Models of Networks of Neurons

Networks of neurons

- Neurons are organized in large networks. A typical neuron is cortex receives thousands of inputs.
- Aim of modeling networks: explore the computational potential of such connectivity.

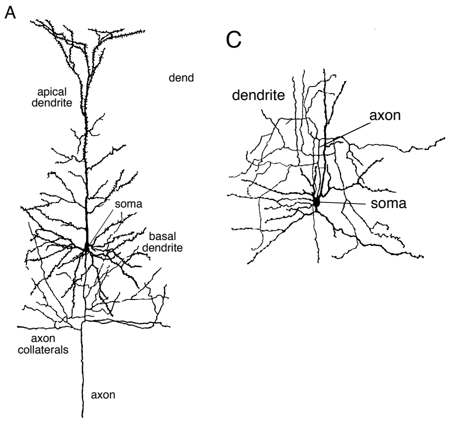
- What computations? (e.g. gain modulation, integration, selective amplification of some signal, memory etc..)
- What dynamics ? (e.g. spontaneous acticity, variability, oscillations)

- Tools:

- models of neurons and synapses : spiking neurons (IAF) or firing rate
- analytical solutions, numerical integration

What's a network ?

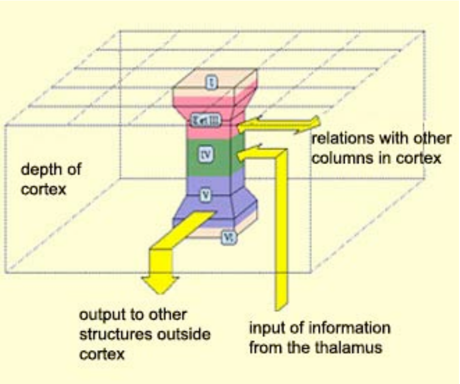
- In cortex, ~80% excitatory cells (pyramidal neurons), ~20% inhibitory neurons (smooth stellate + large variety of other types)/ a.k.a interneurons.

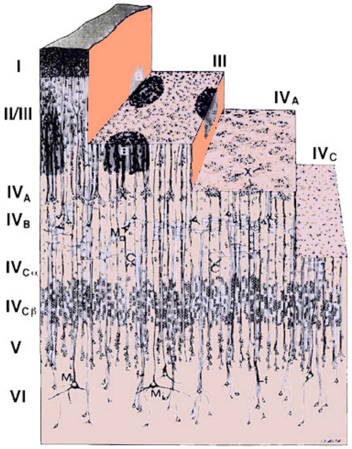


What's a network ?

- Laminar Organization.

Cortex is divided into 6 layers.
Models usually pool all layers together.

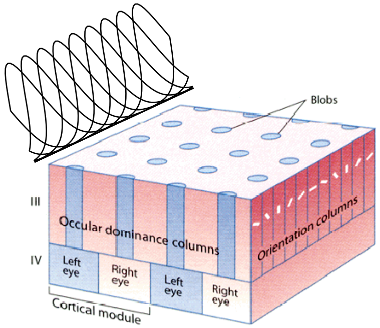




What's a network ?

- Columnar Organization.

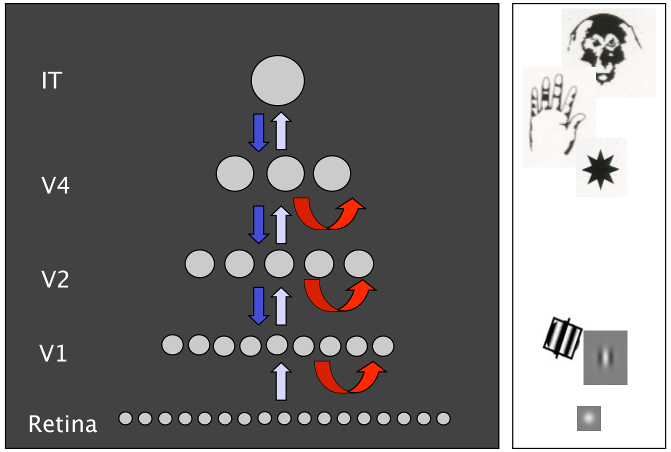
Neurons in small (30-100 micrometers) columns perpendicular to the layers (across all layers) respond to similar stimulus features.

