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## Models of Networks of Neurons

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Readings: D&A, chapter 7.

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## Networks of Neurons

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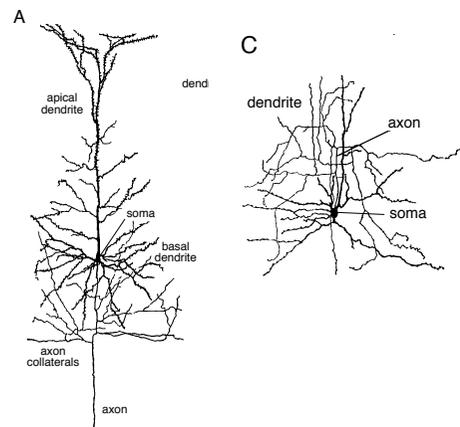
- Neurons are organized in **large networks**. A typical neuron in cortex receives thousands of inputs.
- Aim of modelling networks: explore the computational potential of such connectivity.
  - What **computations**? (e.g. gain modulation, integration, selective amplification of some signal, memory etc..)
  - What **dynamics**? (e.g. spontaneous activity, variability, oscillations)
- Tools:
  - models of neurons and synapses : spiking neurons (IAF) or firing rate
  - analytical solutions, numerical integration

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## What's a network ?

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

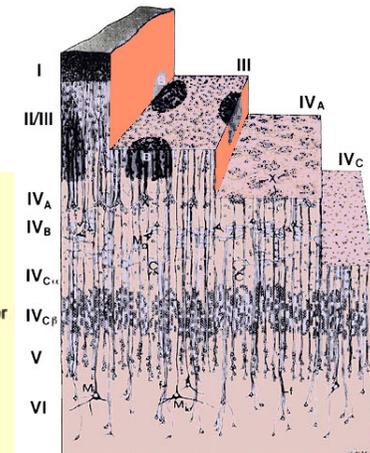
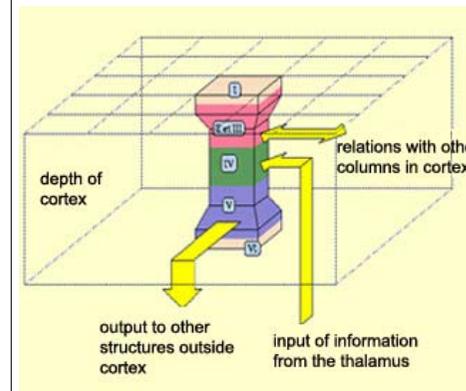


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## What's a network ?

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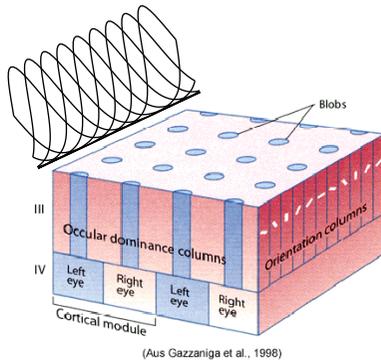
- **Laminar Organization**.  
Cortex is divided into 6 layers.  
Models usually pool all layers together.



