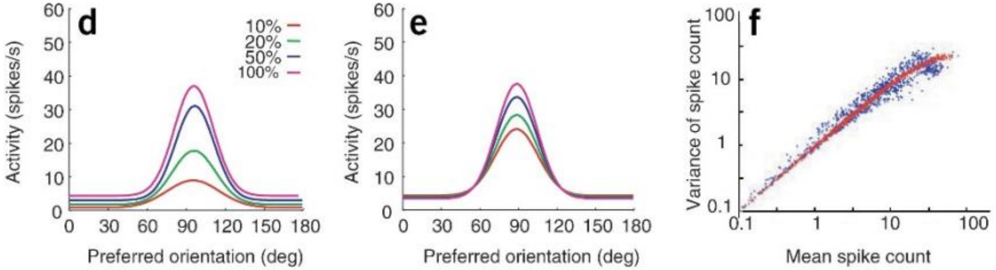
e.g. What connectivity can create irregularity of spiking aka Poisson variability?

How does connectivity and variability impact information?

Do fwd and recurrent models transmit as much information?



[Somers, Nelson & Sur, 1995]



[Seriès, Latham & Pouget, 2004]

ARTICLES

nature neuroscience

http://www.nature.com/natureneuroscience

Tuning curve sharpening for orientation selectivity: coding efficiency and the impact of correlations

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Several studies have shown that the information conveyed by bell-shaped tuning curves increases as their width decreases, leading to the notion that sharpening of tuning curves improves population codes. This notion, however, is based on assumptions that the noise distribution is independent among neurons and independent of the tuning curve width. Here we reexamine these assumptions in networks of spiking neurons by using orientation selectivity as an example. We compare two principal classes of model: one in which the tuning curves are sharpened through cortical lateral interactions, and one in which they are not. We report that sharpening through lateral interactions does not improve population codes but, on the contrary, leads to a severe loss of information. In addition, the sharpening models generate complicated codes that rely extensively on pairwise correlations. Our study generates several experimental predictions that can be used to distinguish between these two classes of model.

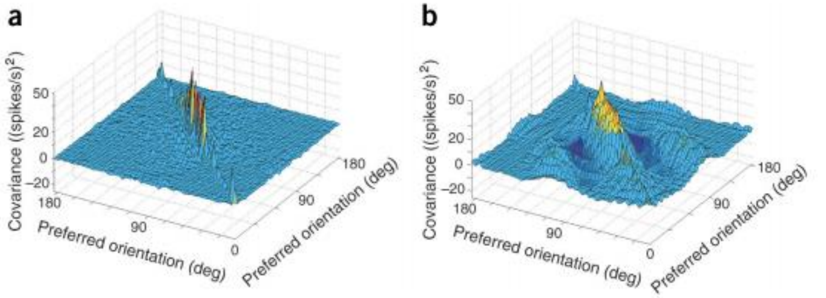

Figure 3 Covariance matrices of the V1 cells in both models. **(a)** In the no-sharpening network, correlations are mostly positive and confined to cells with similar preferred orientations. **(b)** In the sharpening model, correlations tend to be longer range and are both negative and positive.

- “Although feedforward models for the emergence of orientation selectivity are able to account for many aspects of V1 orientation selectivity, interactions within the visual cortex, particularly between nearby neurons, also sculpt selectivity”.
- A diversity of mechanisms, depending on species, layer and cell type.

Mechanisms of Orientation Selectivity in the Primary Visual Cortex

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Abstract

The mechanisms underlying the emergence of orientation selectivity in the visual cortex have been, and continue to be, the subjects of intense scrutiny. Orientation selectivity reflects a dramatic change in the representation of the visual world: Whereas afferent thalamic neurons are generally orientation insensitive, neurons in the primary visual cortex (V1) are extremely sensitive to stimulus orientation. This profound change in the receptive field structure along the visual pathway has positioned V1 as a model system for studying the circuitry that underlies neural computations across the neocortex. The neocortex is characterized anatomically by the relative uniformity of its cir-

Network models - summary

- Network models: to understand the implications of connectivity in terms of computation and dynamics.

- 2 Main strategies: Spiking vs Firing rate models.

- The issue of the emergence of orientation selectivity as a model problem, extensively studied theoretically and experimentally.

- Two main models: feed-forward and recurrent.
- The problem has been investigated with a firing rate model, a.k.a. the 'ring model' which has attractor dynamics and is now taken as a model of connectivity throughout the brain.
- Detailed spiking/ integrate-and-fire models have also been constructed which can be directly compared to electrophysiology.