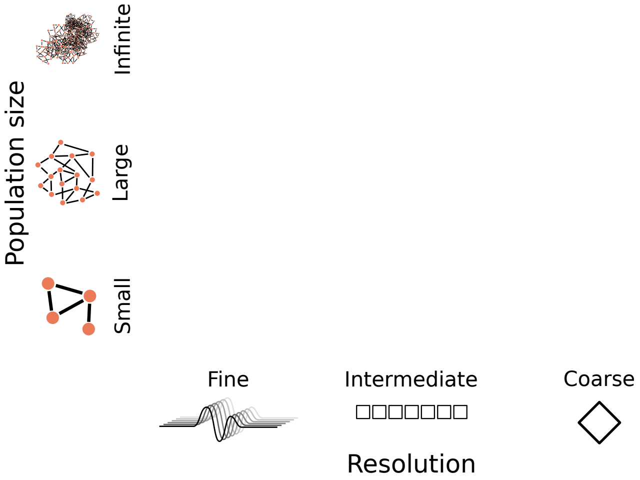
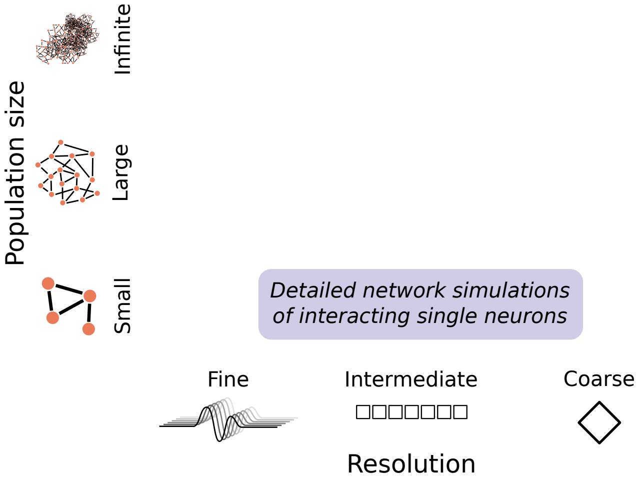
Statistical Mechanics and Inference in Models of Neural Dynamics

M Rule

Understand emergence of **collective neural dynamics**

Tens, thousands, billions of neurons.... any hope?


Population size
Infinite
Large
Small
Fine
Intermediate
Coarse
Resolution


Population size
Infinite
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Small
Detailed network simulations of interacting single neurons
Fine
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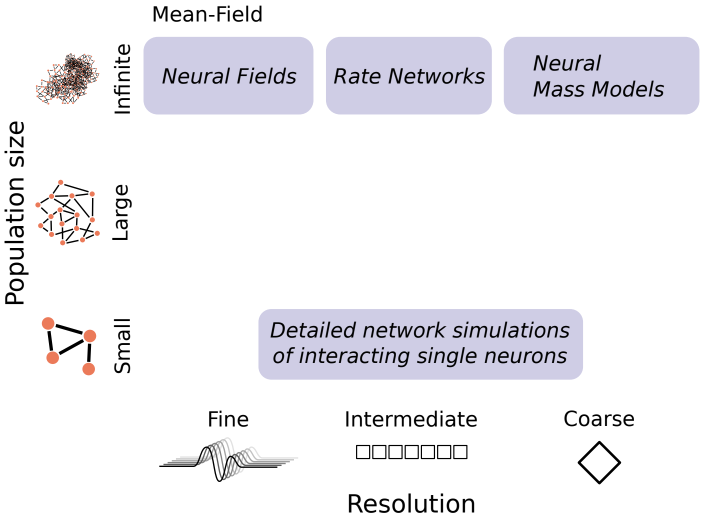
Mean-Field
Neural Fields
Rate Networks
Neural Mass Models
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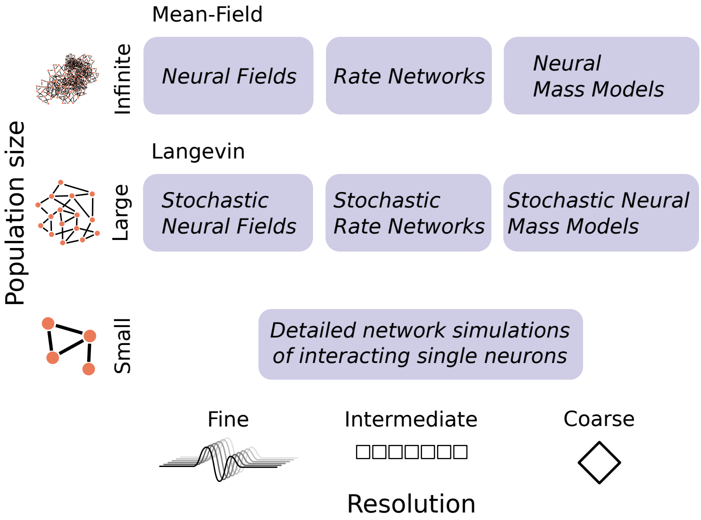
Mean-Field
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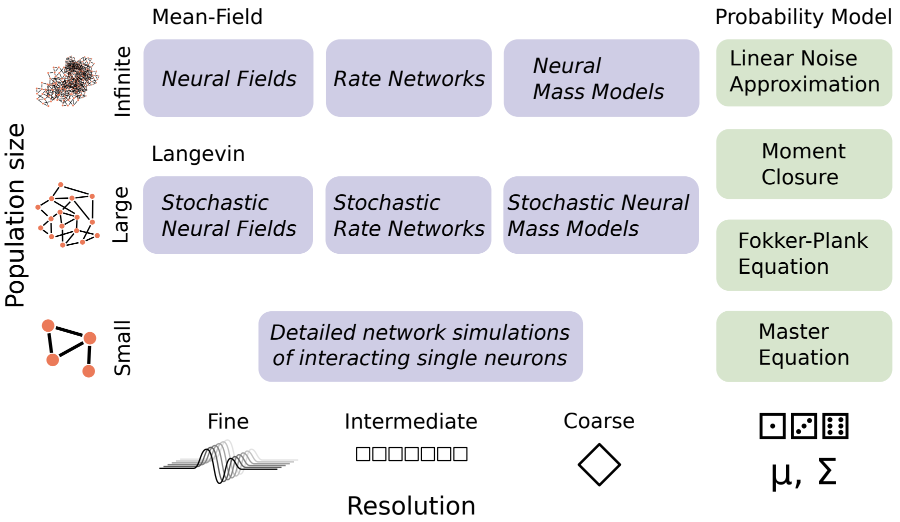

Mean-Field
Probability Model
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Linear Noise Approximation
Langevin
Moment Closure
Large
Stochastic Neural Fields
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Fokker-Plank Equation
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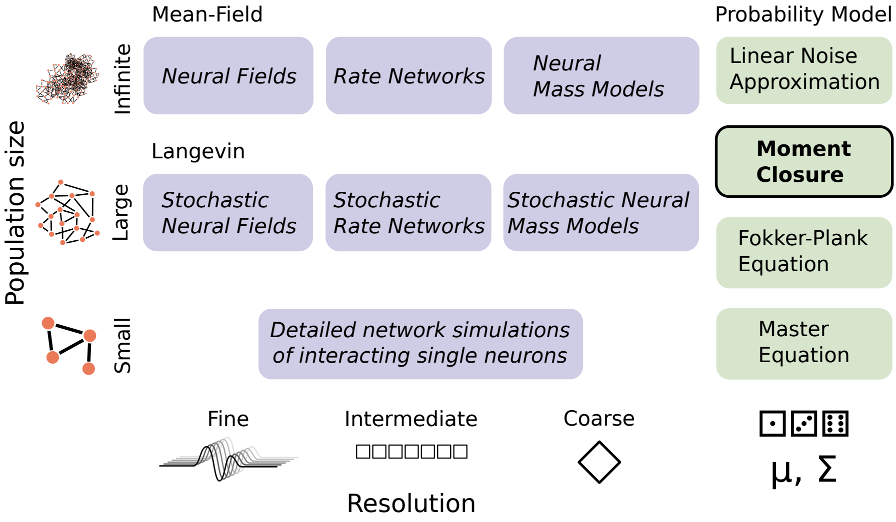
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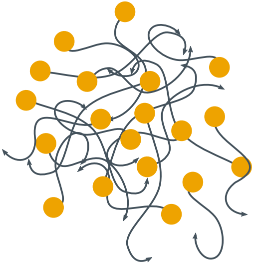
Moment approximations of population dynamics

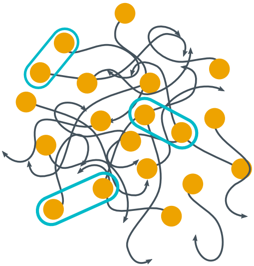
$$\partial_t x = f(x) + \text{noise}$$

Moment approximations of population dynamics



$$\partial_t \vec{x} = f\left(\vec{x}\right) + \text{noise}$$

Moment approximations of population dynamics



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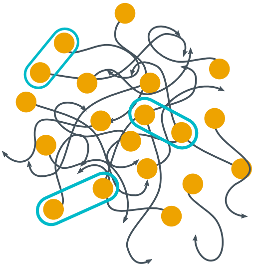
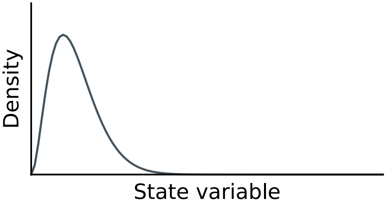
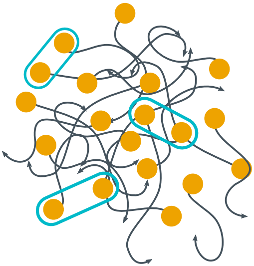
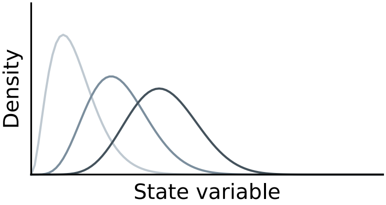




$$\partial_t \Pr(x) = f\left(\Pr(x)\right)$$

Moment approximations of population dynamics





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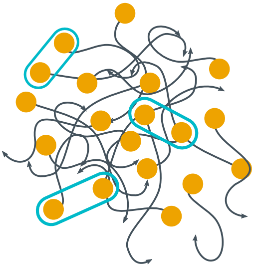

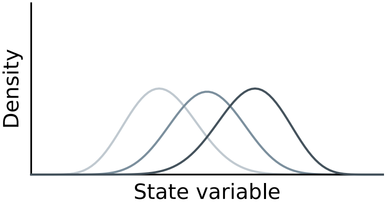

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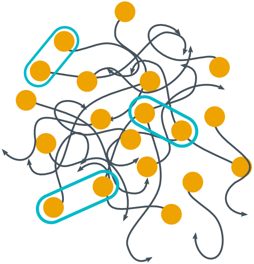

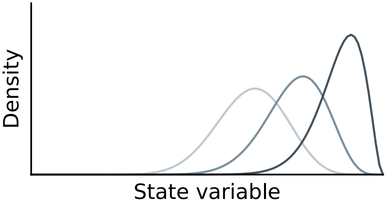

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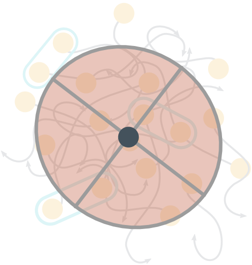
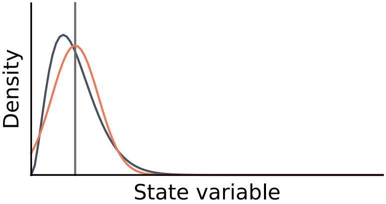
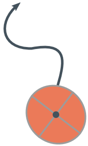
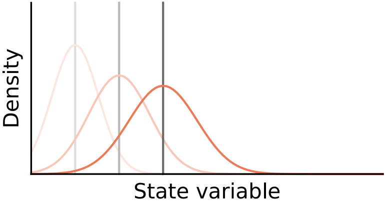




$$\partial_t \langle x \rangle = f\left(\langle x \rangle, \left\langle xx^\top \right\rangle\right)$$
$$\partial_t \left\langle xx^\top \right\rangle = g\left(\langle x \rangle, \left\langle xx^\top \right\rangle\right)$$

Moment approximations of population dynamics





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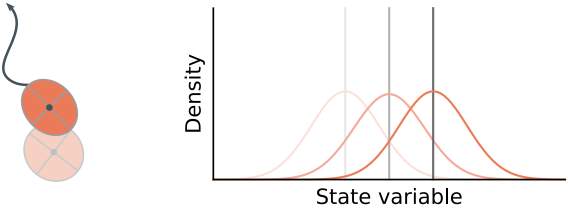

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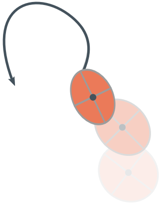

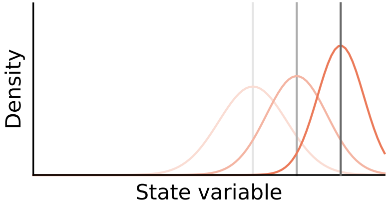

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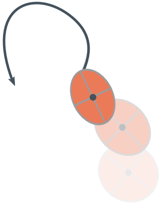
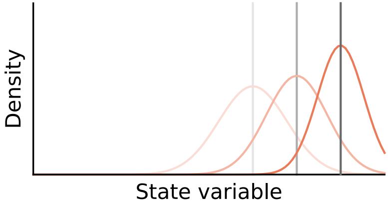
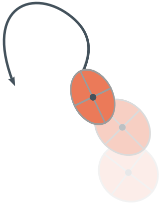
Moment approximations of population dynamics

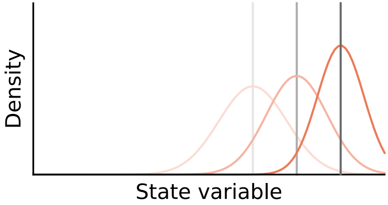




$$\partial_t \langle x \rangle = f\left(\langle x \rangle, \left\langle x x^\top \right\rangle, \text{higher moments?}\right)$$
$$\partial_t \left\langle x x^\top \right\rangle = g\left(\langle x \rangle, \left\langle x x^\top \right\rangle, \text{higher moments?}\right)$$

Moment approximations of population dynamics

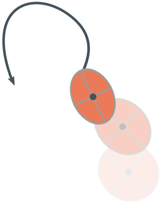


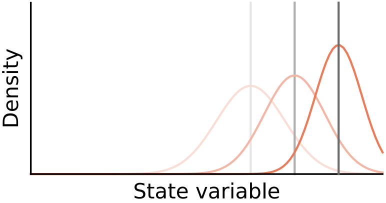


Moment Closure:

- Assume distributional form for x
- Match low-order moments
- Compute effect of higher-order moments under assumed distribution