## What's a network ?

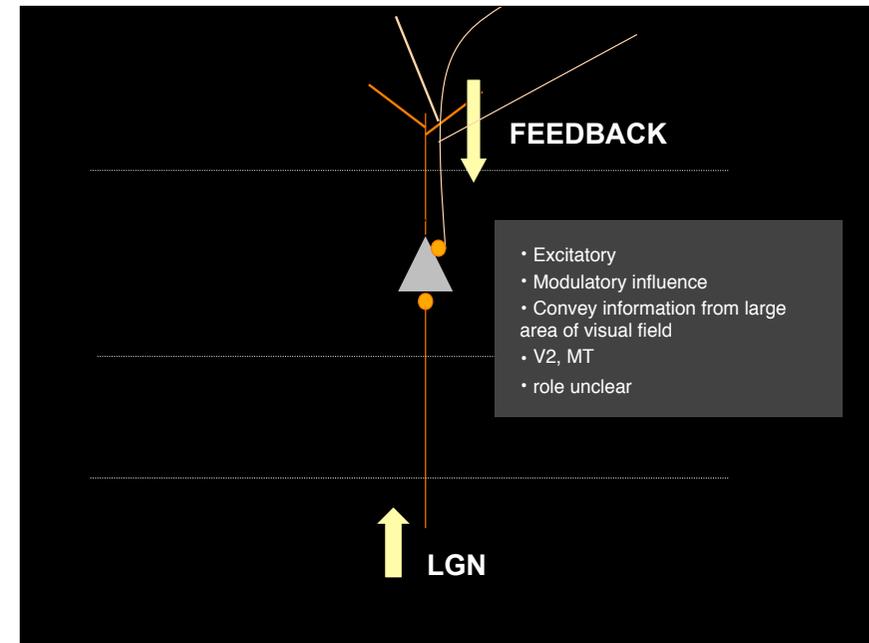
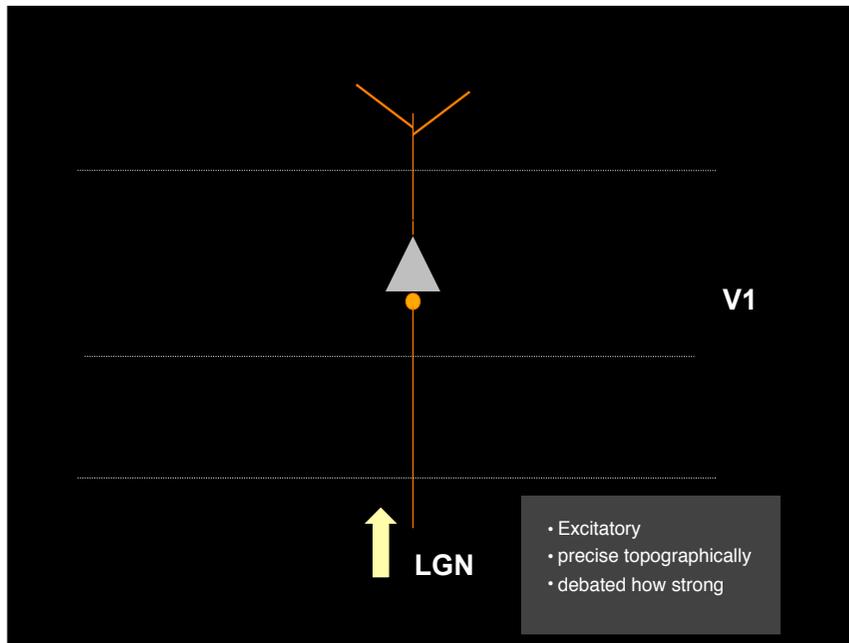
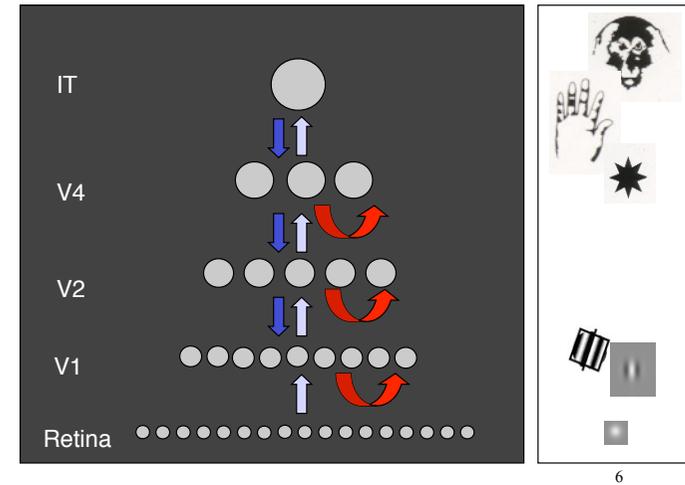
- **Columnar Organization.**