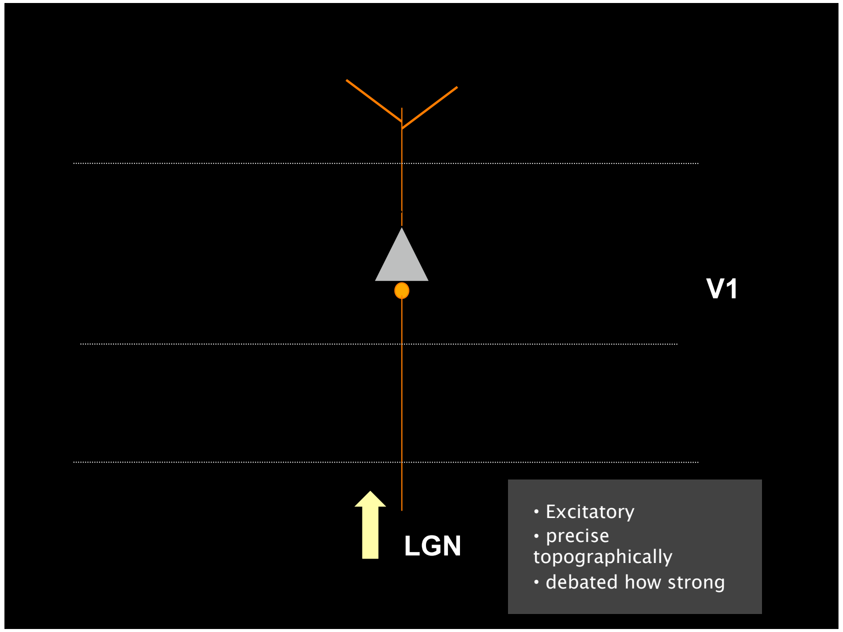


(Aus Gazzaniga et al., 1998)