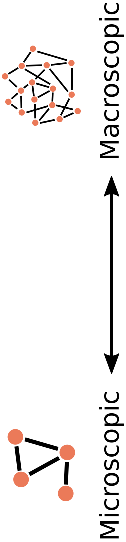
Moment approximations of population dynamics



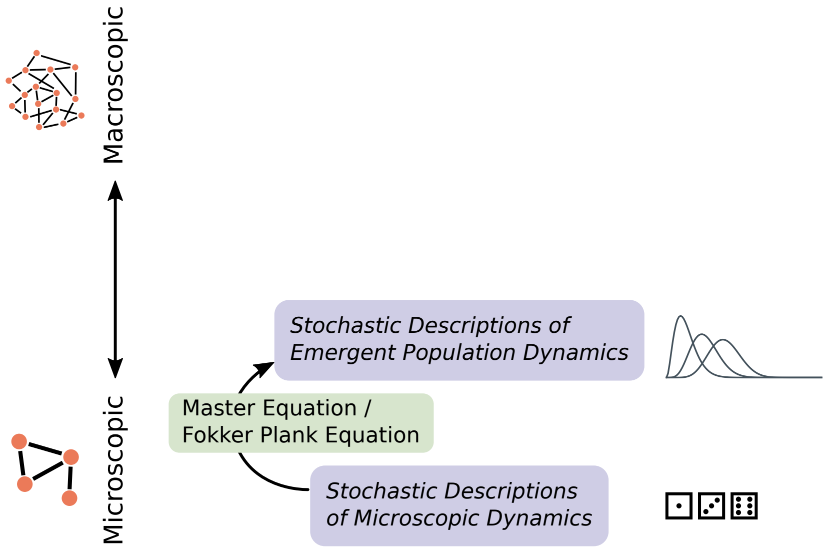


Closed equations:

$$\dot{\mu} = f\left(\mu, \Sigma\right)$$
$$\dot{\Sigma} = g\left(\mu, \Sigma\right)$$



Stochastic Descriptions of Microscopic Dynamics


Macroscopic
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Master Equation /
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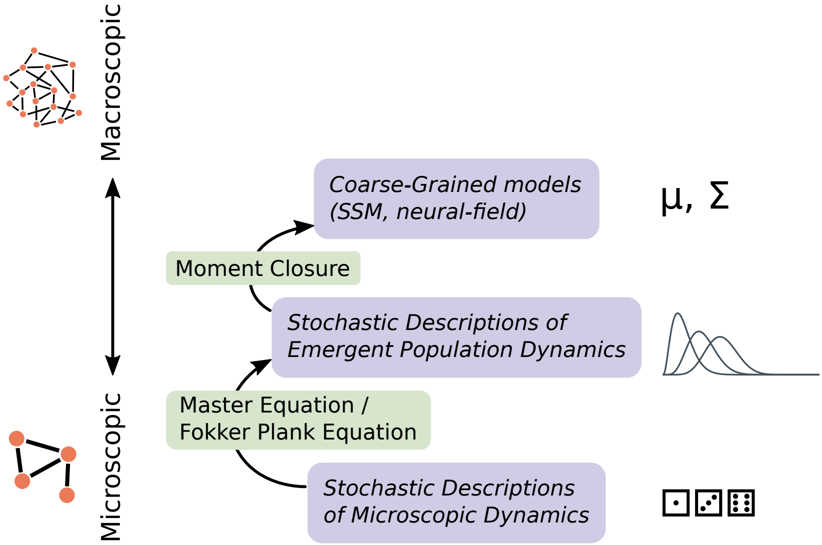
Macroscopic
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Coarse-Grained models
(SSM, neural-field)
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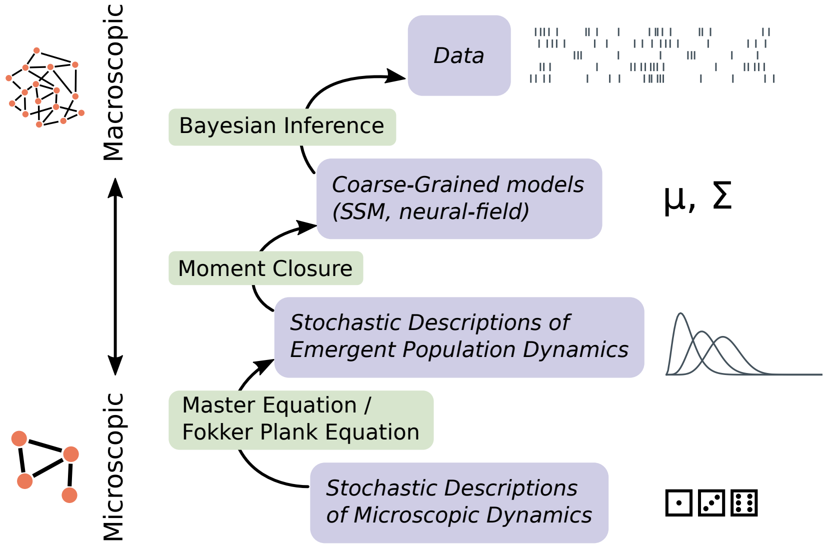
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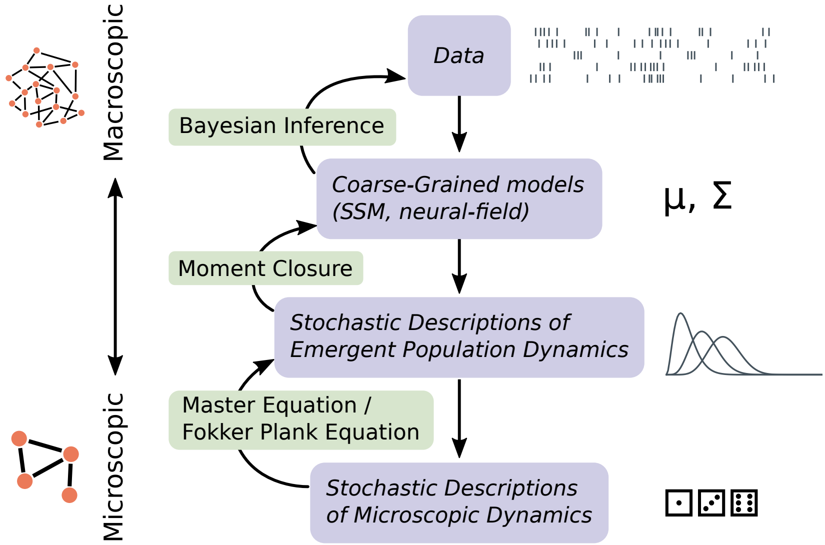
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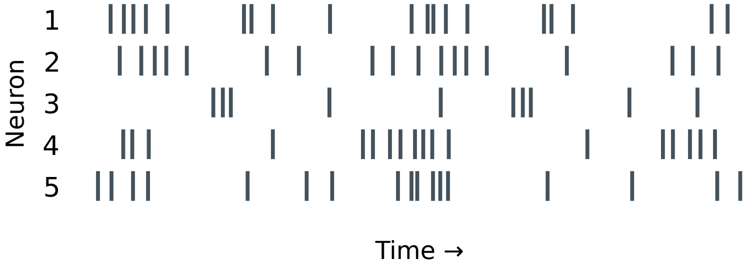
Part 1

A statistical field interpretation of Point-Process models

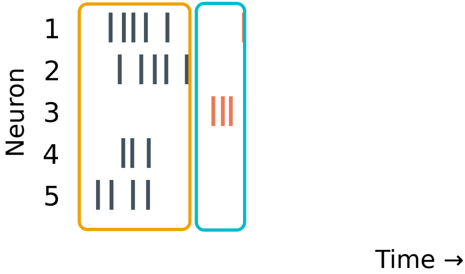
Autoregressive Point Process Models



Conditional intensity given history, inputs

- $\Pr(\text{spike}) = f(\text{history}, \text{input})$

Autoregressive Point Process Models



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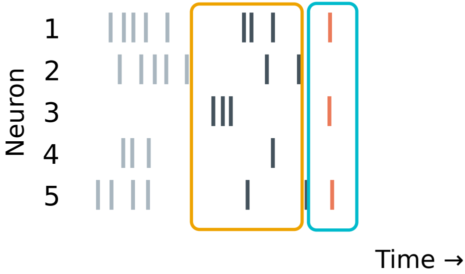

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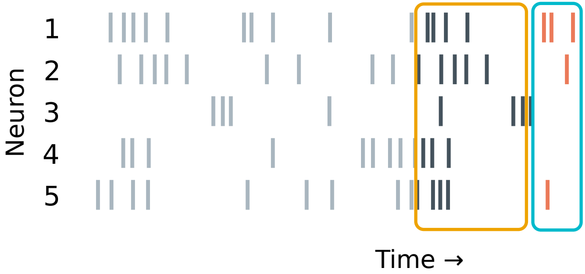

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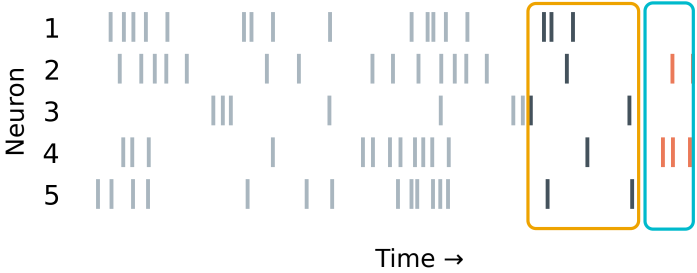
Autoregressive Point Process Models



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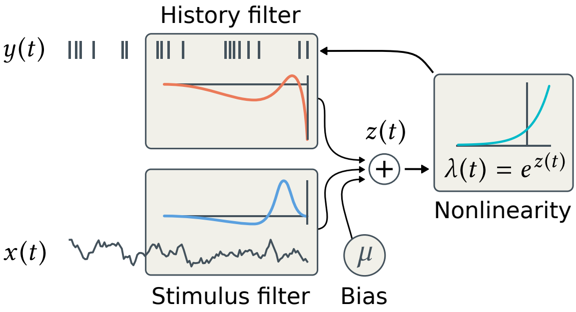
Autoregressive Point Process Models



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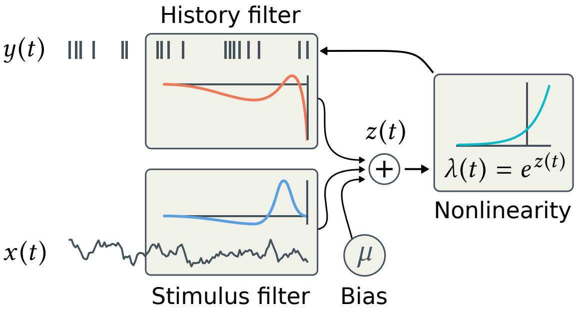

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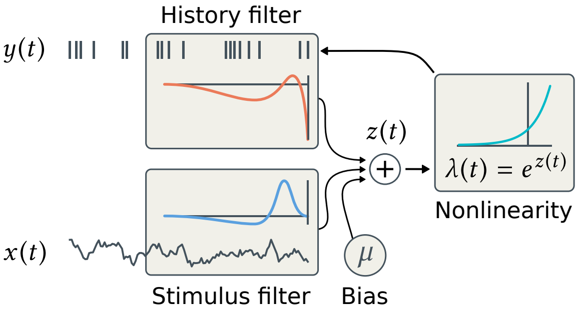
Good

- Fast regression
- Pairwise spiking model

Autoregressive Point Process Models



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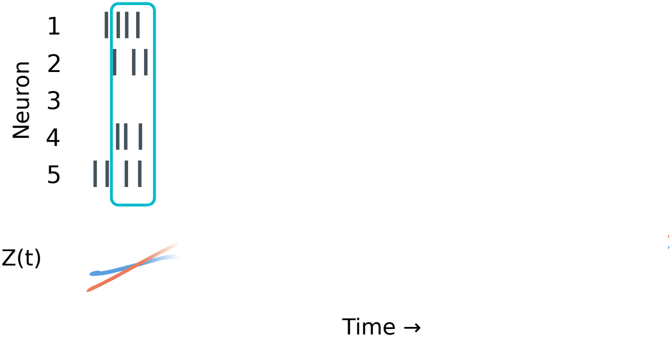
Could improve...

- Large populations?
- Stability?

Latent State-Space Model (SSM)



Latent dynamics drive spiking

- $\dot{x} = f(x)$
- $\Pr(\text{spike}) = g(x)$

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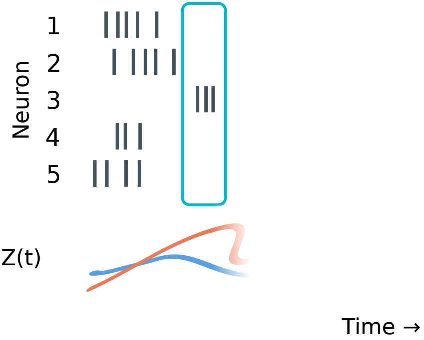

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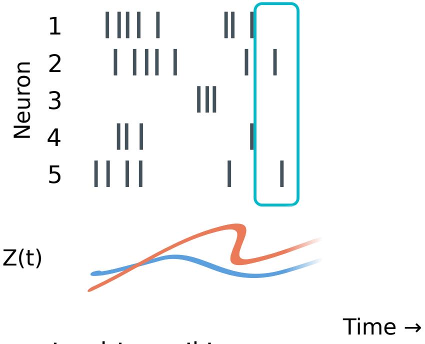

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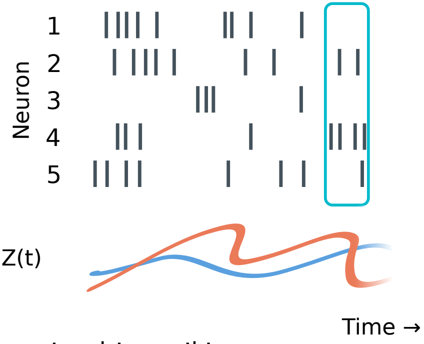

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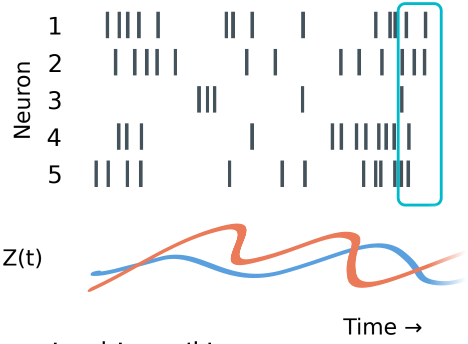

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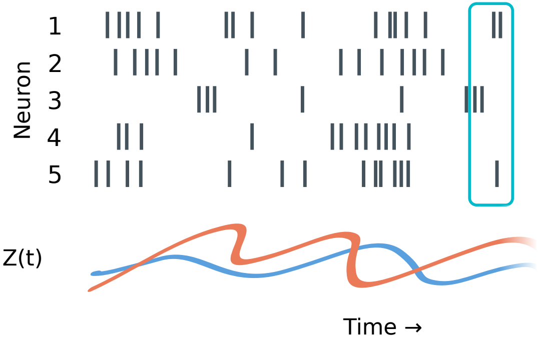