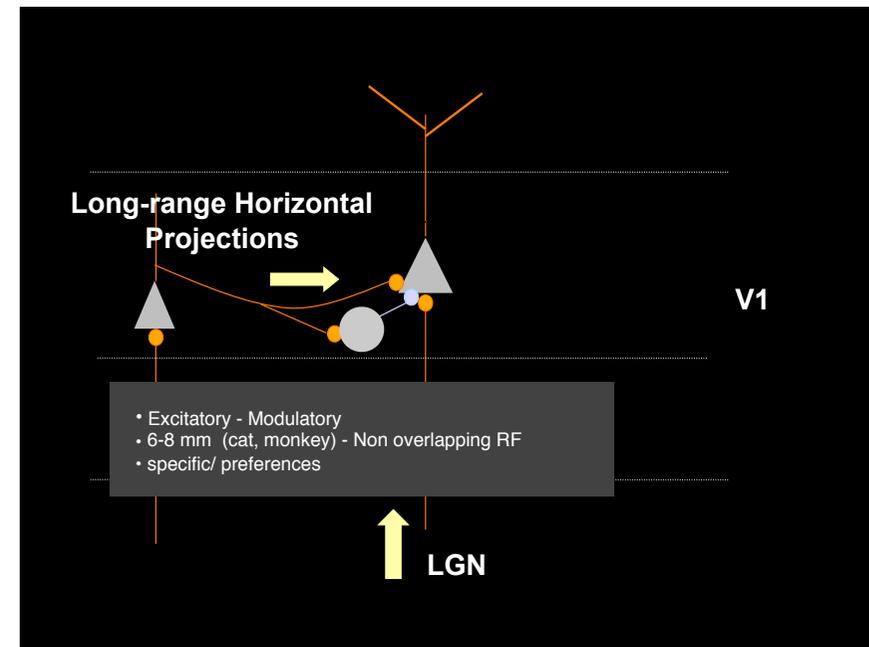
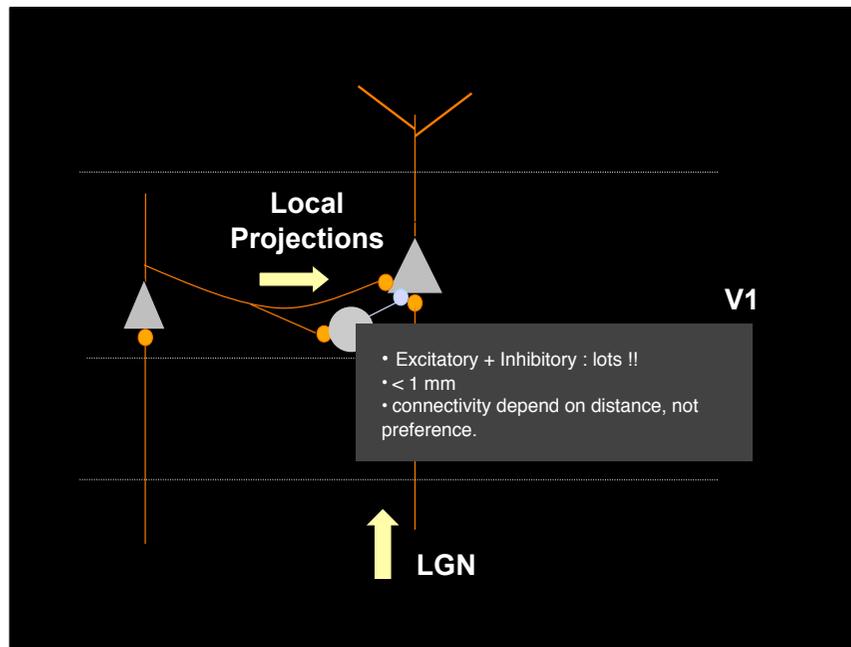
Neurons in small (30-100 micrometers) columns perpendicular to the layers (across all layers) respond to similar stimulus features.



## Connectivity

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





### Network modeling strategies (1)

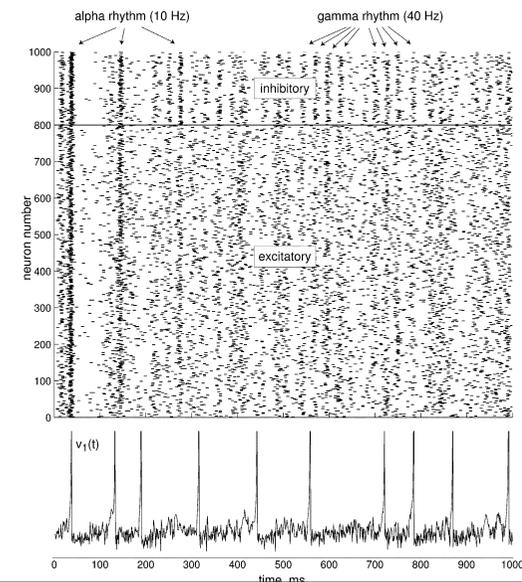
- method 1: **spiking neurons**, e.g. integrate and fire neurons