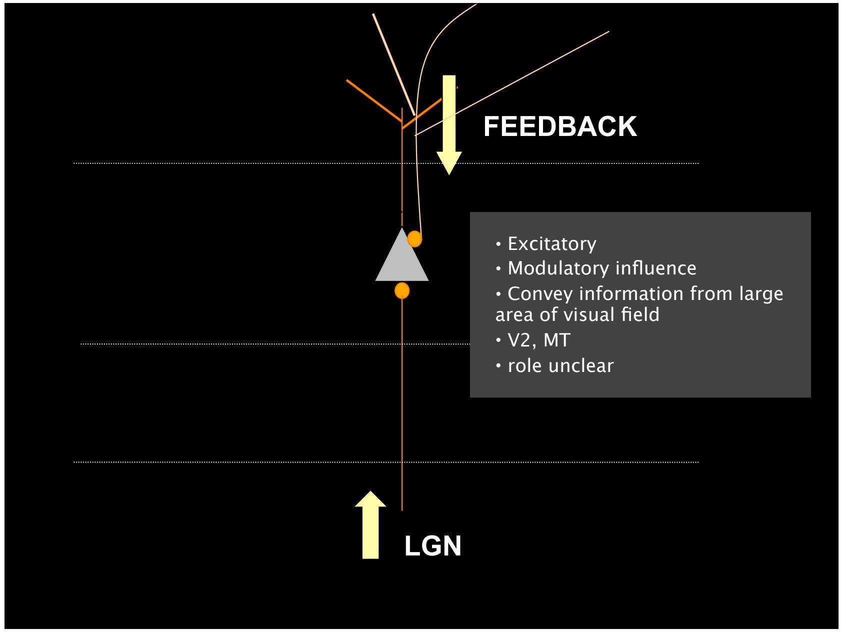
Connectivity

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

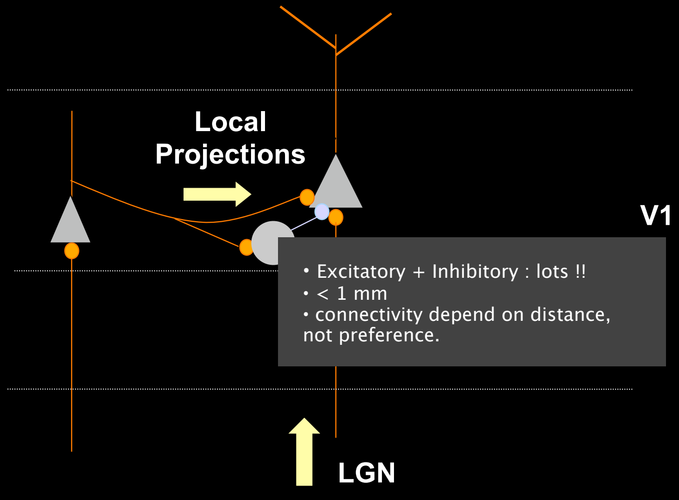




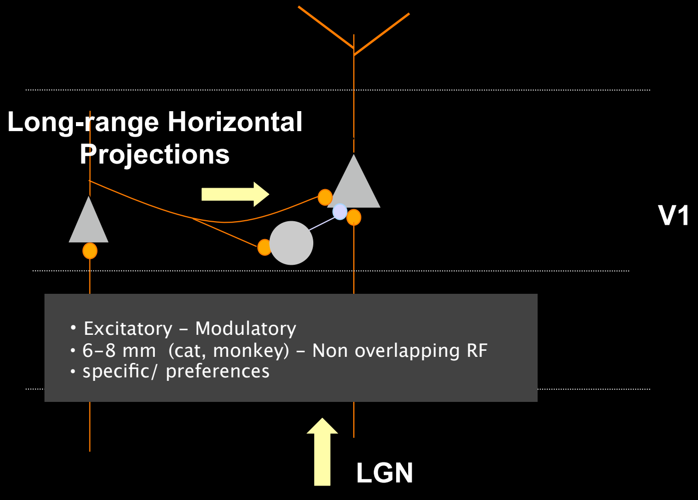
- Excitatory
- precise topographically
- debated how strong



- Excitatory
- Modulatory influence
- Convey information from large area of visual field
- V2, MT
- role unclear



- Excitatory + Inhibitory : lots !!
- < 1 mm
- connectivity depend on distance, not preference.



- Excitatory – Modulatory
- 6-8 mm (cat, monkey) – Non overlapping RF
- specific/ preferences

Network modeling strategies (1)

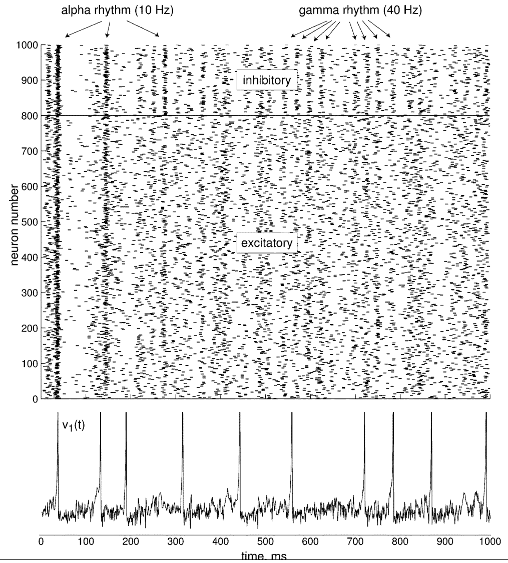
- method 1: spiking neurons, e.g. integrate and fire neurons

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

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

- 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

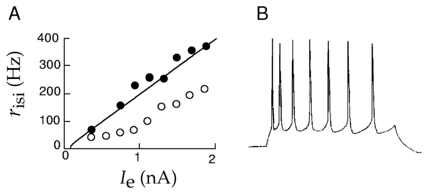
neuron trace

[Izhikevitch, 2003]

