Scale-up of Cortical Representations in Fluctuation Driven Settings

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I. Background

Our group has been modeling a local patch (1mm$^2$) of a single layer of Primary Visual Cortex

Now, we want to “scale-up”

⇒ ⇒ David Cai
    David Lorentz
    Robert Shapley
    Michael Shelley
⇒ ⇒ Louis Tao
    Jacob Wielaard
Local Patch
1mm²

cortical "plane" (surface)
Lateral Connections and Orientation -- Tree Shrew
Bosking, Zhang, Schofield & Fitzpatrick
J. Neuroscience, 1997
From one “input layer” to several layers

Figure 10.12
The cytoarchitecture of the striate cortex. The tissue has been Nissl stained to show cell bodies, which appear as dots. (Source: Adapted from Hubel, 1988, p. 97.)

Why scale-up?
II. Our Large-Scale Model

• A *detailed, fine scale model* of a local patch of *input layer* of Primary Visual Cortex;
• Realistically *constrained by experimental data*;
• *Integrate & Fire, point neuron model (16,000 neurons per sq mm).*

Refs:  
--- PNAS (July, 2000)  
--- J Neural Science (July, 2001)  
--- http://www.cims.nyu.edu/faculty/dmac/
Equations of the Integrate & Fire Model

\[
\frac{dv^j_\sigma}{dt} = -g_R v^j_\sigma - g^{jE}_\sigma(t)[v^j_\sigma - V_E] - g^{jI}_\sigma(t)[v^j_\sigma - V_I]
\]

\(\sigma = \text{E, I}\)

\(v^j_\sigma\) -- membrane potential
-- \(\sigma = \text{Exc, Inhib}\)
-- \(j = 2\) dim label of location on cortical layer
-- 16000 neurons per sq mm (12000 Exc, 4000 Inh)

\(V_E \& V_I\) -- Exc & Inhib Reversal Potentials (Constants)
Integrate & Fire Model

\[
\frac{dv^j_\sigma}{dt} = -g_R v^j_\sigma - g^j_{\sigma E}(t)[v^j_\sigma - V_E] - g^j_{\sigma I}(t)[v^j_\sigma - V_I]
\]

\[\sigma = E, I\]

Spike Times:

\[t^j_k = k^{th} \text{ spike time of } j^{th} \text{ neuron}\]

Defined by:

\[v^j_\sigma(t = t^j_k) = 1,\]
\[v^j_\sigma(t = t^j_k + \varepsilon) = 0\]
Conductances from Spiking Neurons

\[
g^{j}_{EE}(t) = F(t) + S_{EE} \sum_{k} a_{j-k} \sum_{l} G_{E}(t-t_l^k),
\]

\[
g^{j}_{EI}(t) = f^0_{I}(t) + S_{EI} \sum_{k} b_{j-k} \sum_{l} G_{I}(t-T_l^k),
\]

\[
g^{j}_{IE}(t) = F(t) + S_{IE} \sum_{k} c_{j-k} \sum_{l} G_{E}(t-t_l^k),
\]

\[
g^{j}_{II}(t) = f^0_{I}(t) + S_{II} \sum_{k} d_{j-k} \sum_{l} G_{I}(t-T_l^k),
\]

Forcing & Noise  Spatial  Temporal  Cortico-cortical

Here \( t_{l}^{k} \) (\( T_{l}^{k} \)) denote the \( l^{th} \) spike time of \( k^{th} \) neuron.
Elementary Feature Detectors

*Individual* neurons in V1 respond *preferentially to elementary features* of the visual scene (color, direction of motion, speed of motion, spatial wave-length).