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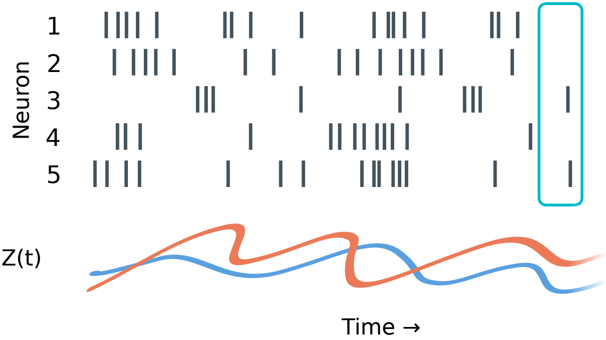

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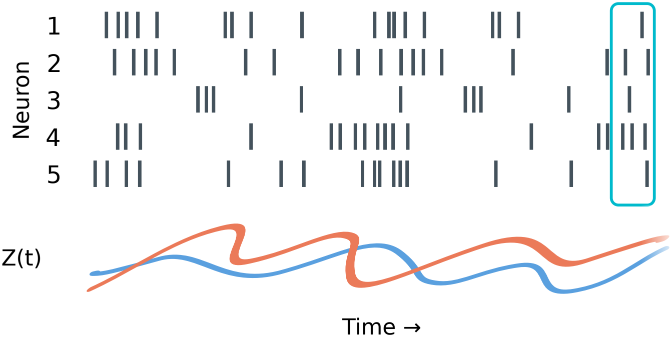

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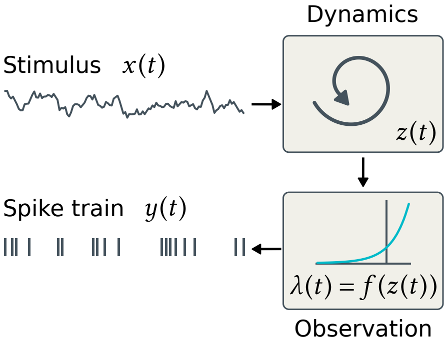

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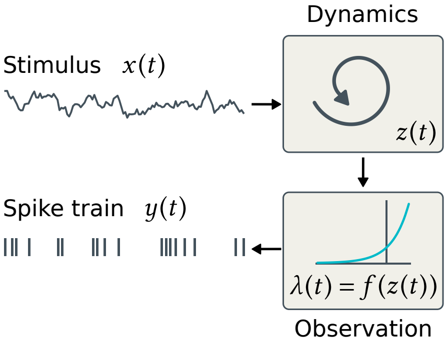

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Good

- **Robust** population models

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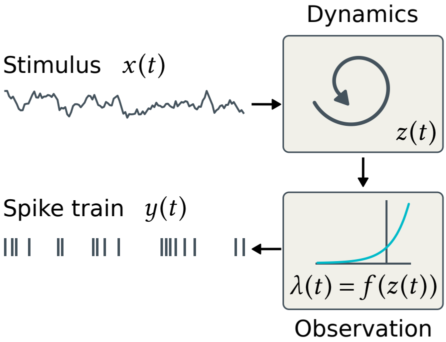

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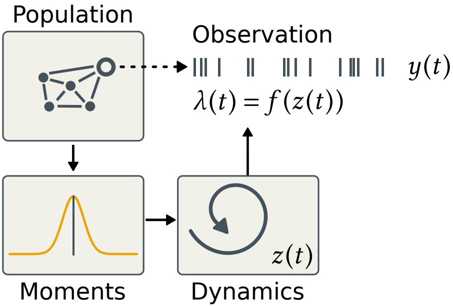
Can we

- Interpret?
- Emergence from single-unit?

Good

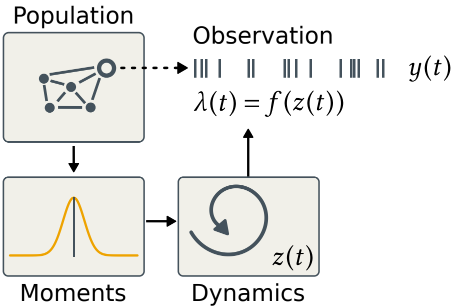
- **Robust** population models



Mean-field limit, e.g. firing rate v

- $\tau \dot{v} = -v + f(Av + \theta)$

Neural mass models



Mean-field limit, e.g. firing rate v

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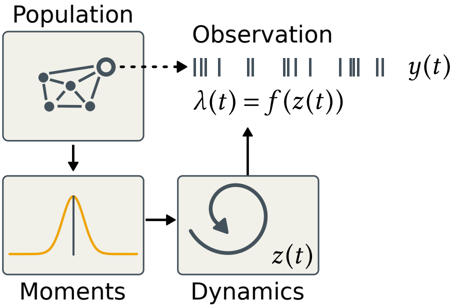
Good

- Analytically tractable
- Physical intuition

Neural mass models



Mean-field limit, e.g. firing rate v

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Good

- Analytically tractable
- Physical intuition

Could improve...

- Data-driven?
- Detail?

Moment-closure on PP-GLM models

Combine aspects ...

- Neural field models:
  - *Analytically tractable ODEs*
  - with mechanistic interpretation
- State-space models:
  - Low dimensional
  - *Data-driven*

Moment-closure on PP-GLM models

Combine aspects ...

- Neural field models:
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  - with mechanistic interpretation
- State-space models:
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  - *Data-driven*

Consider distribution over possible point-process paths

- Describe dynamics of **moments** of PP-GLM models

History process of an autoregressive PP-GLM

Consider a log-linear model

History process of an autoregressive PP-GLM

Consider a log-linear model

$$y(t) \sim \mathrm{Poisson}(\lambda \cdot dt)$$

$$\lambda(t) = \exp\left(H(\tau)^\top h(\tau, t) + I(t)\right)$$

$$H(\tau) : \text{history filter}$$

$$I(t) : \text{input}$$

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History $h(\tau, t)$ of spikes $y(t)$: $\partial_t h(\tau, t) = \delta_{\tau=0} y(t) - \partial_\tau h(\tau, t)$

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Poisson noise → Gaussian: $y(t) \approx \lambda \cdot dt + \sqrt{\lambda} \cdot dW$

Continuous approximation to history process

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Continuous approximation to history process

$$dh(\tau, t) = (\delta_{\tau=0}\lambda - \partial_\tau h(\tau, t)) \cdot dt + \delta_{\tau=0}\sqrt{\lambda} \cdot dW$$

Does it work?

Case study:

- Emergent dynamics from spiking interactions
- PP-GLM emulation of phasic-bursting Izhikevich neuron (?)

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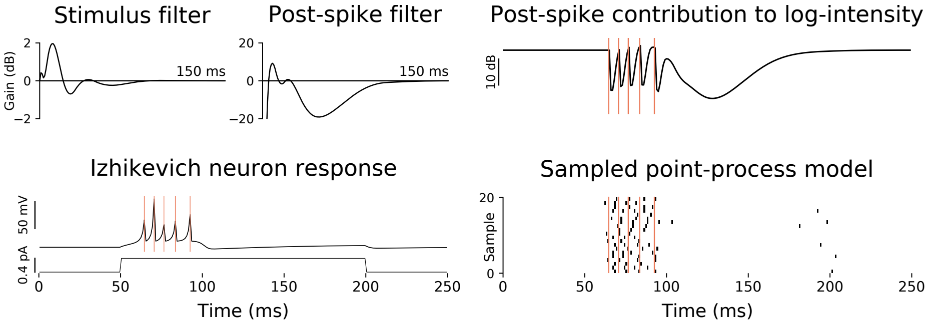
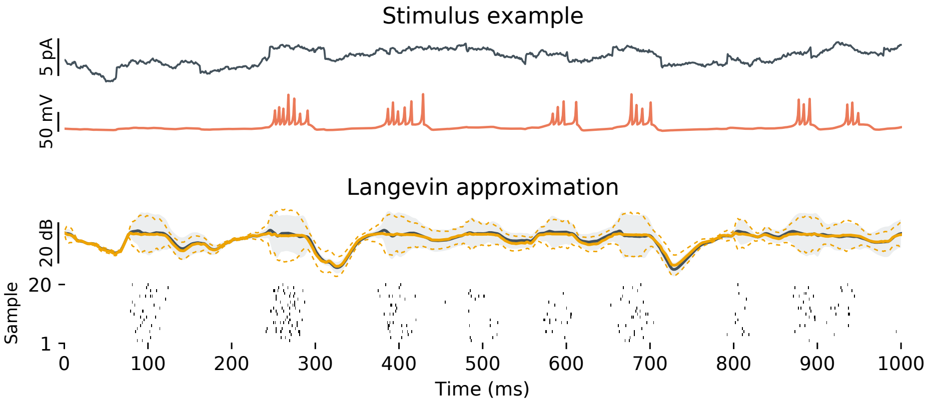
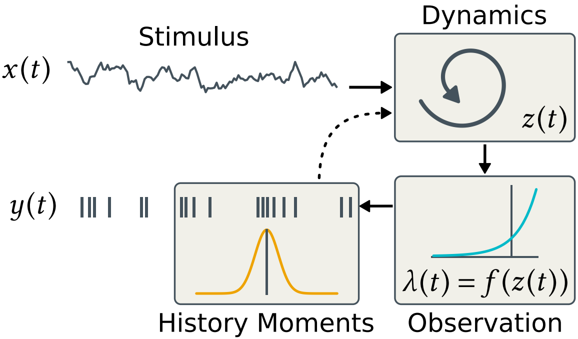



Stimulus example
5 pA
50 mV
Langevin approximation
20 dB
Sample
20
1
0
100
200
300
400
500
600
700
800
900
1000
Time (ms)

?

Moment-closure of autoregressive PP-GLM



Moment closure of PP-GLM history process

$$\partial_t \mu_h = -\partial_\tau \mu_h + \delta_{\tau=0} \langle \lambda \rangle$$

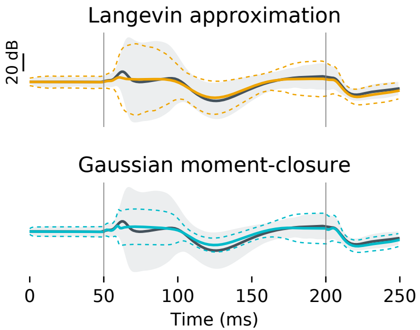
$$\langle \lambda \rangle = \exp\left(H^\top \mu_h + I(t) + \tfrac{1}{2} H^\top \Sigma H \right)$$

$$\partial_t \Sigma_h = J \Sigma_h + \Sigma_h J^\top + Q$$

$$J = \delta_{\tau=0} \langle \lambda \rangle H^\top - \partial_\tau$$

$$Q = \delta_{\tau=0} \langle \lambda \rangle \delta_{\tau=0}^\top$$

Pulse Response



?

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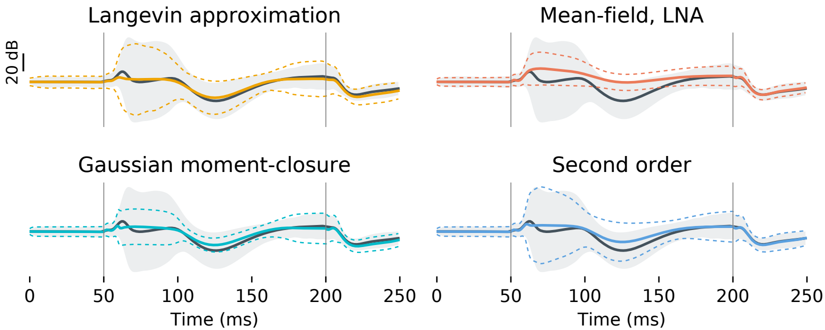
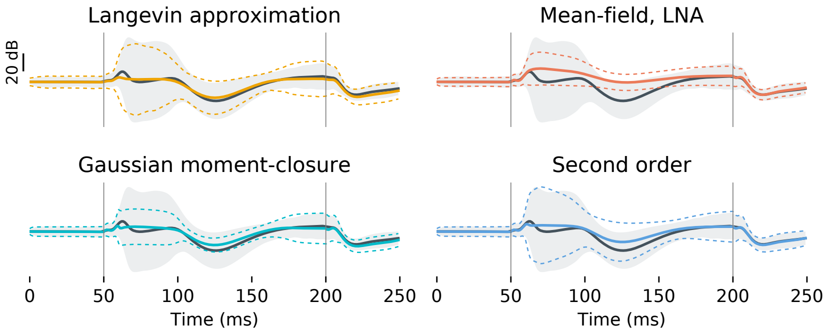


?

$$\langle \lambda \rangle = \langle f(w) \rangle \,, \quad \text{where } w = H^\top h(\tau, t) + I(t)$$

Pulse Response



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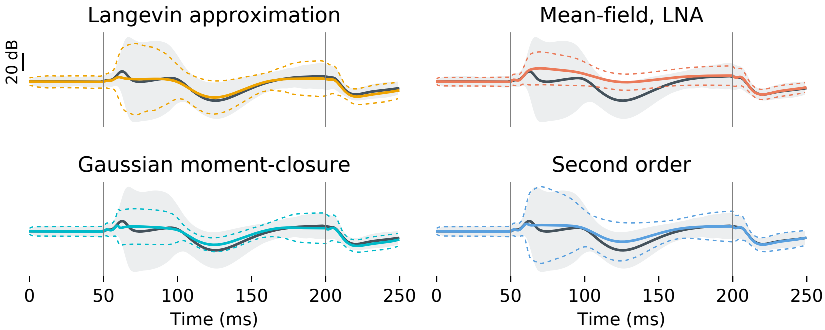
$$\langle \lambda \rangle = \langle f(w) \rangle \,, \quad \text{where } w = H^\top h(\tau, t) + I(t)$$

$$\langle f(w) \rangle \approx f(\mu_w) + \langle w - \mu_w \rangle \, f'(\mu_w) + \tfrac{1}{2} \left\langle (w - \mu_w)^2 \right\rangle f''(\mu_w)$$

Pulse Response



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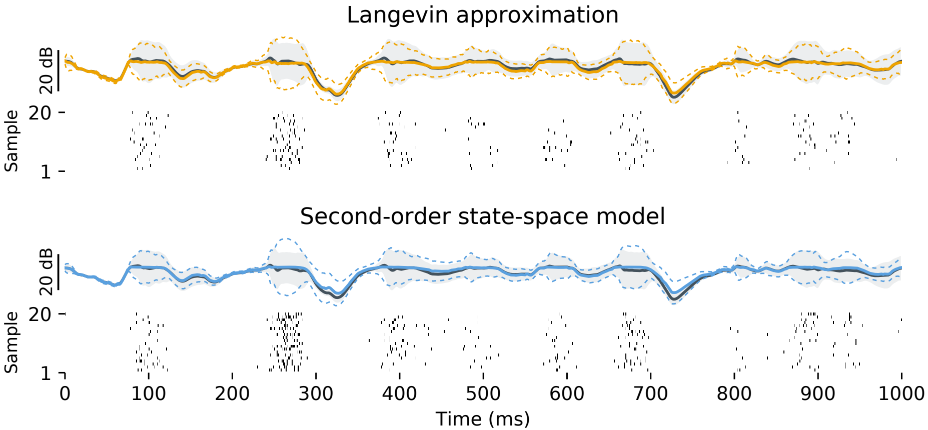
2nd-order approximation

