'Ring' model, attractor networks and working memory

Readings:

- Ben Yishai et al, Theory of orientation tuning in visual cortex, PNAS, 1995
- C.Constandinis and XJ Wang, , "a neural circuit basis for spatial working memory", Neuroscientist, 2004

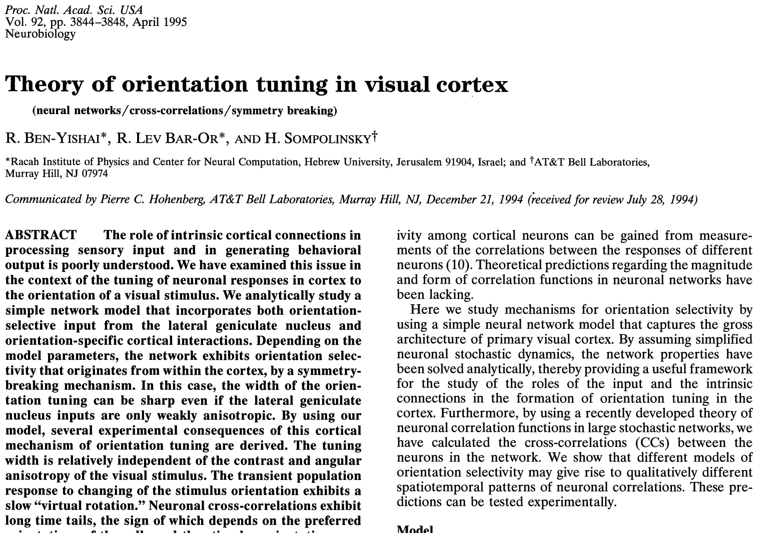
Network models (summary of last lecture)

• 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**

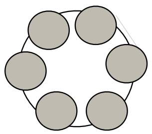
ivity among cortical neurons can be gained from measurements of the correlations between the responses of different neurons (10). Theoretical predictions regarding the magnitude and form of correlation functions in neuronal networks have been lacking.

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

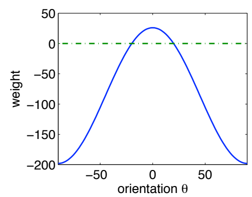
The Ring Model (2)

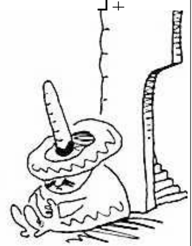
• N neurons, with preferred angle, θ_i ,evenly distributed between $-\pi/2$ and $\pi/2$



• 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)

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

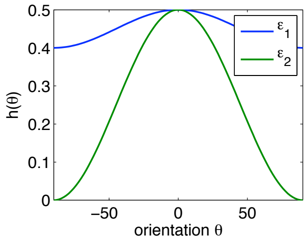




The Ring Model (3)

- 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)

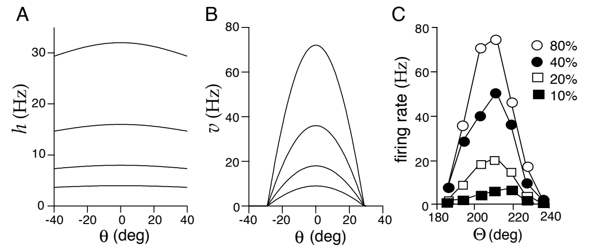
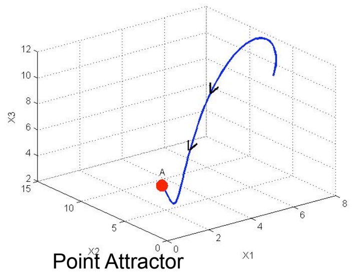


Figure 7.10: The effect of contrast on orientation tuning. A) The feedforward input as a function of preferred orientation. The four curves, from top to bottom, correspond to contrasts of 80%, 40%, 20%, and 10%. B) The output firing rates in response to different levels of contrast as a function of orientation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