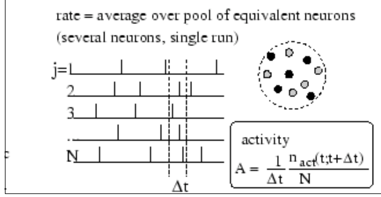
Network modeling strategies (3)

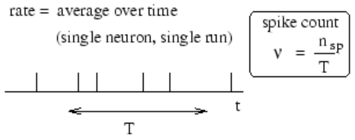
- method 2: reduce the description to describe only rate of spiking r(t), instead of Vm(t).

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



- Interpretation: average over time, average over equivalent neurons

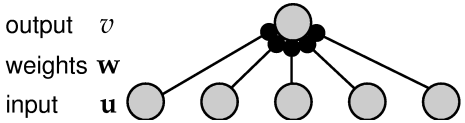




Firing rate model (1)

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

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



- In absence of input, the firing rate relaxes to 0 with a time constant t_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).

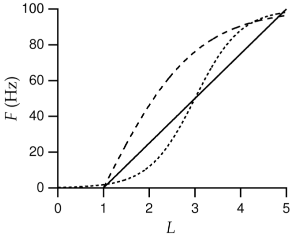
$$\tau_r \frac{dv_i(t)}{dt} = -v_i(t) + F(\sum_{j=1}^{j=N} w_{ij} u_j) = -v_i(t) + F(\mathbf{w}.\mathbf{u})$$

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

$$F(I) = \frac{r_{max}}{1 + \exp(g(I_{1/2} - I))}$$

$$F(I) = G[I - I_0]_+$$



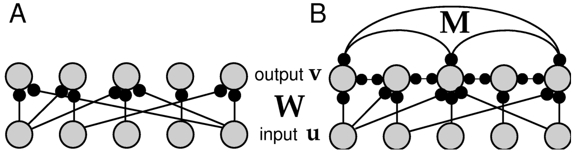
Network Architectures

- 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 problem: spiking networks and ring model

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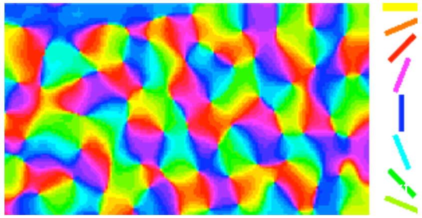
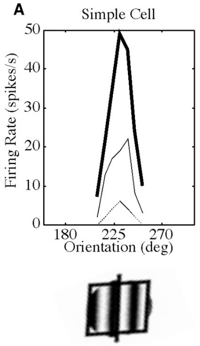
LGN neurons are not selective to orientation, V1’s are: Origin of Orientation selectivity ?



V1

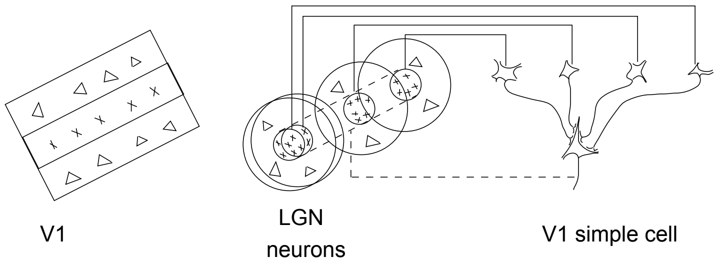


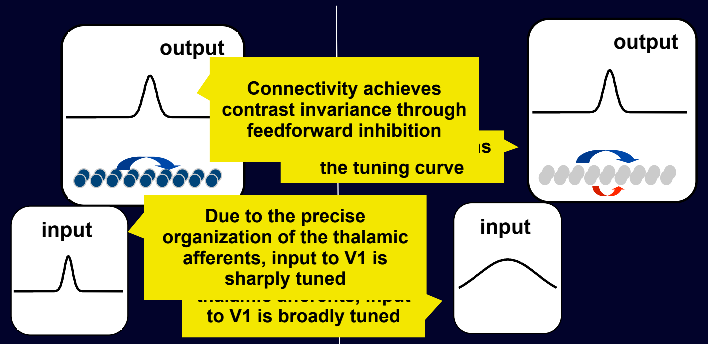
Sclar and Freeman, 1982

- 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.