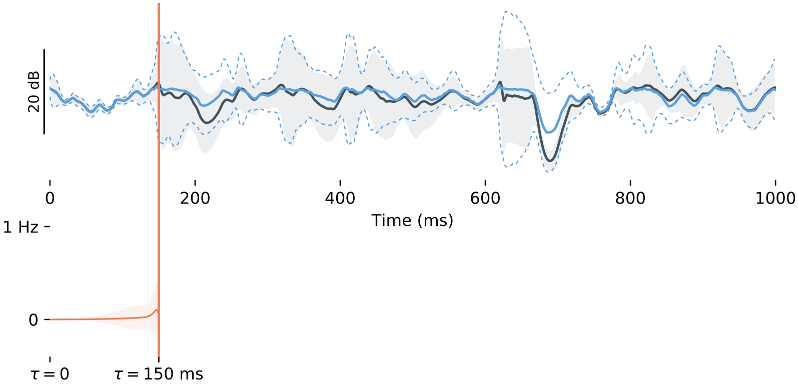
$$\partial_t \mu_h = -\partial_\tau \mu_h + \delta_{\tau=0} \langle \lambda \rangle$$
$$\langle \lambda \rangle = \exp\left(H^\top \mu_h + I(t)\right)\left(1 + \tfrac{1}{2} H^\top \Sigma H\right)$$

$$\partial_t \Sigma_h = J\Sigma_h + \Sigma_h J^\top + Q$$
$$Q = \delta_{\tau=0} \langle \lambda \rangle \delta_{\tau=0}^\top$$
$$J = \delta_{\tau=0} \bar{\lambda} H^\top - \partial_\tau$$
$$\bar{\lambda} = \exp\left(H^\top \mu_h + I(t)\right)$$

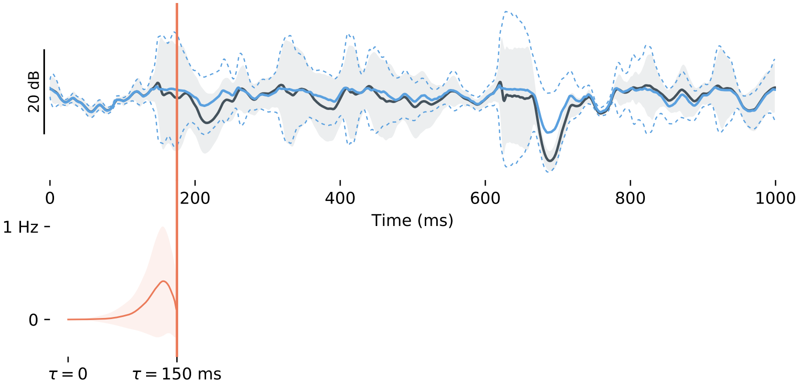

Langevin approximation
20 dB
Sample
20
1
Second-order state-space model
20 dB
Sample
20
1
0
100
200
300
400
500
600
700
800
900
1000
Time (ms)

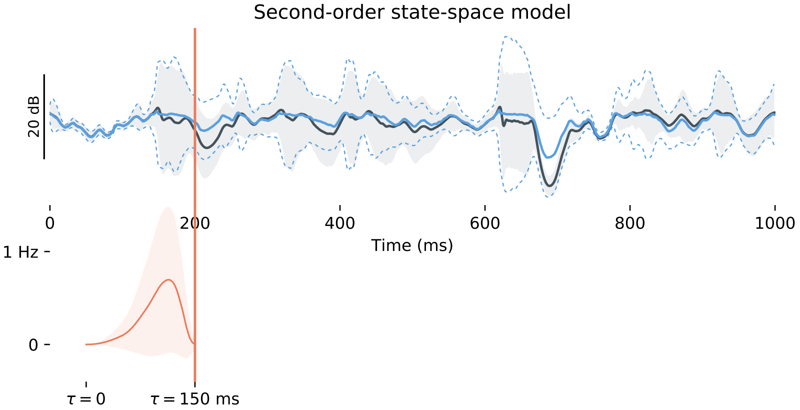
?

Second-order state-space model

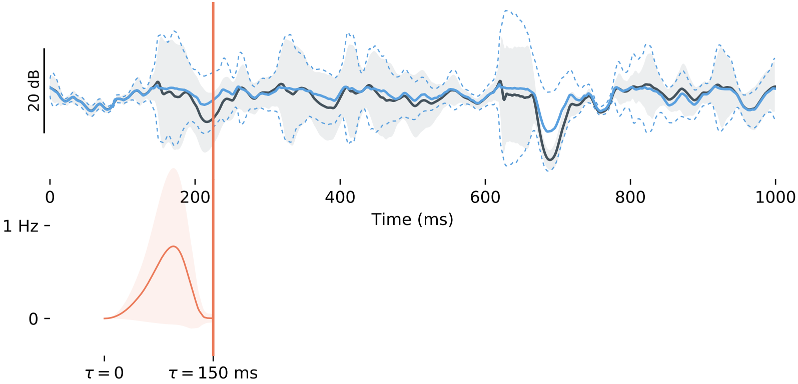


Second-order state-space model




Second-order state-space model
20 dB
0
200
400
600
800
1000
Time (ms)
1 Hz
0
τ = 0
τ = 150 ms

Second-order state-space model



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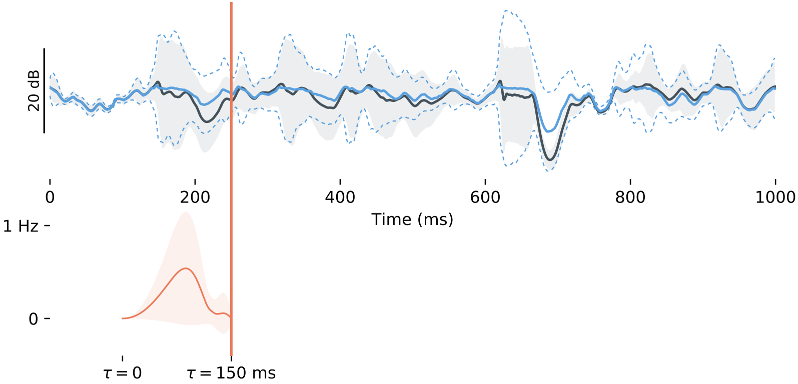

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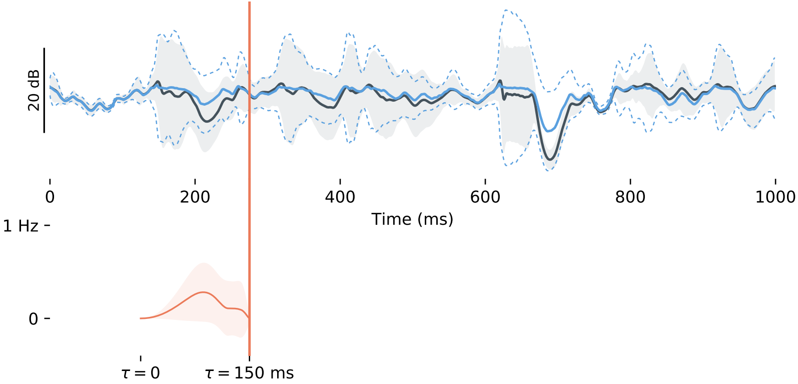

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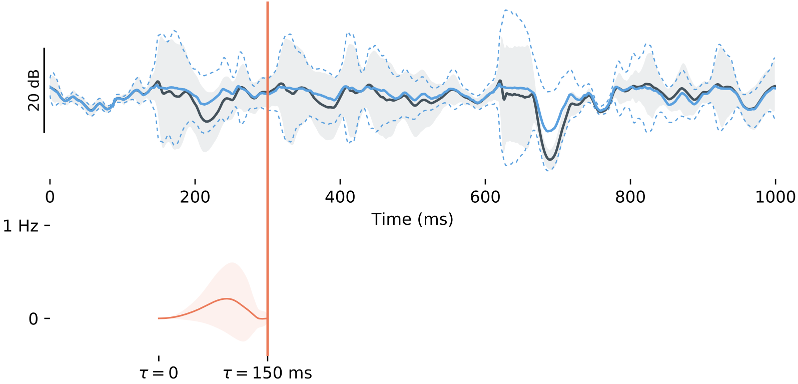

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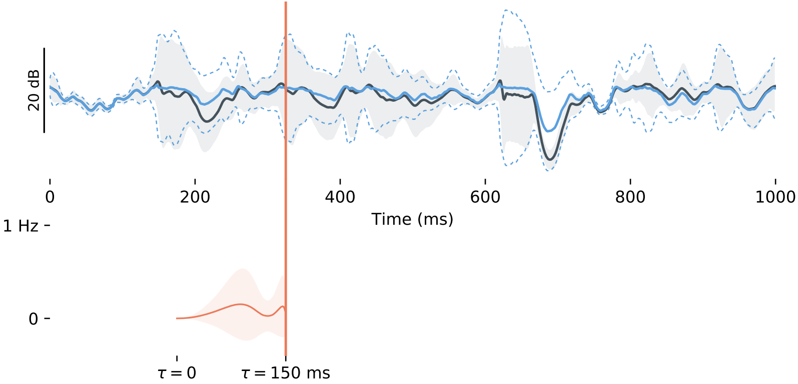

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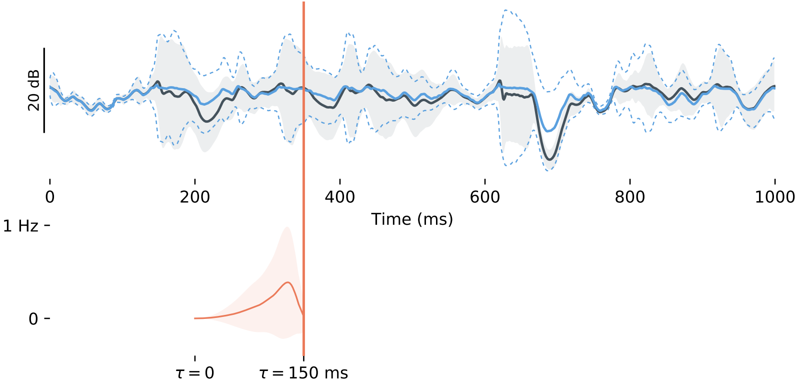

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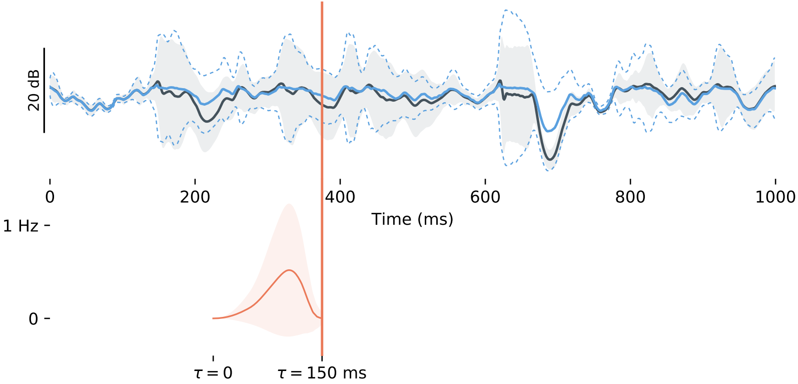

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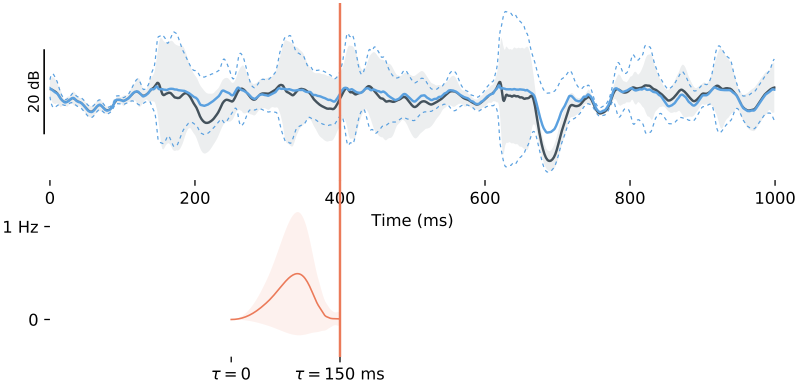

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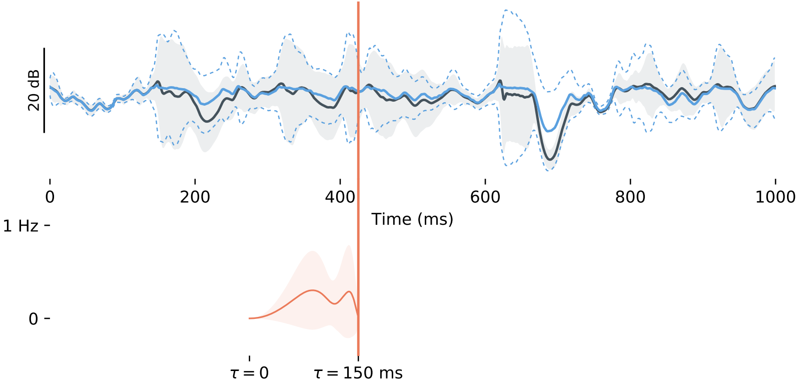

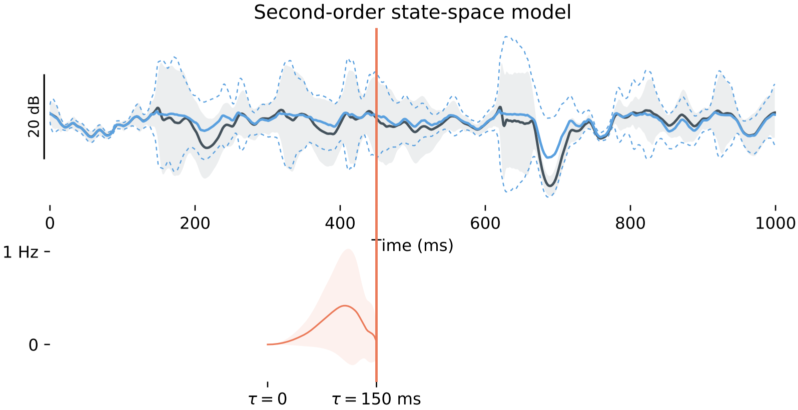
Second-order state-space model
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1 Hz
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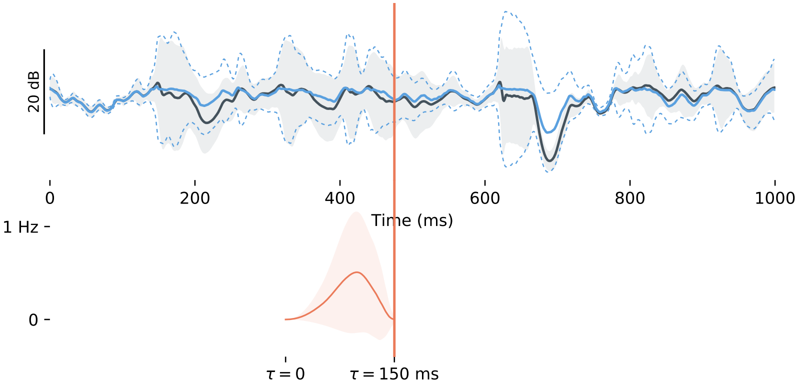