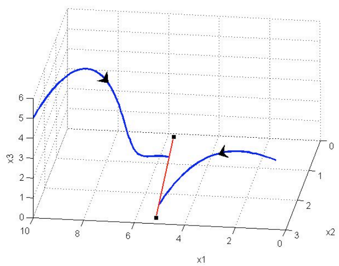
Attractor Networks

- 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

Pergamon
PII: S0042-6989(97)00100-4
Vision Res., Vol. 37, No. 21, pp. 3061–3071, 1997

0042-6989/97 $17.00 + 0.00

Predictions of a Recurrent Model of Orientation Selectivity

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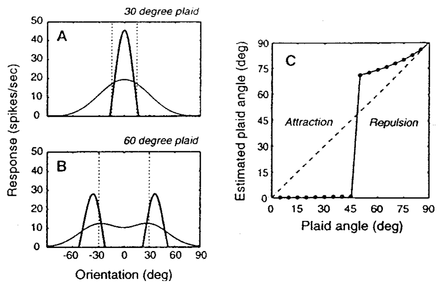
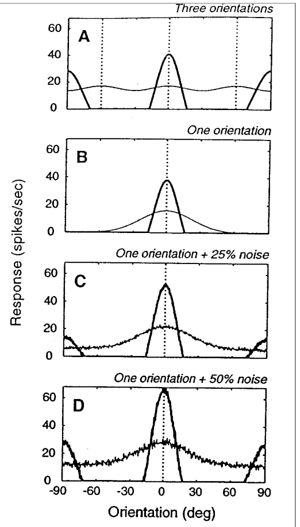
Received 3 January 1997; in revised form 21 March 1997

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

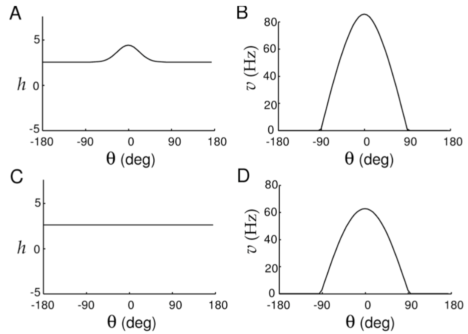




- Model was tested with stimuli containing more than 1 orientation (crosses)
- Model fails to distinguish angles separated by 30 deg, overestimates larger angles
- spurious attractors with noise

The Ring Model (5): Sustained Activity

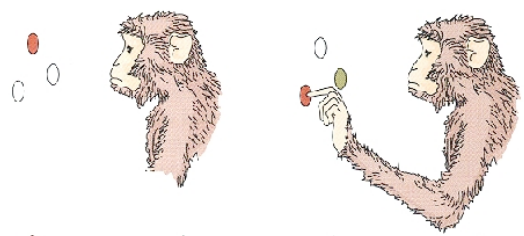
- If recurrent connections are strong enough, the pattern of population activity once established can become independent of the structure of the input. It can persists when input is removed.
- A model of working memory ?



Models of working memory

What is working memory ? (a.k.a. short-term memory)

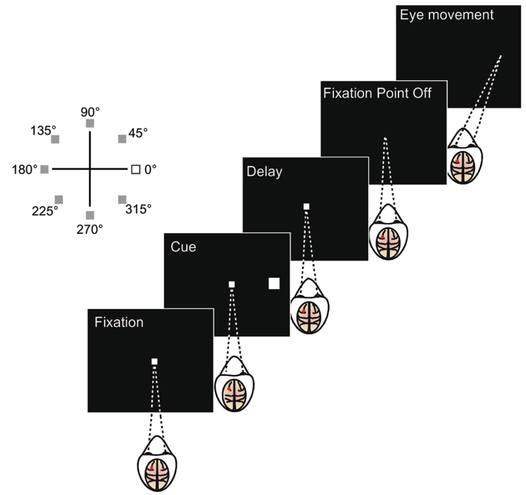
- The ability to hold information over a time scale of seconds to minutes
- a critical component of cognitive functions (language, thoughts, planning etc..)