*Two important features:*

- **Orientation** $\theta$ [of edges in the visual scene]
- **Spatial phase** $\phi$
Grating Stimuli

Standing & Drifting

Angle of orientation -- $\theta$

Angle of spatial phase -- $\phi$

(relevant for standing gratings)
Cortical Maps

• How does a preferred feature, such as the orientation preference $\theta_k$ of the $k^{th}$ cortical neuron, depend upon the neuron’s location $k = (k_1, k_2)$ in the cortical layer?
II. Our Large-Scale Model

• A detailed, fine scale model of a local patch of input layer of Primary Visual Cortex;
• Realistically constrained by experimental data;

Refs:

--- PNAS (July, 2000)
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III. Cortical Networks Have Very Noisy Dynamics

- Strong temporal fluctuations
- On synaptic timescale
- Fluctuation driven spiking
Fluctuation-driven spiking

(fluctuations on the synaptic time scale)

Solid: average
(over 72 cycles)

Dashed: 10 temporal trajectories
IV. Coarse-Grained Asymptotic Representations

For “scale-up” in fluctuation driven systems
A Regular Cortical Map
Firing Times:
\[ t^k_x (\omega) \sim \tau^k x + \phi^k_x (\omega) \]

Firing Rate:
\[ m^k = \frac{1}{\tau^k x} \]
Coarse-Grained Reductions for V1

- *Average firing rate models* (Cowan & Wilson; Shelley & McLaughlin)
  
  \[ m_\sigma(x,t), \quad \sigma = E,I \]

- *PDF representations* (Knight & Sirovich; Nykamp & Tranchina; Cai, McLaughlin, Shelley & Tao)
  
  \[ \rho_\sigma(v,g; x,t), \quad \sigma = E,I \]

- *Sub-network of embedded point neurons* -- in a coarse-grained, dynamical background 
  
  (Cai, McLaughlin & Tao)
• To accurately and efficiently describe these fluctuations, the scale-up method will require pdf representations –

\[ \rho_\sigma(v,g; x,t), \; \sigma = E,I \]

• To “benchmark” these, we will numerically simulate I&F neurons within one CG cell

• As an aside, these single CG cell simulations – as well as their pdf reductions, can give us insight into neuronal mechanisms
For example, consider the difficulties in constructing networks with both simple (linear) and complex (nonlinear) cells:

- Too few complex cells;
- Cells not selective enough for orientation (not well enough “tuned”);
- Particularly true for complex cells, and when looking ahead to other cortical layers.
• Need a better cortical amplifier;
• But cortical amplification produces instabilities, such as synchrony & far too rapid firing rates.
To begin to address these issues:

We turn to smaller, idealized networks – of two types:

i) One “coarse-grained cell” holding hundreds of neurons;

ii) Idealized “ring-models”

First, one “coarse-grained cell” with only two classes of cells -- “pure” simple and “pure” complex
For the rest of the talk, consider one coarse-grained cell, containing several hundred neurons.
• We’ll replace the 200 neurons in this CG cell by an effective pdf representation.
• For convenience of presentation, I’ll sketch the derivation of the reduction for 200 excitatory Integrate & Fire neurons.
• Later, I’ll show results with inhibition included – as well as “simple” & “complex” cells.
• N excitatory neurons (within one CG cell)
• all toall coupling;
• AMPA synapses (with time scale $\sigma$)

$$
\tau \frac{\partial}{\partial t} v_i = -(v - V_R) - g_i (v-V_E)
$$

$$
\sigma \frac{\partial}{\partial t} g_i = - g_i + \Sigma_l f \delta(t - t^l) + (S\sigma/N) \Sigma_{l,k} \delta(t - t^l_k)
$$

$$
\rho(g,v,t) \equiv N^{-1} \sum_{i=1,N} E\{ \delta[v - v^i(t)] \delta[g - g^i(t)] \},
$$

Expectation “E” taken over modulated incoming (from LGN neurons) Poisson spike train.
\[ \tau \partial_t v_i = -(v - V_R) - g_i (v - V_E) \]
\[ \sigma \partial_t g_i = -g_i + \sum_l f \delta(t - t^l) + (S_a/N) \sum_{l,k} \delta(t - t^l_k) \]

**Evolution of pdf -- \( \rho(g,v,t) \):**
\[ \partial_t \rho = \tau^{-1} \partial_v \{ [(v - V_R) + g (v - V_E)] \rho \} + \partial_g \{ (g/\sigma) \rho \} \]
\[ + \nu_0(t) [\rho(v, g-f/\sigma, t) - \rho(v,g,t)] \]
\[ + N m(t) [\rho(v, g-Sa/N\sigma, t) - \rho(v,g,t)] \]
where