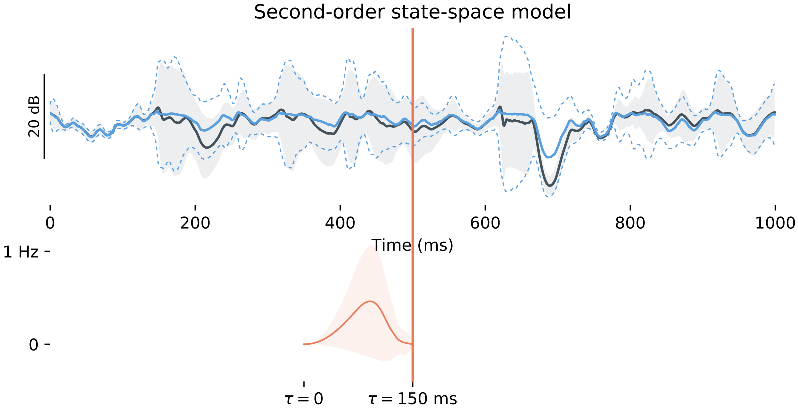
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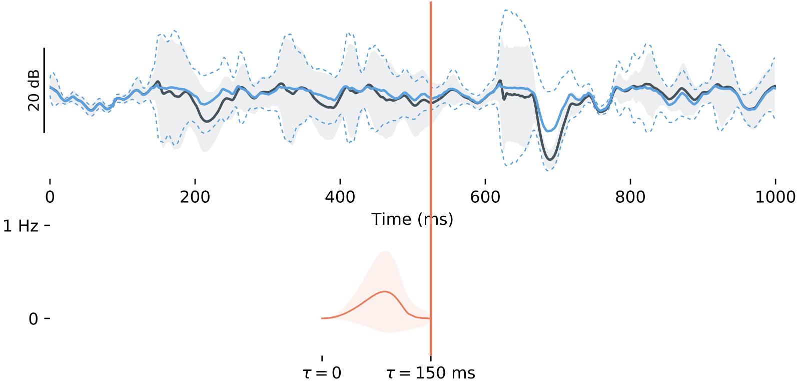

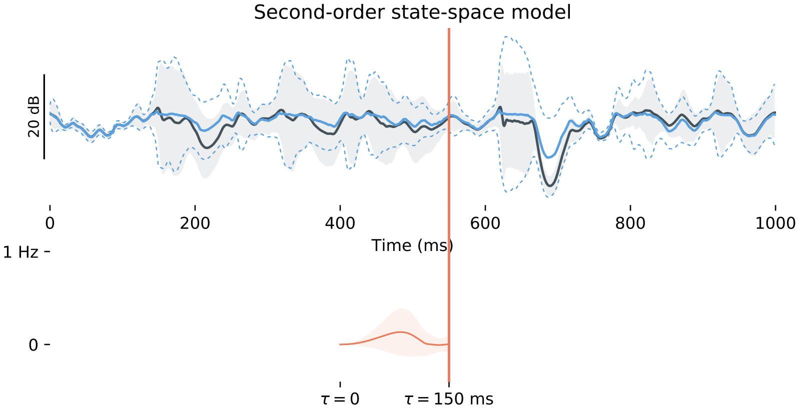
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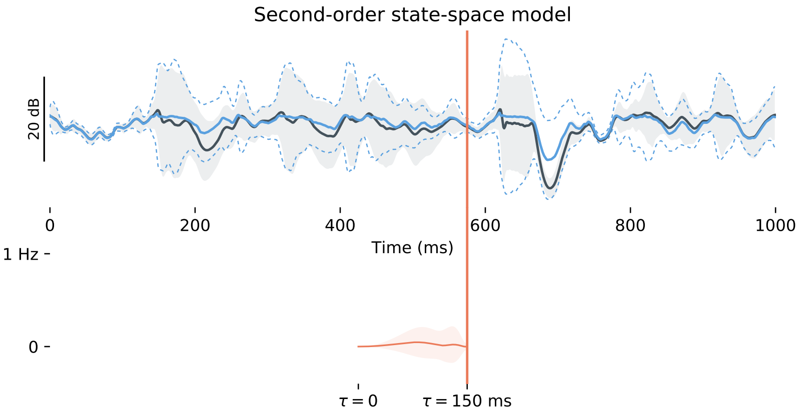
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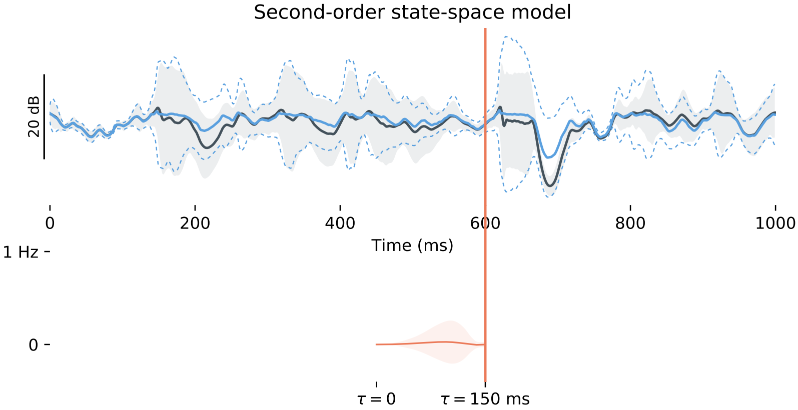

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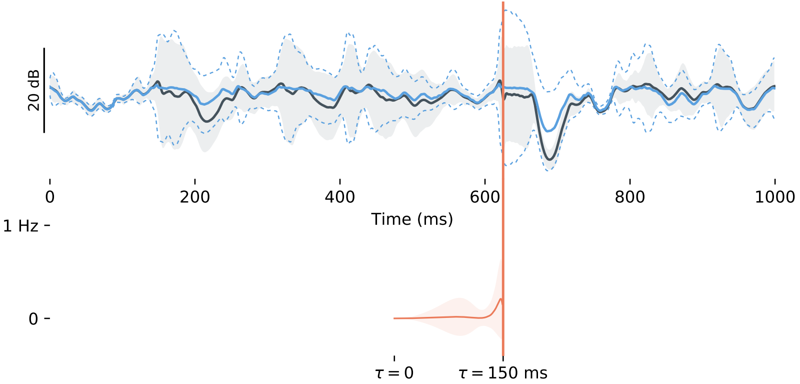

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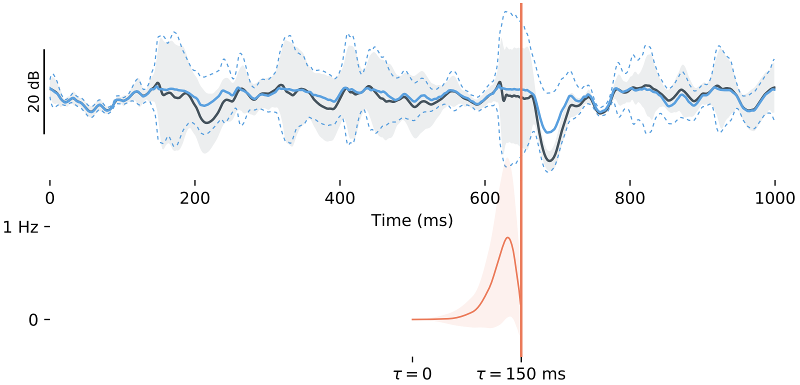

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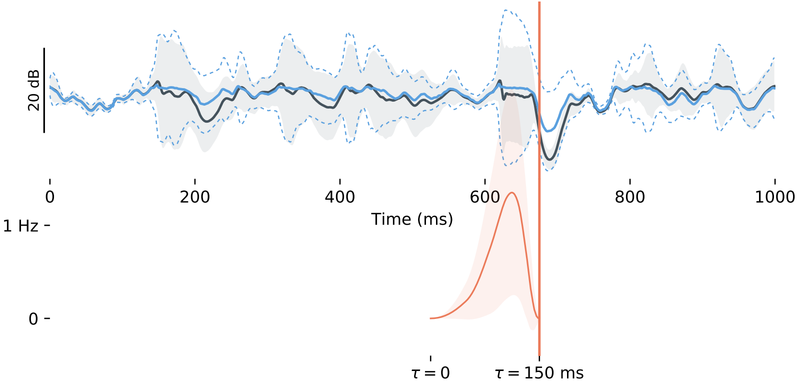

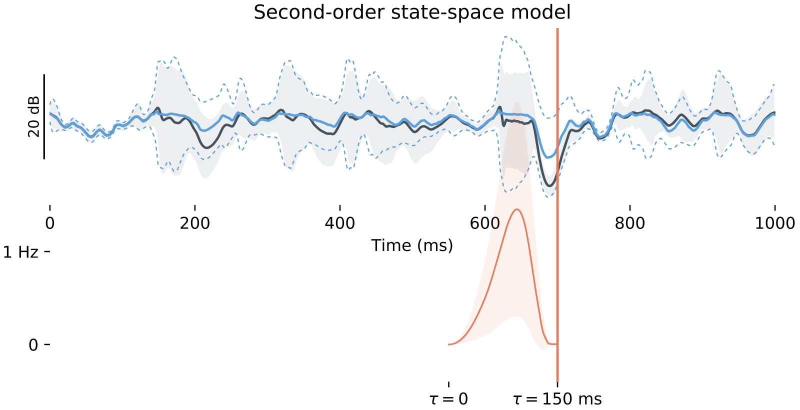
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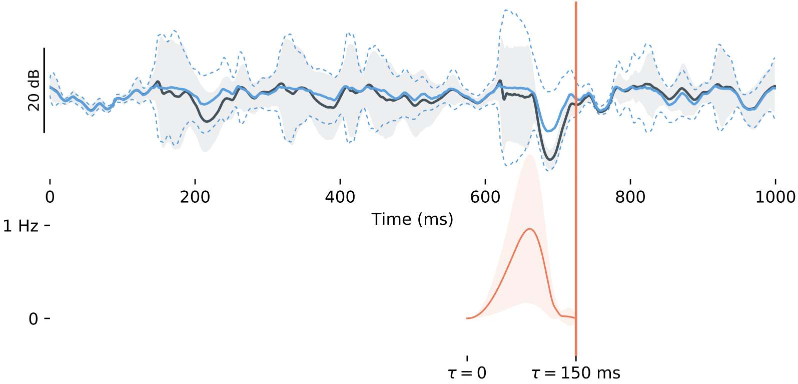

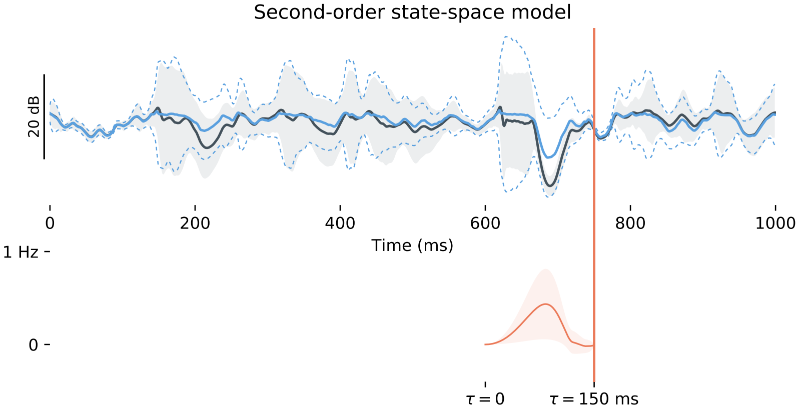

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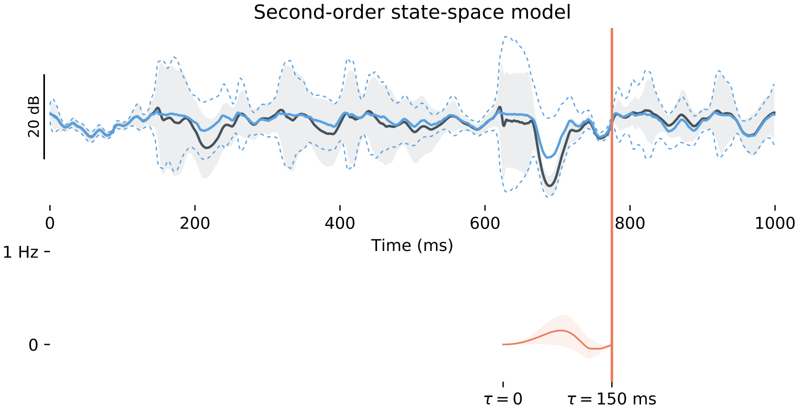
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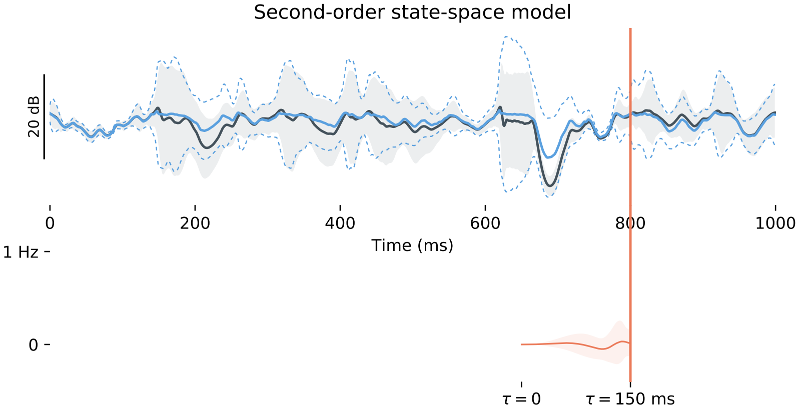
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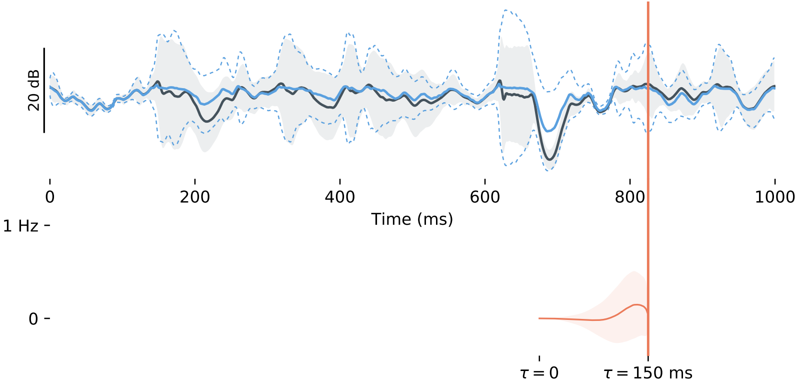

