‘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

Theory of orientation tuning in visual cortex

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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, in 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. 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 architectures 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 spatio-temporal patterns of neuronal correlations. These predictions can be tested experimentally.

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)

The Ring Model (2)

- N neurons, with preferred angle, , evenly distributed between and
- Neurons receive thalamic inputs.
- Recurrent connections, with excitatory weights between nearby cells and inhibitory weights between cells that are further apart (mexican-hat profile)

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

- Attractor network: a network of neurons, usually recurrently connected, whose time dynamics settles to a stable pattern. That pattern may be stationary (fixed point), time-varying (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 steady-state can be solved analytically.

\[ h(t) = c(1 - e^{-t}) \cos(2\pi t) \]

- Model achieves: orientation selectivity; contrast invariance of tuning even if input is very broad.

- The width of orientation selectivity depends on the shape of the mexican-hat.

- The ring model analyzed like a physical system.

- Model analyzed like a physical system.

The Ring Model (3)

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

- Symmetry breaking / Attractor dynamics.

The Ring Model (4)

- The effect of contrast on orientation tuning. A/B. The bandwidth of the model as a function of contrast as a function of orientation preference. Contrast is defined in the caption. (redrawn from Shapley and Enroth-Cugell, 1978 based on data from Star and Freeman, 1982.)

- The effect of contrast on orientation tuning. Figure 7.10. The effect of contrast on orientation tuning. A/B. The bandwidth of the model as a function of contrast as a function of orientation preference. Contrast is defined in the caption. (redrawn from Shapley and Enroth-Cugell, 1978 based on data from Star and Freeman, 1982.)

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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?

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.)

Models of working memory

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).
- 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, Premotor cortex, SMA, SC, basal ganglia...
- The distinct and cooperative roles of these areas remain unresolved.

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