\( \nu_0(t) \) = modulated rate of incoming Poisson spike train;
\( m(t) \) = average firing rate of the neurons in the CG cell

\[ = \int J^{(v)}(v,g; \rho) \bigg|_{(v=1)} dg \]
where \( J^{(v)}(v,g; \rho) = -\{ [(v - V_R) + g (v - V_E)] \rho \} \)
\[ \partial_t \rho = \tau^{-1} \partial_v \left\{ [(v - V_R) + g (v-V_E)] \rho \right\} + \partial_g \left\{ (g/\sigma) \rho \right\} \]
\[ + \nu_0(t) [\rho(v, g-f/\sigma, t) - \rho(v,g,t)] \]
\[ + N m(t) [\rho(v, g-Sa/N\sigma, t) - \rho(v,g,t)], \]

N\gg1; \quad f \ll 1; \quad \nu_0 f = O(1); \]

\[ \partial_t \rho = \tau^{-1} \partial_v \left\{ [(v - V_R) + g (v-V_E)] \rho \right\} \]
\[ + \partial_g \left\{ [g - G(t)]/\sigma \right\} \rho \right\} + \sigma g^2/\sigma \partial_{gg} \rho + \ldots \]

where \[ \sigma g^2 = \nu_0(t) f^2/(2\sigma) + m(t) (Sa)^2/(2N\sigma) \]
\[ G(t) = \nu_0(t) f + m(t) Sa \]
Moments

- \( \rho(g,v,t) \)
- \( \rho^{(g)}(g,t) = \int \rho(g,v,t) \, dv \)
- \( \rho^{(v)}(v,t) = \int \rho(g,v,t) \, dg \)
- \( \mu_1^{(v)}(v,t) = \int g \rho(g,t \mid v) \, dg \)

where \( \rho(g,v,t) = \rho(g,t \mid v) \rho^{(v)}(v,t) \)

Integrating \( \rho(g,v,t) \) eq over \( v \) yields:

\[
\sigma \partial_t \rho^{(g)} = \partial_g \left\{ [g - G(t)] \rho^{(g)} \right\} + \sigma_g^2 \partial_{gg} \rho^{(g)}
\]
Fluctuations in $g$ are Gaussian

$$\sigma \frac{\partial}{\partial t} \rho^{(g)} = \frac{\partial}{\partial g} \{ [g - G(t)] \rho^{(g)} \} + \sigma_g^2 \frac{\partial}{\partial g g} \rho^{(g)}$$

PDF of $g_{EXC}$
Integrating $\rho(g,v,t)$ eq over $g$ yields:

$$\partial_t \rho^{(v)} = \tau^{-1} \partial_v \left[ (v - V_R) \rho^{(v)} + \mu_1^{(v)} (v - V_E) \rho^{(v)} \right]$$

Integrating $[g \rho(g,v,t)]$ eq over $g$ yields an equation for

$$\mu_1^{(v)}(v,t) = \int g \rho(g,t \mid v) \, dg,$$

where $\rho(g,v,t) = \rho(g,t \mid v) \rho^{(v)}(v,t)$
\[ \partial_t \mu_1^{(v)} = -\sigma^{-1}[\mu_1^{(v)} - G(t)] \]
\[ + \tau^{-1}\left\{[(v - V_R) + \mu_1^{(v)}(v-V_E)] \partial_v \mu_1^{(v)}\right\} \]
\[ + \Sigma^2(v)/ (\tau\rho^{(v)}) \partial_v [(v-V_E) \rho^{(v)}] \]
\[ + \tau^{-1}(v-V_E) \partial_v \Sigma^2(v) \]

where \[ \Sigma^2(v) = \mu_2^{(v)} - (\mu_1^{(v)})^2. \]

**Closure:**

(i) \[ \partial_v \Sigma^2(v) = 0; \]