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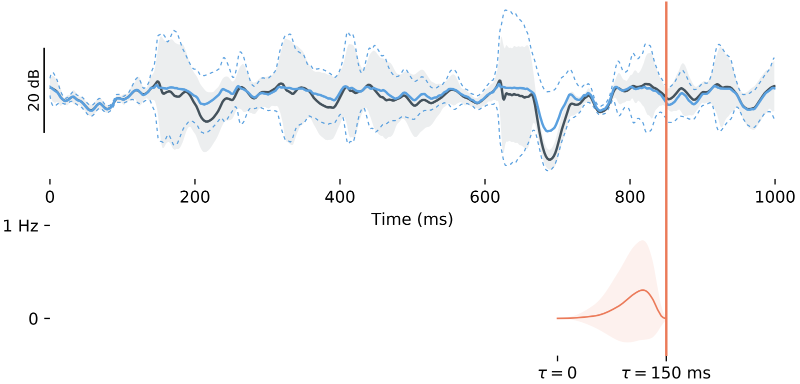

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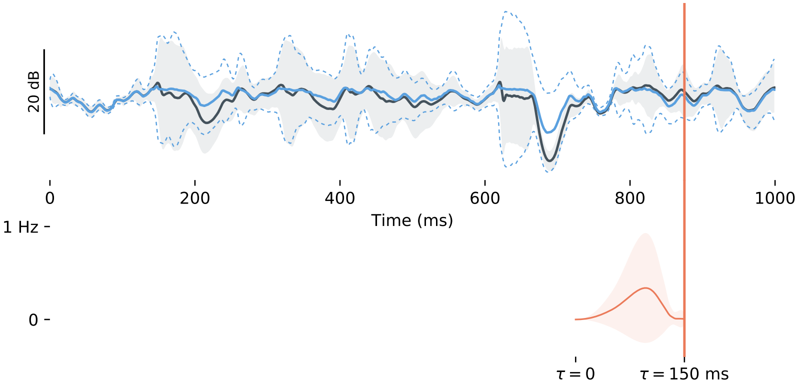

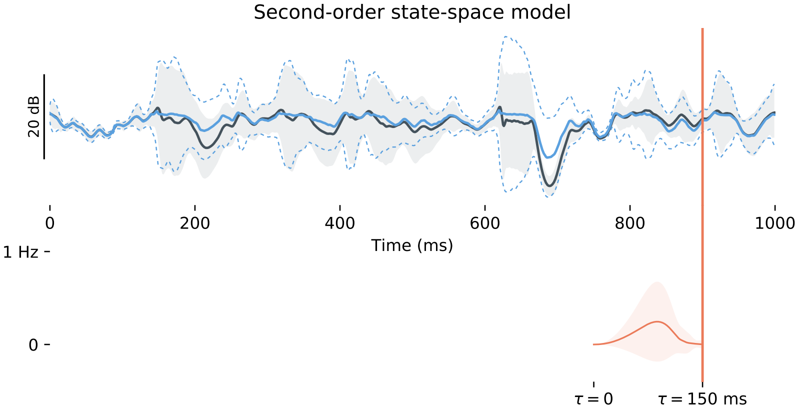
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A SSM with point-process moment interpretation

Add Poisson noise to recurrent linear model (?)

$$dx = [Ax + C\lambda] \cdot dt + C\sqrt{\lambda} \cdot dW$$
$$w = Hx + m$$
$$\lambda = \exp(w)$$

Second-order state-space equations for extended Kalman filtering

$$\partial_t \mu_x = A\mu_x + C\langle\lambda\rangle$$
$$\mu_w = H\mu_x + m$$
$$\Sigma_w = H^\top \Sigma_x H$$
$$\langle\lambda\rangle = \exp\left(\mu_w + \tfrac{1}{2}\Sigma_w\right)$$

$$\partial_t \Sigma_x = J\Sigma_x + \Sigma_x J^\top + Q$$
$$J = C\langle\lambda\rangle H^\top + A$$
$$Q = C\langle\lambda\rangle C^\top$$

A SSM with point-process moment interpretation

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$$\partial_t \Sigma_x = J\Sigma_x + \Sigma_x J^\top + Q$$
$$J = Cf'(\mu_w)H^\top + A$$
$$Q = C\langle\lambda\rangle C^\top$$

A statistical field interpretation of Point-Process models

PP-GLM $\rightarrow$ Langevin $\rightarrow$ **moment-closure** $\rightarrow$ $\dot{\mu}_h$, $\dot{\Sigma}_h$

- **Closed equations** for 'statistical fields' (history moments)

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2nd-order SSM with *mechanistic interpretation*

- Spikes are Poisson **measurements**
- Spiking interaction $\rightarrow$ field coupling (?)

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2nd-order SSM with *mechanistic interpretation*

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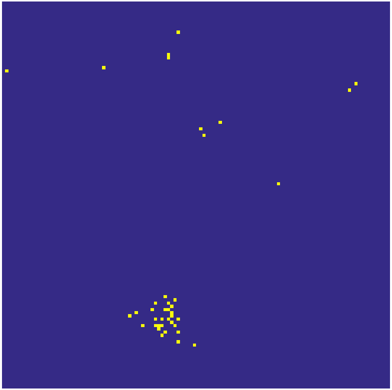
New directions

- Detect **instability**
- Bayesian estimation
- Analytic tools for **reduction** of population models?

Part 2

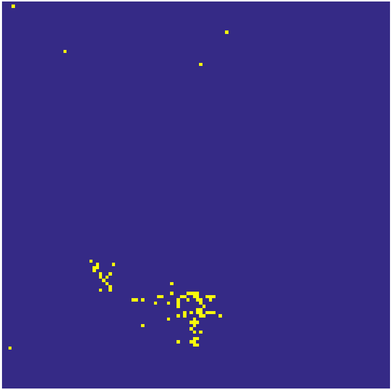
Bayesian State-Space Inference for Stochastic Neural fields

Developing retina exhibits spatiotemporal waves



$10\times$ real-time

Developing retina exhibits spatiotemporal waves



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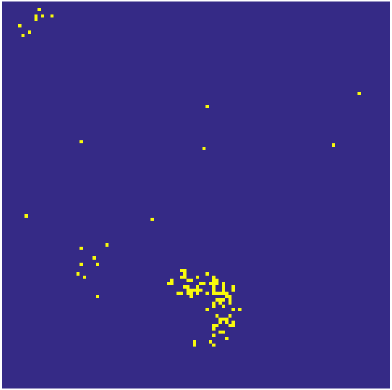
Developing retina exhibits spatiotemporal waves



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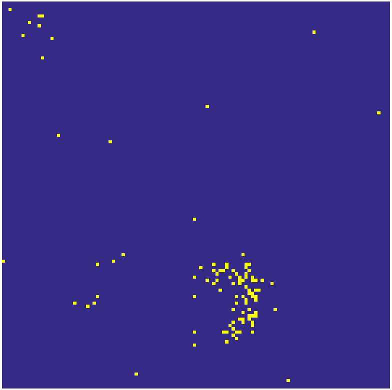

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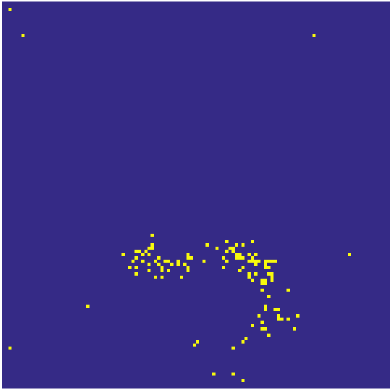

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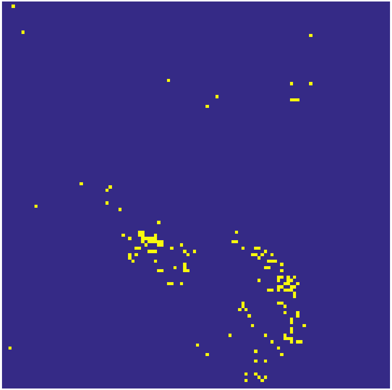

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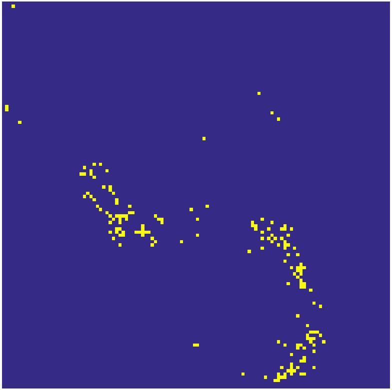

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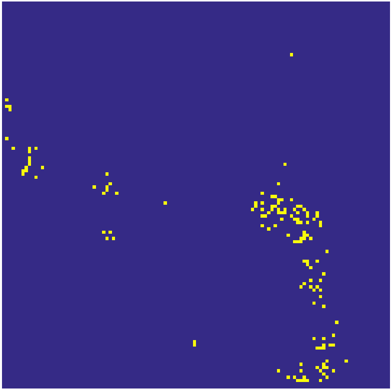

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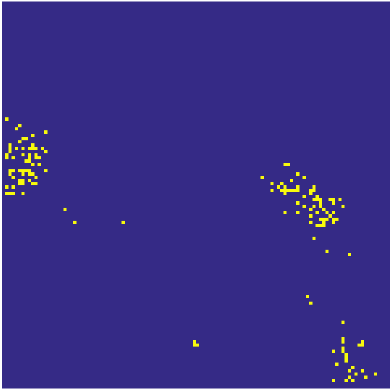

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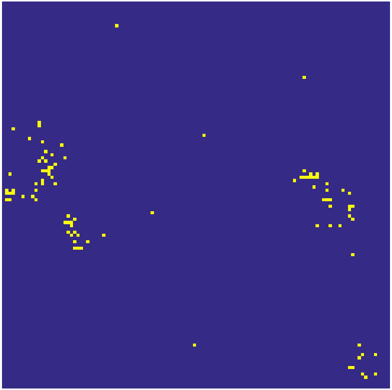

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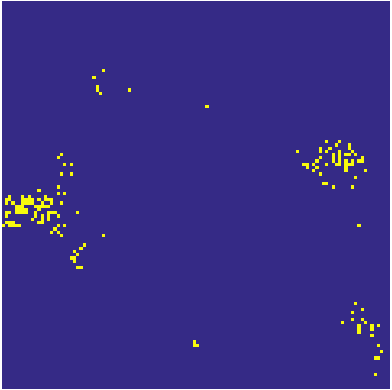

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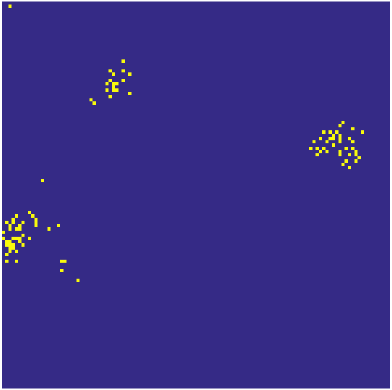

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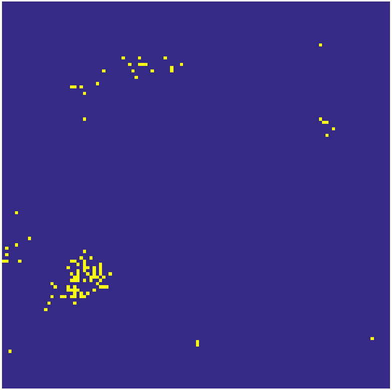

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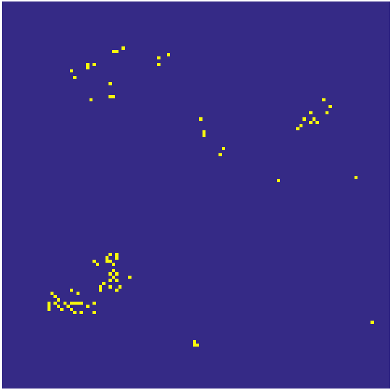

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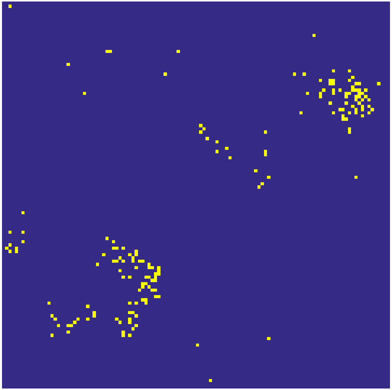

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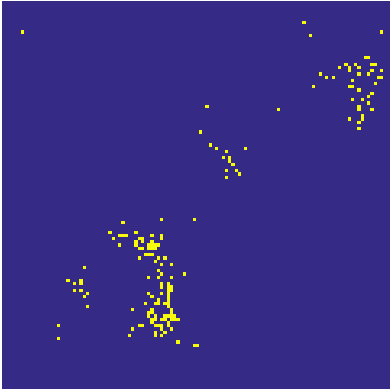

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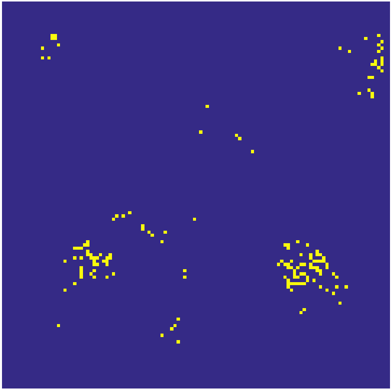

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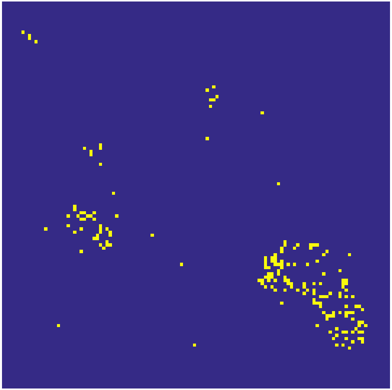

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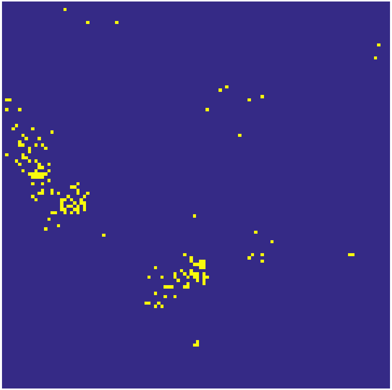