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

$$g_{ij}(t) = \bar{g}_{ij} \sum_l [t - t'_j]^+ \left( \frac{e}{\tau_{\text{peak}}} \right) \exp\left( -\frac{t - t'_j}{\tau_{\text{peak}}} \right).$$

- 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

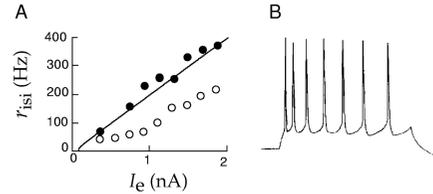
neuron trace

[Izhikevitch, 2003]

### Network modeling strategies (3)

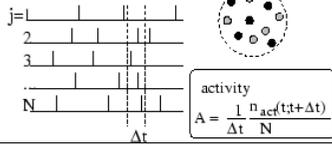
- method 2: reduce the description to describe only **rate of spiking  $r(t)$**  (also confusingly sometimes denoted  $v(t)$ ), instead of  $V_m(t)$ .

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

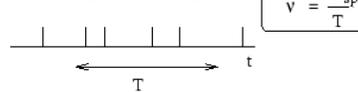


- Interpretation: **average over equivalent neurons or over time**

rate = average over pool of equivalent neurons (several neurons, single run)



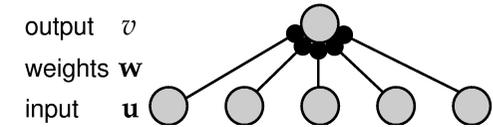
rate = average over time (single neuron, single run)



### 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  $\tau_r$**  - 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  $v(t)$ .

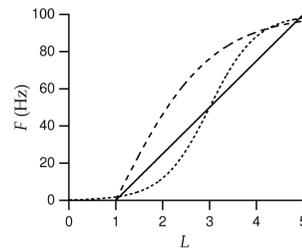
$$\tau_r \frac{dv_i(t)}{dt} = -v_i(t) + F\left(\sum_{j=1}^{j=N} w_{ij} u_j\right) = -v_i(t) + F(\mathbf{w} \cdot \mathbf{u})$$

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**

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

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



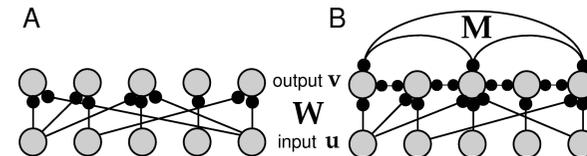
### Network Architectures

- A: **Feedforward**

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

- B: **Recurrent**

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



## 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,  $M_{EE}$ ,  $M_{IE}$ ,  $M_{II}$ ,  $M_{EI}$

$$\tau_E \frac{dv_E}{dt} = -v_E + F_E (h_E + M_{EE} \cdot v_E + M_{EI} \cdot v_I)$$

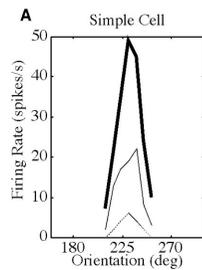
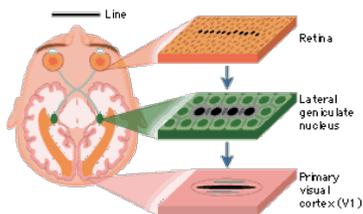
and

$$\tau_I \frac{dv_I}{dt} = -v_I + F_I (h_I + M_{IE} \cdot v_E + M_{II} \cdot v_I)$$

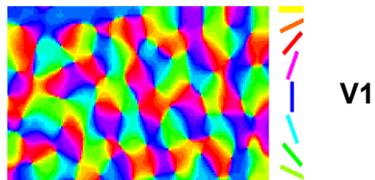
Example:

Orientation selectivity as a model problem:  
spiking networks and ring model

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



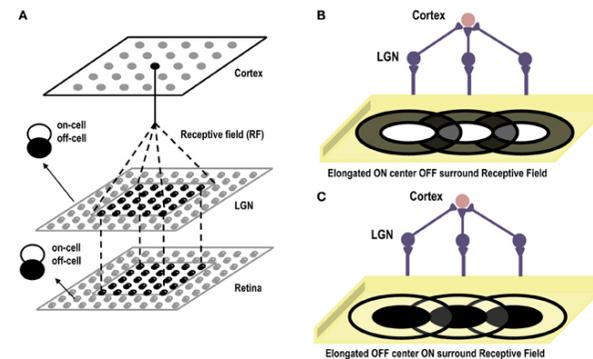
Sclar and Freeman, 1982



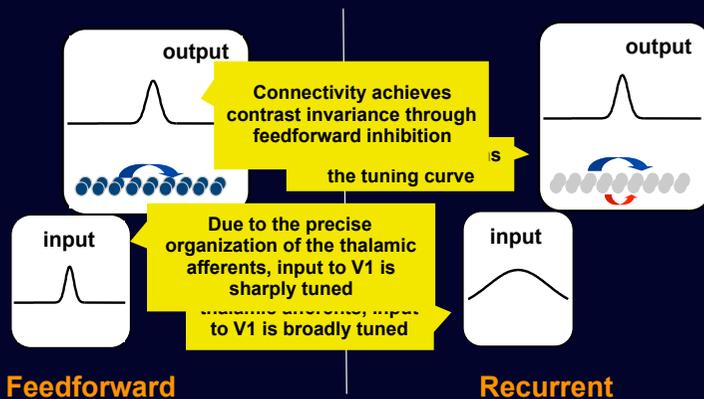
- Example of a computation, emergence of a new property.

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.



## Feedforward vs Recurrent models of Orientation Selectivity



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

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 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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**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

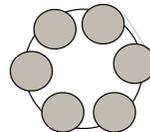
orientation among cortical neurons can be gained from measurements of the correlations between the responses of different neurons (10). Theoretical predictions regarding the magnitude and form of correlation functions in neuronal networks have been lacking.

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.

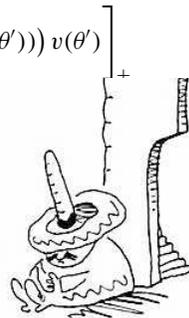
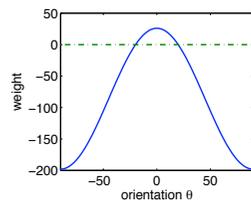
Model

## The Recurrent/ Ring Model of orientation selectivity (2)

- N neurons, with preferred angle,  $\theta_i$ , 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)



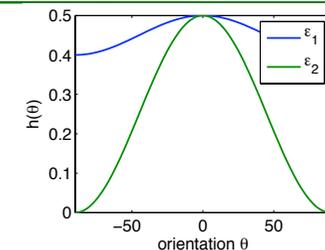
$$\tau_r \frac{dv(\theta)}{dt} = -v(\theta) + \left[ h(\theta) + \int_{-\pi/2}^{\pi/2} \frac{d\theta'}{\pi} (-\lambda_0 + \lambda_1 \cos(2(\theta - \theta'))) v(\theta') \right]$$



## 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)

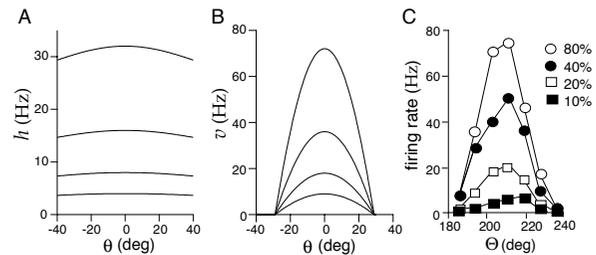
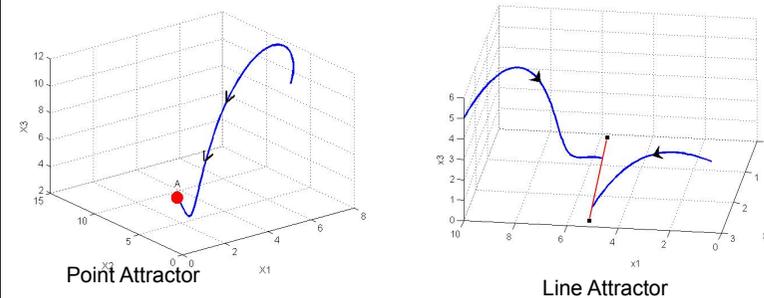