(ii) \[ \Sigma^2(v) = \sigma_g^2 \]
Thus, eqs for $\rho^{(v)}(v,t)$ & $\mu_1^{(v)}(v,t)$:

\[
\partial_t \rho^{(v)} = \tau^{-1} \partial_v [(v - V_R) \rho^{(v)} + \mu_1^{(v)}(v-V_E) \rho^{(v)}]
\]

\[
\partial_t \mu_1^{(v)} = -\sigma^{-1}[\mu_1^{(v)} - G(t)]
\]

\[
+ \tau^{-1}\{[(v - V_R) + \mu_1^{(v)}(v-V_E)] \partial_v \mu_1^{(v)}\}
\]

\[
+ \sigma^2_g / (\tau \rho^{(v)}) \partial_v [(v-V_E) \rho^{(v)}]
\]

Together with a diffusion eq for $\rho^{(g)}(g,t)$:

\[
\sigma \partial_t \rho^{(g)} = \partial_g \{[g - G(t)] \rho^{(g)}\} + \sigma^2_g \partial_{gg} \rho^{(g)}
\]
But we can go further for AMPA \((\sigma \to 0)\):

\[ \sigma \partial_t \mu_1^{(v)} = - [\mu_1^{(v)} - G(t)] \]
\[ + \sigma \tau^{-1} \left\{ \left[ (v - V_R) + \mu_1^{(v)}(v - V_E) \right] \partial_v \mu_1^{(v)} \right\} \]
\[ + \sigma \sigma_g^2 / (\tau \rho^{(v)}) \partial_v \left[ (v - V_E) \rho^{(v)} \right] \]

Recall \(\sigma_g^2 = f^2 / (2\sigma) \nu_0(t) + m(t) (Sa)^2 / (2N\sigma)\);
Thus, as \(\sigma \to 0\), \(\sigma \sigma_g^2 = O(1)\).

Let \(\sigma \to 0\): Algebraically solve for \(\mu_1^{(v)}\):

\[ \mu_1^{(v)} = G(t) + \sigma \sigma_g^2 / (\tau \rho^{(v)}) \partial_v \left[ (v - V_E) \rho^{(v)} \right] \]
Result: A Fokker-Planck eq for $\rho^{(v)}(v,t)$:

$$\tau \partial_t \rho^{(v)} = \partial_v \left\{ \left[ (1 + G(t) + \sigma \sigma^2_g / \tau ) \ v - \left( V_R + V_E (G(t) + \sigma \sigma^2_g / \tau ) \right) \right] \rho^{(v)} \\
+ \sigma \sigma^2_g / \tau (v - V_E)^2 \partial_v \rho^{(v)} \right\}$$

$\sigma \sigma^2_g / \tau$ -- Fluctuations in $g$

Seek steady state solutions – ODE in $v$, which will be good for scale-up.
Remarks: (i) Boundary Conditions;
(ii) Inhibition, spatial coupling of CG cells, simple & complex cells have been added;
(iii) $N \to \infty$ yields “mean field” representation.

Next, use one CG cell to
(i) Check accuracy of this pdf representation;
(ii) Get insight about mechanisms in fluctuation driven systems.
**New Pdf Representation**

- $\rho(g,v,t)$ -- (i) Evolution eq, with jumps from incoming spikes;
  (ii) Jumps smoothed to diffusion in $g$ by a “large N expansion”
- $\rho^{(g)}(g,t) = \int \rho(g,v,t) \, dv$ -- diffuses as a Gaussian
- $\rho^{(v)}(v,t) = \int \rho(g,v,t) \, dg$ ; $\mu^{(v)}(v,t) = \int g \rho(g,t \mid v) \, dg$
- Coupled (moment) eqs for $\rho^{(v)}(v,t)$ & $\mu^{(v)}(v,t)$, which are not closed [but depend upon $\mu^{(v)}_2(v,t)$]
- Closure -- (i) $\partial_v \Sigma^2(v) = 0$; (ii) $\Sigma^2(v) = \sigma_g^2$
  where $\Sigma^2(v) = \mu^{(v)}_2 - (\mu^{(v)}_1)^2$.
- $\sigma \to 0 \Rightarrow$ eq for $\mu^{(v)}_1(v,t)$ solved algebraically in terms of $\rho^{(v)}(v,t)$, resulting in a Fokker-Planck eq for $\rho^{(v)}(v,t)$
• Local temporal asynchrony enhanced *by synaptic failure* – permitting *better amplification*
Bistability and Hysteresis