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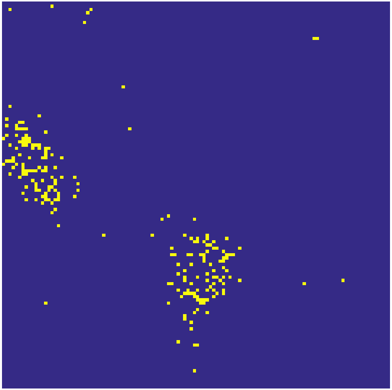

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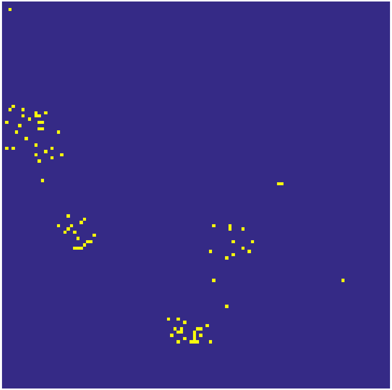

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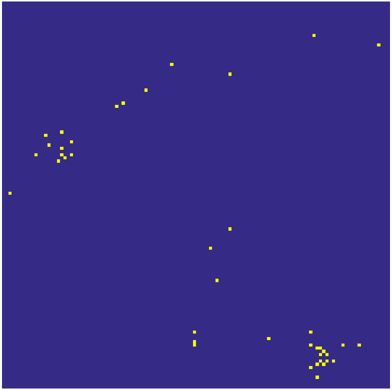

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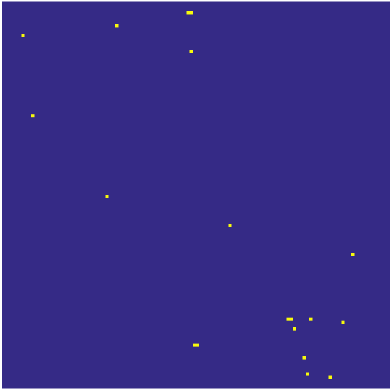

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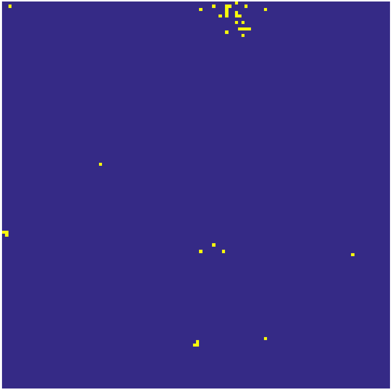

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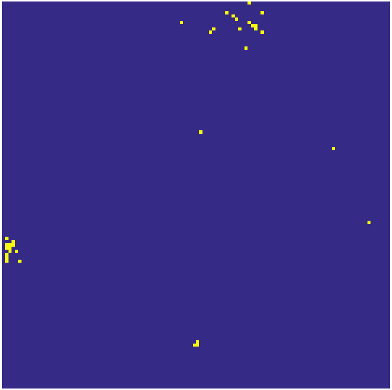

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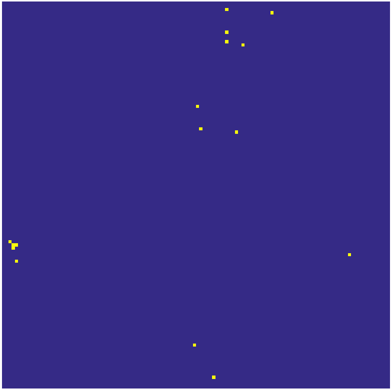

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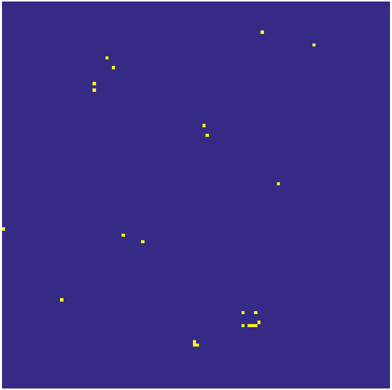

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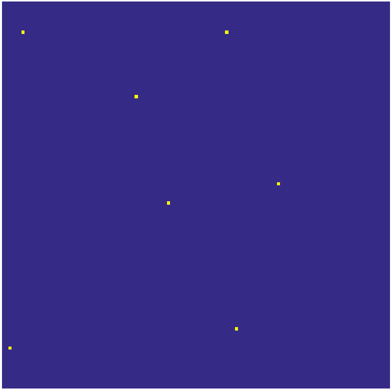

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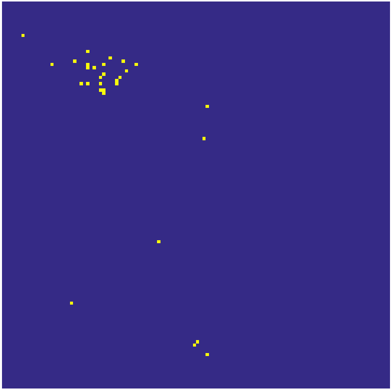

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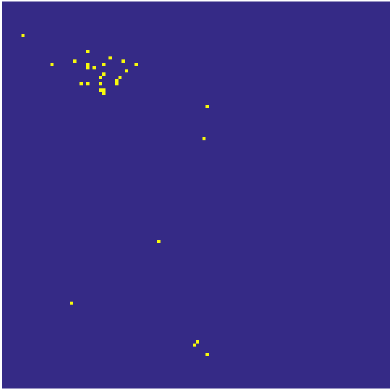

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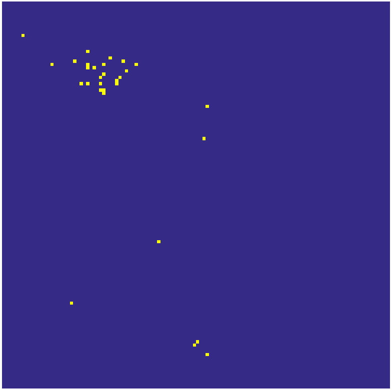
Frequent: small events that do not propagate

Developing retina exhibits spatiotemporal waves



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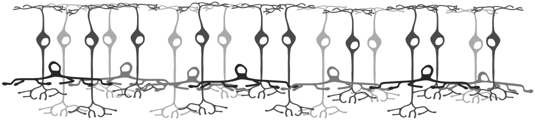
Frequent: small events that do not propagate

Rare: large waves that cover the retina

Waves emerge in inner nuclear layer

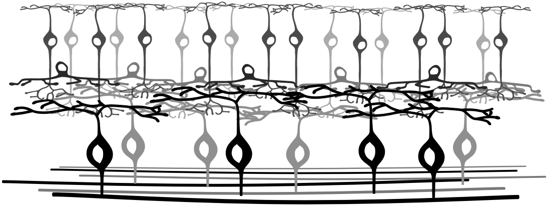
Bipolar and
amacrine cells
(generate waves)

Waves emerge in inner nuclear layer



Bipolar and amacrine cells (generate waves)

Waves induce spiking in ganglion cell outputs



Bipolar and
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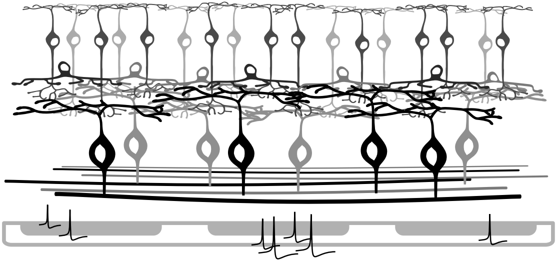
Retinal Ganglion Cells

4096-electrode MEAs record RGC outputs



Bipolar and amacrine cells (generate waves)

Retinal Ganglion Cells

Multi-electrode array (spiking observations)

Objective: infer latent states

State inference

- Given spiking data and model parameters,
- Can we infer voltage, conductance, current?

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Conductance models

- *Hennig et al. '09:* **Realistic** discrete neurons (too complex)
  - Slow refractory dynamics; rare, random depolarization
- *Lansdell et al. '14:* Continuum field approach
  - Conductance dynamics *still too complicated*

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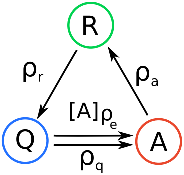
Something simpler?

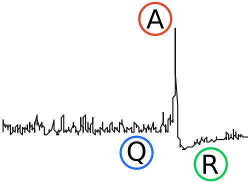
Buice & Cowan '09: a simple model for retinal waves

3-state model of retinal waves (?)

- Q "Quiescent" (not spiking)
- A "Active" (spiking)
- R "Refractory"

Buice & Cowan '09: a simple model for retinal waves





3-state model of retinal waves (?)

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4 rates

- ρ_q Spontaneous activation ■ $\rightarrow$ ■
- ρ_a Cells become refractory ■ $\rightarrow$ ■
- ρ_r Refractory cells become Quiescent ■ $\rightarrow$ ■
- ρ_e Excitation of Quiescent cells ■■ $\rightarrow$ ■■

Spatially extended 3-state mean-field model

Model ***fraction*** of N neurons in each state

- Let ρ_{qa} denote **effective** excitation $\rho_{qa} = \rho_q + f[A]\rho_e$
- Means evolve as

$$\partial_t Q = -\rho_{qa} Q + \rho_r R$$
$$\partial_t A = -\rho_a A + \rho_{qa} Q$$
$$\partial_t R = -\rho_r R + \rho_a A$$

Space:

- Extend Q, A, and R fields be defined over a 2D (x,y) domain
- **Nonlocal** excitation kernel k radius σ_i

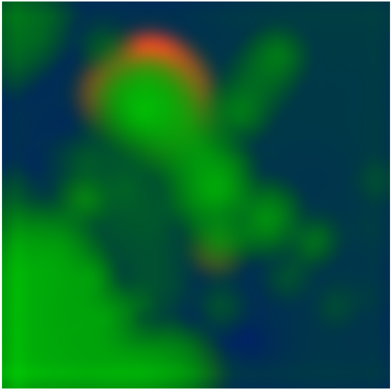
$$f[A] = k * A, \qquad k(x,y) \propto \exp\left(-\frac{1}{2}\frac{x^2+y^2}{\sigma_i^2}\right)$$

Incorporate a threshold, random initiation

$$f[A] = \begin{cases} A - \varepsilon, & \text{if } A \geq \varepsilon \\ 0 & \text{elsewise} \end{cases}$$

$$\Pr(Q \to A) \sim \rho_q \cdot \delta,$$

$$\delta \sim \text{Poisson}\left(\lambda_q\right)$$



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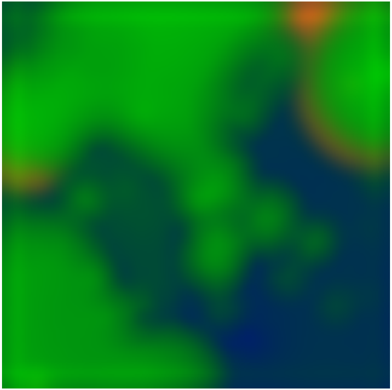

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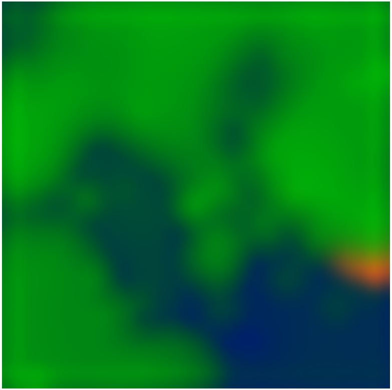

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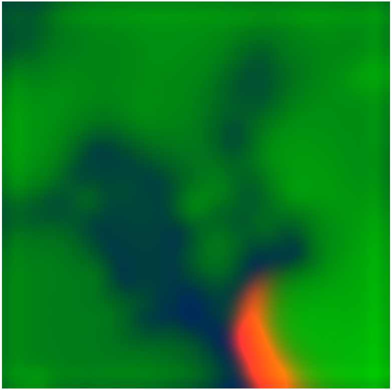

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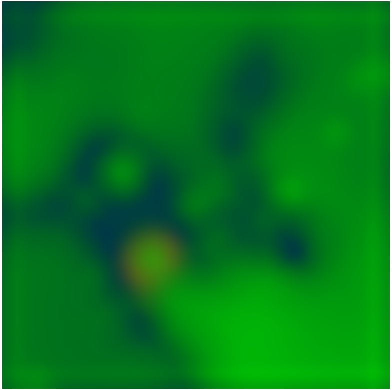

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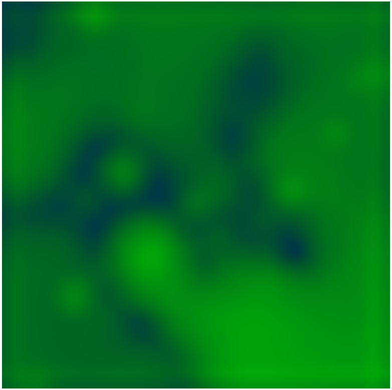

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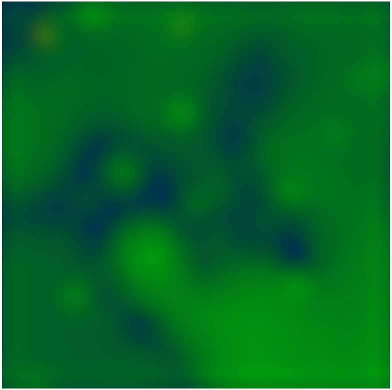

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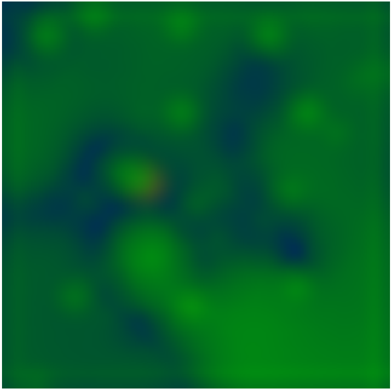

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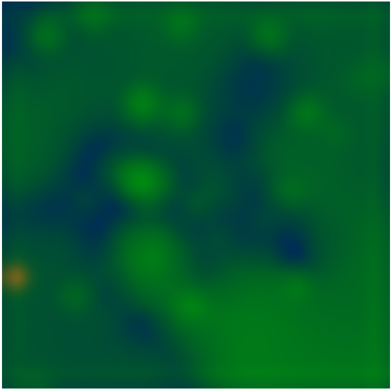

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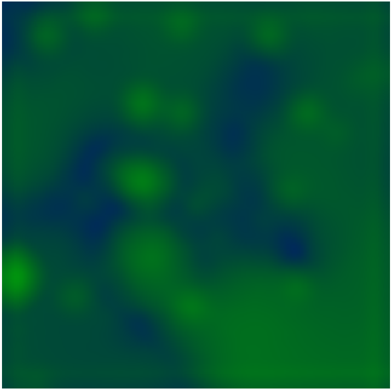