Connectivity achieves contrast invariance through feedforward inhibition

…s the tuning curve

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

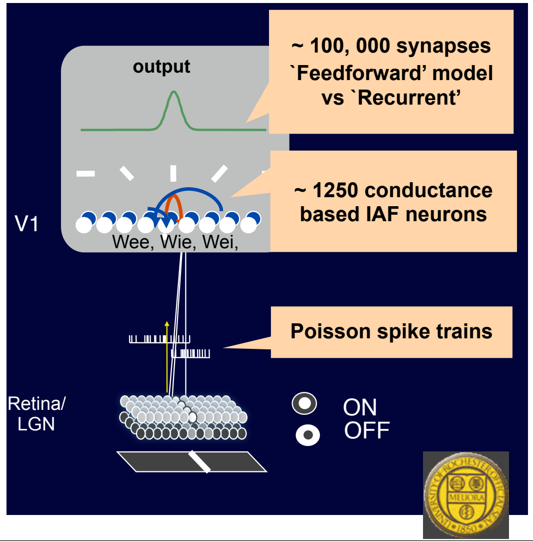
…to V1 is broadly tuned

Feedforward

Recurrent

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

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

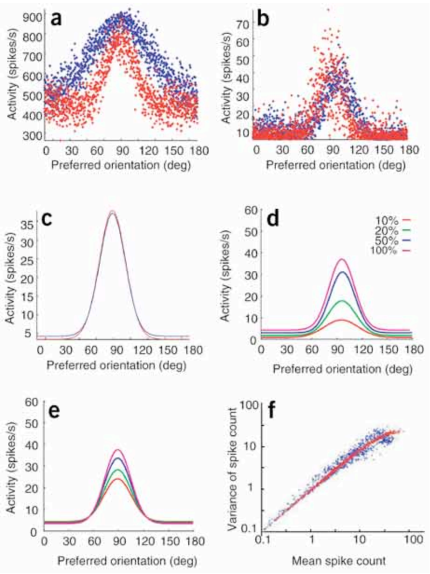


~ 100, 000 synapses `Feedforward' model vs `Recurrent'

~ 1250 conductance based IAF neurons

Poisson spike trains

Seriès, Latham and Pouget - *Nature Neuroscience* 2004



- **Explore physiological and anatomical plausibility**:

- cortical connectivity scheme,

- thalamocortical connectivity,

- properties of inhibition in Cx (inactivation)

…

(Sompolinsky and Shapley, 1997; Ferster and Miller, 2000).

- **Coding efficiency**

(are these models making different predictions in terms of information transmission?)