Figure 7.10: The effect of contrast on orientation tuning. A) The feedforward input as a function of preferred orientation. The four curves, from top to bottom, correspond to contrasts of 80%, 40%, 20%, and 10%. B) The output firing rates in response to different levels of contrast as a function of orientation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

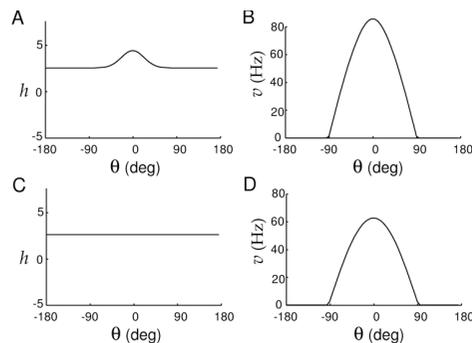
## Attractor Networks

- **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) attractor network**. Its stable states are also sometimes referred to as '**bump attractors**'.

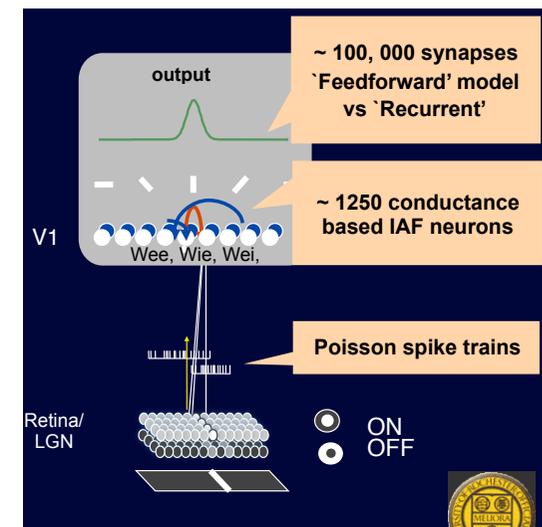


## The Ring Model (5): Sustained Activity

- 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** ?

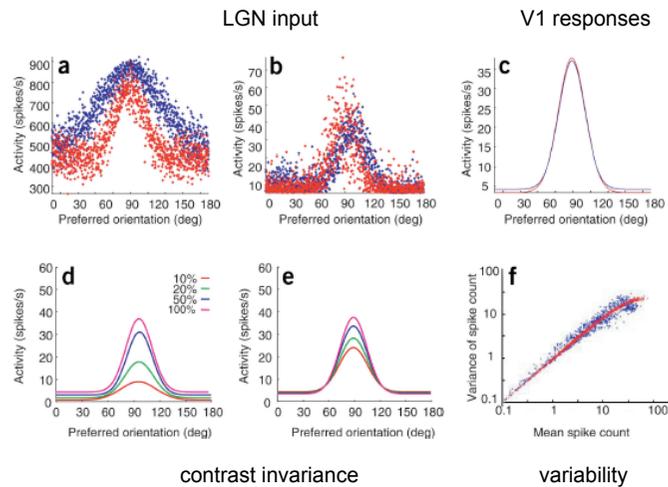


## Recurrent vs Feedforward models of orientation selectivity with spiking neurons



Seriès, Latham and Pouget - *Nature Neuroscience* 2004

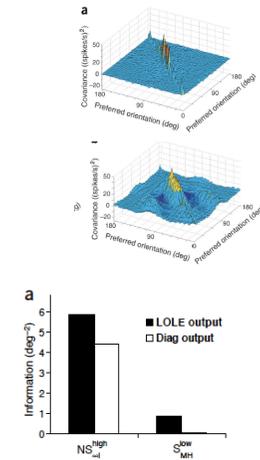
- Both models can generate tuned responses, contrast invariance, and realistic variability of spike count



## Recurrent vs Feedforward models of orientation selectivity with spiking neurons

- **Explore physiological and anatomical plausibility:**
  - cortical connectivity scheme,
  - thalamocortical connectivity,
  - properties of inhibition in Cx (inactivation)
- 
- (Sompolinsky and Shapley, 1997; Ferster and Miller, 2000).

- **Variability**
- **Coding efficiency**
- are these models making different predictions in terms of (Fisher) information transmission? (Yes).



## 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'.