Mean-field bistability certainly exists, but …

Red: I&F, \( N = 1024 \)
Blue: Mean-Field
solid - stable
dashed - unstable
Hysteresis in Fluctuation-Driven Bistable System

Fluctuation-Driven Bistable System

Firing Rate (Hz)

G_{Input}
Firing Rate Comparison

- N = 64 I&F Network
- Theory $N_V = 100$
- Mean–Field
**Bistability and Hysteresis**

- Network of Simple and Complex — Excitatory only

Fluctuation-Driven Hysteresis

- Relatively Strong Cortical Coupling: N=16

Fluctuation-Driven: Mean-Driven:

![Graph showing Fluctuation-Driven Hysteresis](image-url)
Bistability and Hysteresis

Network of Simple and Complex — Excitatory only

N=16!

Relatively Strong Cortical Coupling:

Fluctuation-Driven Hysteresis

Mean-Driven:
Blue = Large N Limit
Red = Finite N,
$P(V)$ Comparison: $f = 0.01$, $\nu = 120$, $g_L = 5$

- N = 64 I&F Network ($m = 1.66/sec$)
- Theory $N_v = 1000$ ($m = 1.76/sec$)
Fluctuation-Driven Dynamics

Firing Rate Comparison

N = 64 I&F Network
Theory NV = 100

Firing Rate (Hz)

N=64

P(V) Comparison: f = 0.01, ν = 120, g_L = 5

N = 64 I&F Network
Theory NV = 100

P(V)

Mean-Field

Probability Density:

Theory → I&F

N=64

N=64

V, Membrane Potential

P(V)

N=64

Theory

I&F

- Mean-driven limit (\))[480x565]:

Hard thresholding

- Fluctuation

Driven Dynamics

Driven Dynamics

N=64

G_{input}

N=64

Theory

I&F

N=64

Theory

I&F
Three Levels of Cortical Amplification:

1) Weak Cortical Amplification
   No Bistability/Hysteresis
2) Near Critical Cortical Amplification
3) Strong Cortical Amplification
   Bistability/Hysteresis

Excitatory Cells Shown

Possible Mechanism
for Orientation Tuning of Complex Cells
Regime 2 for far-field/well-tuned Complex Cells
Regime 1 for near-pinwheel/less-tuned
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory
- Complex:
  - Excitatory
  - Inhibitory
Pre-hysterisis in Models

Center: Fluctuation-driven (single Complex neuron, 1 realization & trial-average)

Ring Model

Large-scale Model Cortex
Fluctuation-Driven Tuning Dynamics

Near Critical Amplification vs. Weak Cortical Amplification

Sensitivity to Contrast

Ring Model of Orientation Tuning:

- A well-tuned complex cell
- A less-tuned complex cell
- A complex cell in the far-field

Large V1 Model

Ring Model — far field

Contrast vs. Firing Rate (Hz)
Fluctuations and Correlations

\[ J_V \propto \left[ \varphi \left\{ g_m \left( \frac{\partial}{\partial V} \right) \left( \frac{\partial}{\partial V} \right) \right\} \left( \frac{\varphi}{\partial V} \right) \right] \]

Outer Solution:

Existence of a **Boundary Layer**

– induced by correlation

Firing Rate Comparison

\[ P(V) \text{ vs. } -1/(g_L + g_E (V - V_E)) \]
New Pdf for fluctuation driven systems -- accurate and efficient

• $\rho(g,v,t)$ -- (i) Evolution eq, with jumps from incoming spikes;
  (ii) Jumps smoothed to diffusion in $g$ by a “large N expansion”

• $\rho^{(g)}(g,t) = \int \rho(g,v,t) \, dv$ -- diffuses as a Gaussian

• $\rho^{(v)}(v,t) = \int \rho(g,v,t) \, dg$ ; $\mu_1^{(v)}(v,t) = \int g \, \rho(g,t \mid v) \, dg$

• Coupled (moment) eqs for $\rho^{(v)}(v,t)$ & $\mu_1^{(v)}(v,t)$, which are not closed [but depend upon $\mu_2^{(v)}(v,t)$ ]

• Closure -- (i) $\partial_v \Sigma^2(v) = 0$; (ii) $\Sigma^2(v) = \sigma_g^2$,
  where $\Sigma^2(v) = \mu_2^{(v)} - (\mu_1^{(v)})^2$.