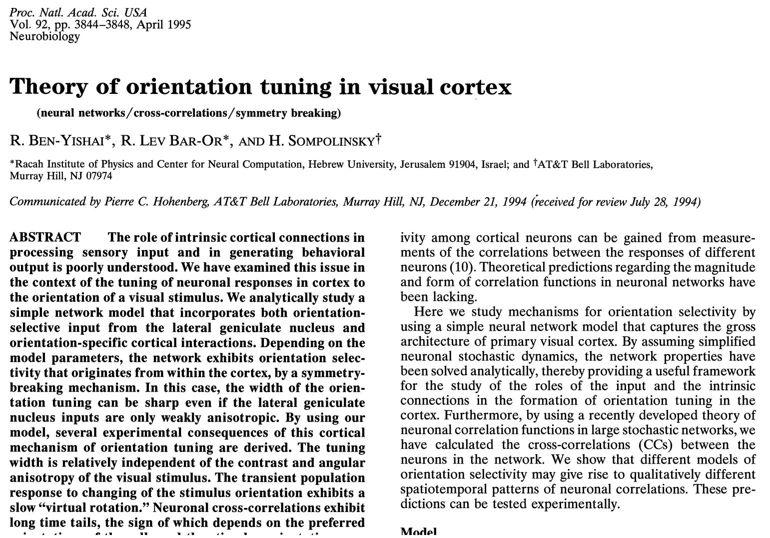
Network models - summary

- 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.
- Detailed spiking models have been constructed which can be directly compared to electrophysiology
- The same problem is also investigated with a firing rate model, a.k.a. the ‘ring model’.

The Ring Model (1)



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)

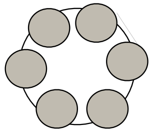
ABSTRACT The role of intrinsic cortical connections in processing sensory input and in generating behavioral output is poorly understood. We have examined this issue in the context of the tuning of neuronal responses in cortex to the orientation of a visual stimulus. We analytically study a simple network 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

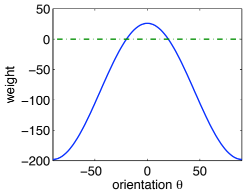
The Ring Model (2)

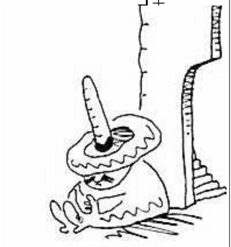


- N neurons, with preferred angle, θ_i ,evenly distributed between $-\pi/2$ and $\pi/2$
- Neurons receive thalamic inputs *h.*

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

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

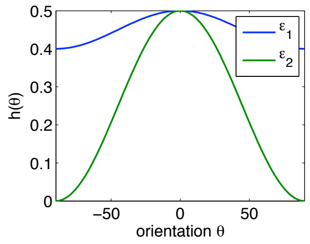




The Ring Model (3)

- 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 Ring Model (4)

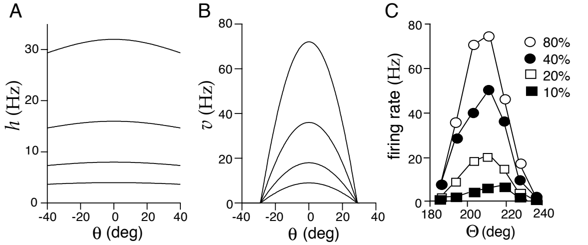
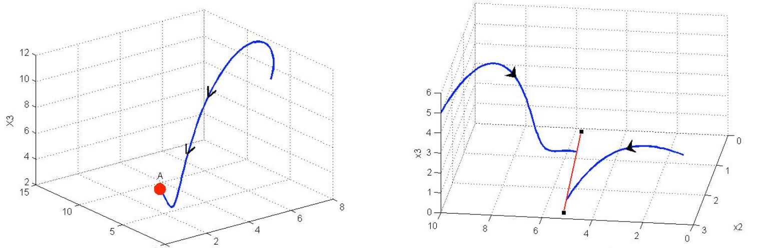


Figure 7.10: The effect of contrast on orientation tuning. A) The feedforward input as a function of preferred orientation. The four curves, from top to bottom, correspond to contrasts of 80%, 40%, 20%, and 10%. B) The output firing rates in response to different levels of contrast as a function of orientation 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

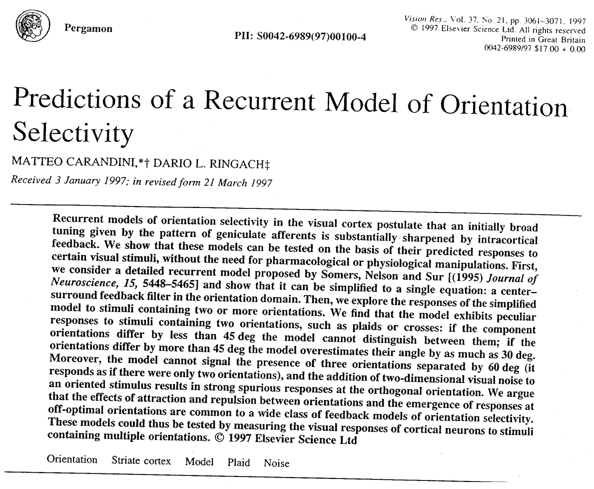
- •Attractor network : a network of neurons, usually recurrently connected, whose time dynamics settle to a stable pattern.
- That pattern may be stationary (fixed points), time-varying (e.g. cyclic), or even stochastic-looking (e.g., chaotic).
- The particular pattern a network settles to is called its ‘attractor’.