Delayed match-to sample task:
remember 'red'

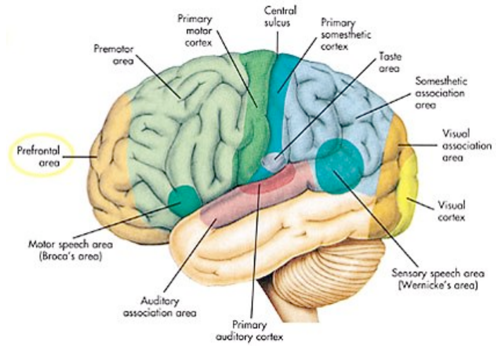
Oculomotor delayed response task:

remember location of cue.



Sustained activity in PFC (1)

• Lesion and inactivation studies demonstrate crucial role of Prefrontal Cortex (PFC) in working memory, in particular dorsolateral PFC (PFdl).



Sustained activity in PFC (1)

• Lesion and inactivation studies demonstrate crucial role of Prefrontal Cortex (PFC) in working memory, in particular dorsolateral PFC (PFdl).

• Electrophysiology in macaques show that neurons in (PFC) continue to discharge even after the offset of transient sensory stimuli that animals are required to remember.

-- interpreted as cellular basis of working memory.

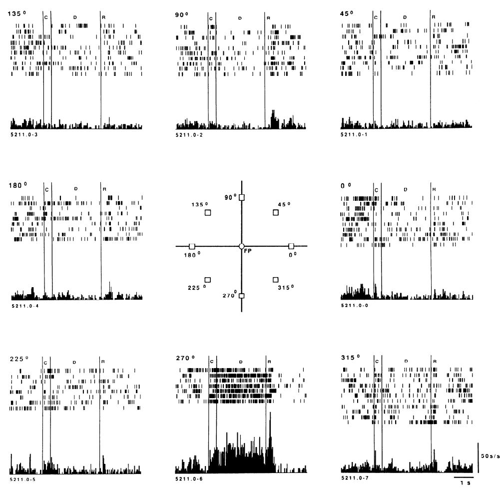
• PET and fMRI studies confirm this in humans.

• E.g. Oculo-motor delayed response task.

Neurons in PFC show activity during the delay -- tuned 'memory fields'.

This activity was shown to represent the memory of the cued location, not the preparation of the motor response.

Sustained activity in PFC (2)



Funahashi et al, 1989

Sustained activity is very widespread

- Sustained activity is a widespread phenomenon

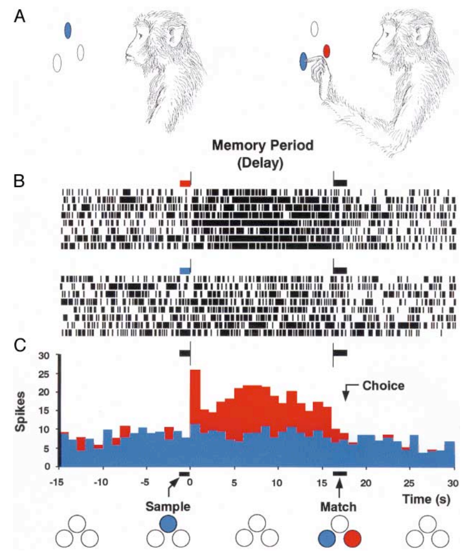
- LIP and PP also have neurons which direction-specific memory fields, similar to PFC.

- Also found in inferotemporal cortex (IT), see e.g. Fuster and Jervey 1982. Example of a discrete working memory.

- Memory related activity is also described in V3A, MT, V1, entorhinal cortex, Pre motor cortex, SMA, SC, basal ganglia...

- The distinct and cooperative roles of these areas remain unresolved.

Sustained activity in IT



Fuster and Jervey 1982

How does a transient stimulus cause a lasting change in neural activity?