• $\sigma \to 0 \Rightarrow$ eq for $\mu_1^{(v)}(v,t)$ solved algebraically in terms of $\rho^{(v)}(v,t)$, resulting in a Fokker-Planck eq for $\rho^{(v)}(v,t)$
Second type of idealized models -- “Ring” Models
A Ring Model of Orientation Tuning

- $I \& F$ network on a Ring, neuron preferred $\theta_i$
- 4 Populations: Exc./Inh, Simple/Complex
- Network coupling strength $A_{ij} \sim A(\theta_i - \theta_j)$ Gaussian
Mean-Driven Bump State

Fluctuation-Driven Bump State
Six ring models:
From near pinwheels to far from pinwheels
Summary Points for Coarse-Grained Reductions needed for Scale-up

1. Neuronal networks are *very noisy, with fluctuation driven effects.*
2. Temporal *scale-separation emerges* from network activity.
3. Local temporal *asynchrony* needed for the asymptotic reduction, and it results from *synaptic failure.*
4. Cortical *maps -- both spatially regular and spatially random* -- tile the cortex; asymptotic reductions must handle both.
5. *Embedded neuron representations* may be needed to capture spike-timing codes and coincidence detection.
6. *PDF representations* may be needed to capture synchronized fluctuations.
Preliminary Results

• Synaptic failure (and/or sparse connections) lessen synchrony, allowing better cortical amplification;
• Bistability both “in mean” and “in fluctuation dominated” systems;
• Complex cells related to bistability – or to “pre-bistability”
• In this model, tuned simple cells reside near pinwheel centers – while tuned complex cells reside far from pinwheel centers.
Scale-up & Dynamical Issues for Cortical Modeling of V1

- Temporal emergence of visual perception
- Role of spatial & temporal feedback -- within and between cortical layers and regions
- Synchrony & asynchrony
- Presence (or absence) and role of oscillations
- Spike-timing vs firing rate codes
- Very noisy, fluctuation driven system
- Emergence of an activity dependent, separation of time scales
- But often no (or little) temporal scale separation
Fluctuation-driven spiking

(very noisy dynamics, on the synaptic time scale)

Solid: average (over 72 cycles)

Dashed: 10 temporal trajectories
**Expt. Results**

**Shapley’s Lab (unpublished)**

# of cells

CV (Orientation Selectivity)

Simple | Complex

⇐ 4B

⇐ 4C
PDF of $g_{\text{EXC}}$

$P(g_{\text{EXC}})$

$3.5 \times 10^{-3}$

$g_{\text{EXC}}$ (sec$^{-1}$)

$P(g_{\text{EXC}})$

Gaussian
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory

- Complex:
  - Excitatory
  - Inhibitory

Complex Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory

- Complex:
  - Excitatory
  - Inhibitory

Complex Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory

- Complex:
  - Excitatory
  - Inhibitory

Complex Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory
- Complex:
  - Excitatory
  - Inhibitory

Complex Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory
- Complex:
  - Excitatory
  - Inhibitory

Simple Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory

- Complex:
  - Excitatory
  - Inhibitory

Simple Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory
- Complex:
  - Excitatory
  - Inhibitory

Simple Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory
- Complex:
  - Excitatory
  - Inhibitory

Simple Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

• Simple:
  ➢ Excitatory
  ➢ Inhibitory

• Complex:
  ➢ Excitatory
  ➢ Inhibitory

Simple Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
  - Inhibitory

- Complex:
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Complex Excitatory Cells
Incorporation of Inhibitory Cells

4 Population Dynamics

- Simple:
  - Excitatory
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Simple Excitatory Cells