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



Point Attractor

Line Attractor



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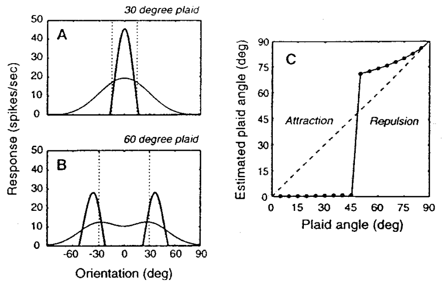
Predictions of a Recurrent Model of Orientation Selectivity

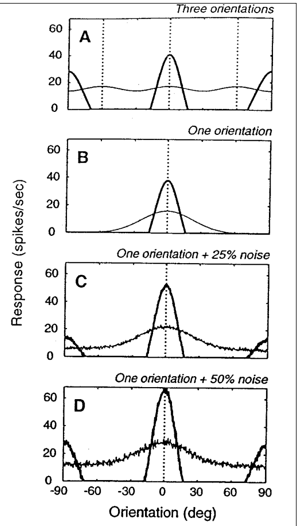
MATTEO CARANDINI,*† DARIO L. RINGACH‡

Received 3 January 1997; in revised form 21 March 1997

Recurrent models of orientation selectivity in the visual cortex postulate that an initially broad tuning given by the pattern of geniculate afferents is substantially sharpened by intracortical feedback. We show that these models can be tested on the basis of their predicted responses to certain visual stimuli, without the need for pharmacological or physiological manipulations. First, we consider a detailed recurrent model proposed by Somers, Nelson and Sur [(1995) *Journal of Neuroscience, 15,* 5448–5465] and show that it can be simplified to a single equation: a center–surround feedback filter in the orientation domain. Then, we explore the responses of the simplified model to stimuli containing two or more orientations. We find that the model exhibits peculiar responses to stimuli containing two orientations, such as plaids or crosses: if the component orientations differ by less than 45 deg the model cannot distinguish between them; if the orientations differ by more than 45 deg the model overestimates their angle by as much as 30 deg. Moreover, the model cannot signal the presence of three orientations separated by 60 deg (it responds as if there were only two orientations), and the addition of two-dimensional visual noise to an oriented stimulus results in strong spurious responses at the orthogonal orientation. We argue that the effects of attraction and repulsion between orientations and the emergence of responses at off-optimal orientations are common to a wide class of feedback models of orientation selectivity. These models could thus be tested by measuring the visual responses of cortical neurons to stimuli containing multiple orientations. © 1997 Elsevier Science Ltd

Orientation Striate cortex Model Plaid Noise

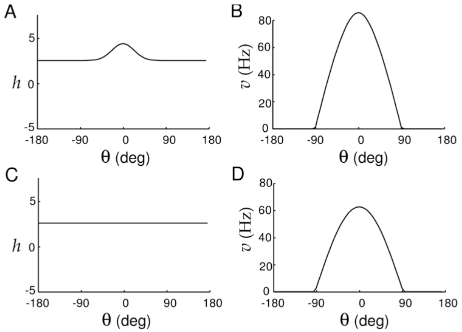




- Model was tested with stimuli containing more than 1 orientation (crosses)
- •Model fails to distinguish angles separated by 30 deg, overestimates larger angles
- •spurious attractors with noise

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 persists when input is removed.
- A model of working memory ?



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