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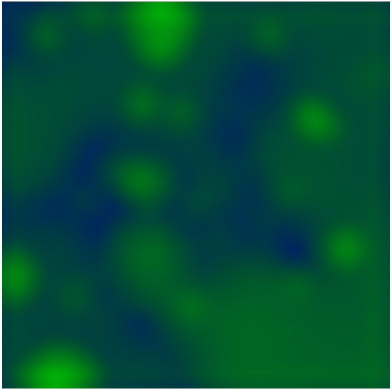

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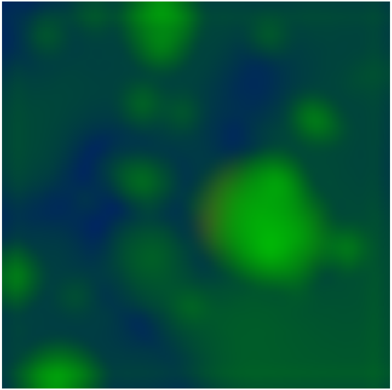

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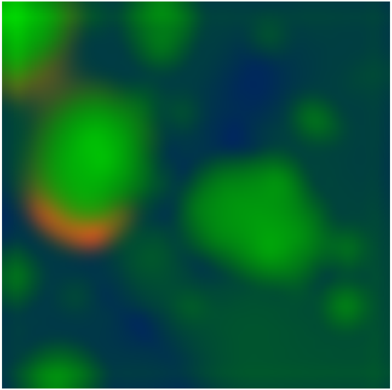

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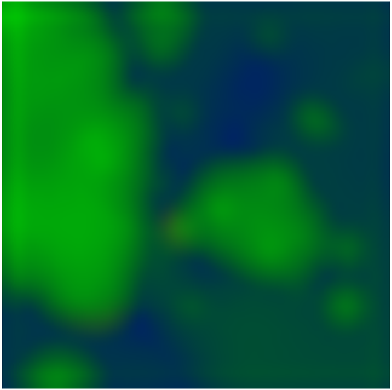

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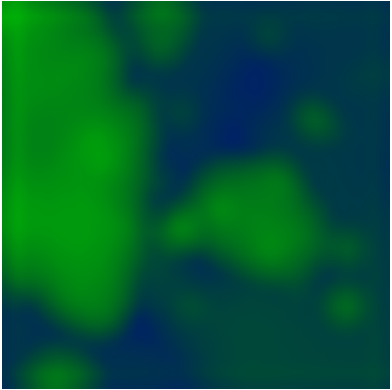

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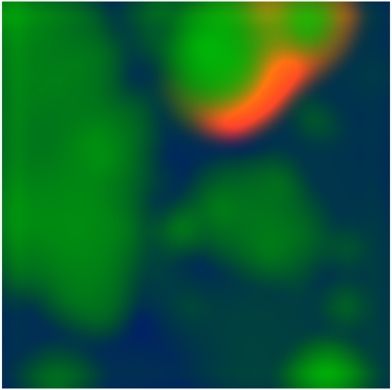

Stochastic 3-state model

Finite, discrete nature of the retina leads to **fluctuations**

Stochastic 3-state model

Finite, discrete nature of the retina leads to **fluctuations**

Restore fluctuation effects as **noise**

- State transition $\sim$ **Poisson**
- Variance $=$ mean $\sim$ rate $\cdot$ concentration

Stochastic 3-state model

Finite, discrete nature of the retina leads to **fluctuations**

Restore fluctuation effects as **noise**

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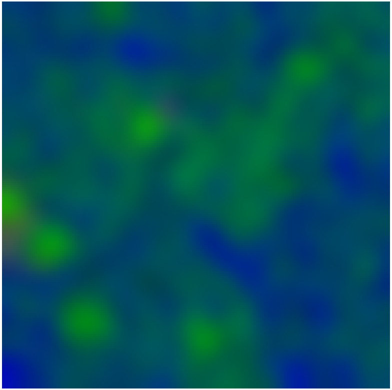
Langevin approximation:

- Approximate Poisson (jump) noise with Gaussian (continuous)
- Fluctuations $\sim \mathcal{O}\left(\sqrt{N}\right)$ for N transitions

Stochastic 3-state model recapitulates retinal waves



Quiescent

Active

Refractory

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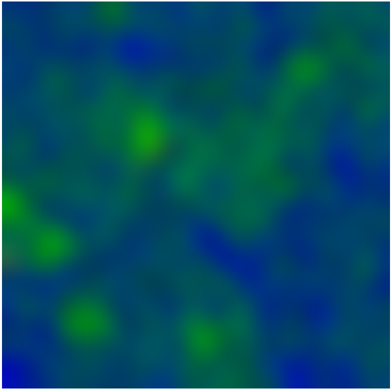

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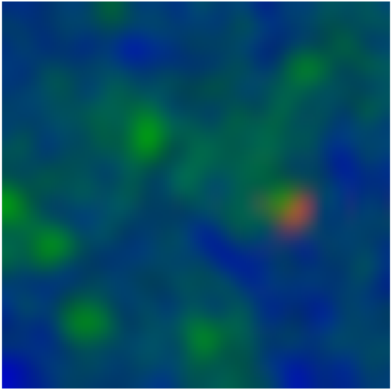

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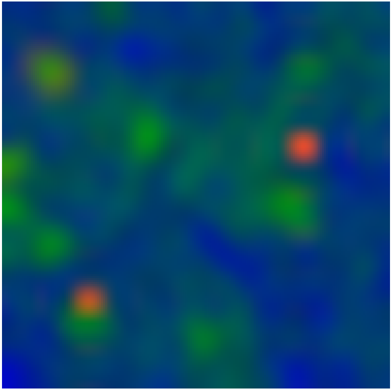

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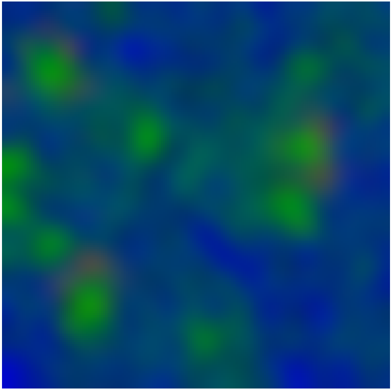

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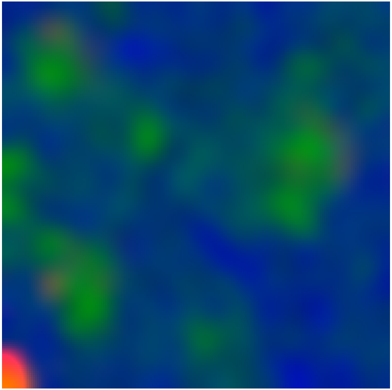

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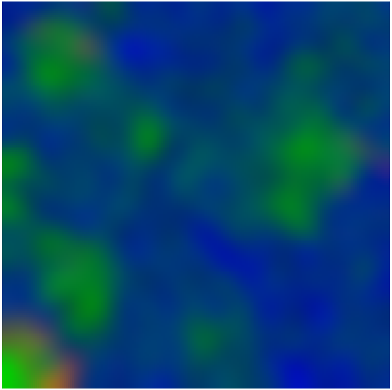

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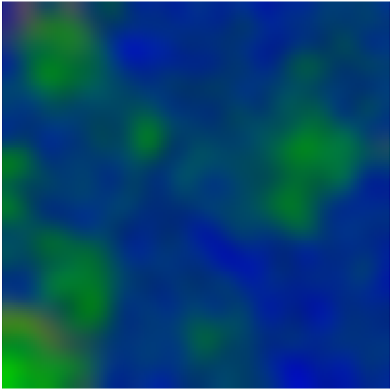

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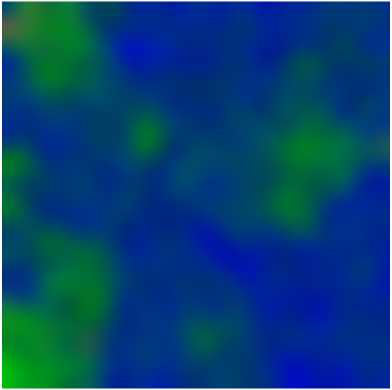

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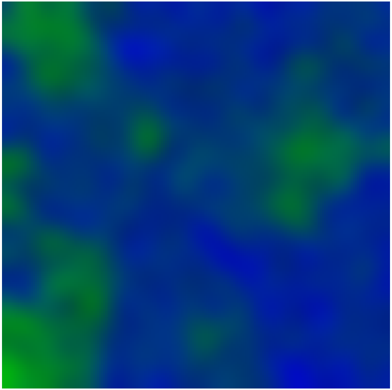

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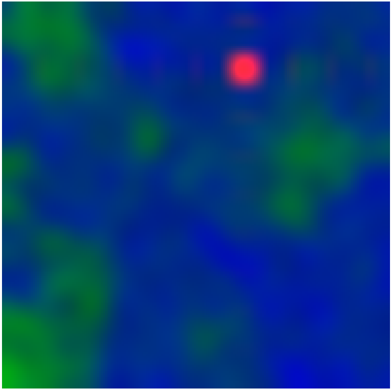

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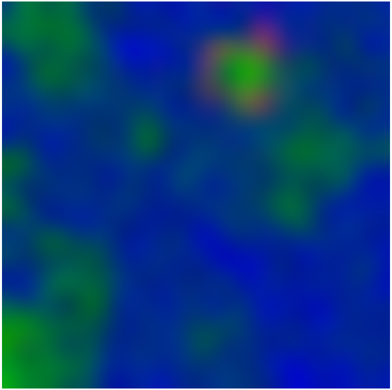

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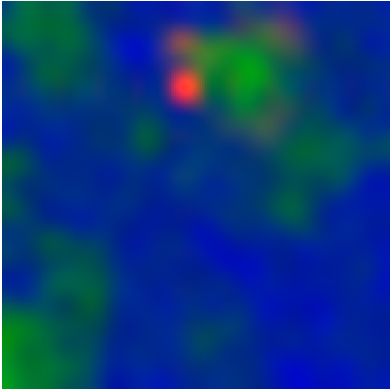

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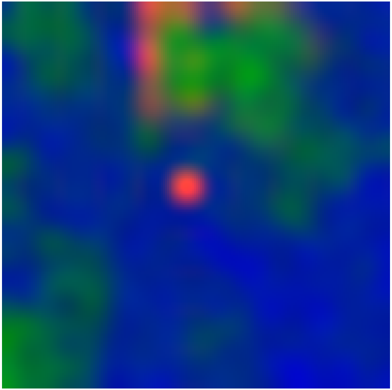

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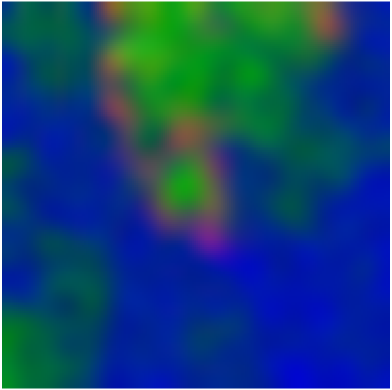

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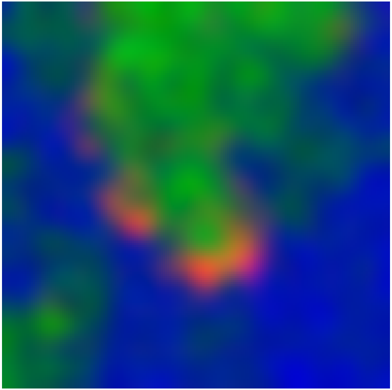

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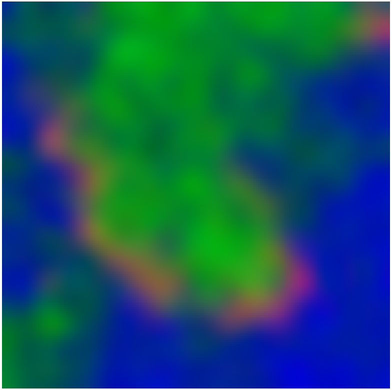

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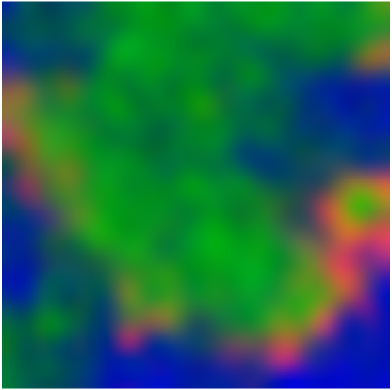

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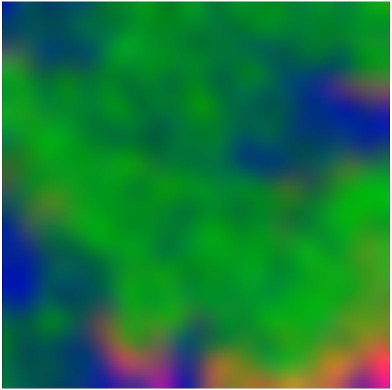

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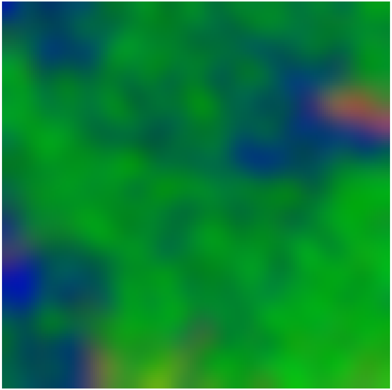

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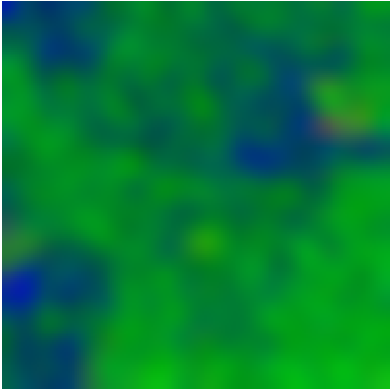

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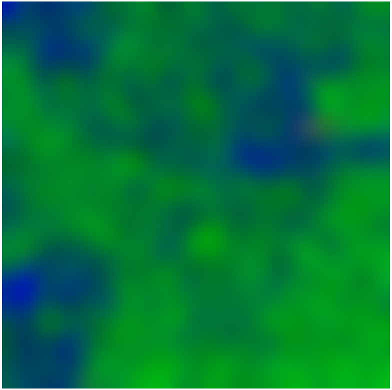

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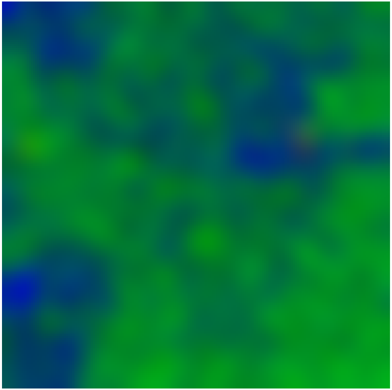

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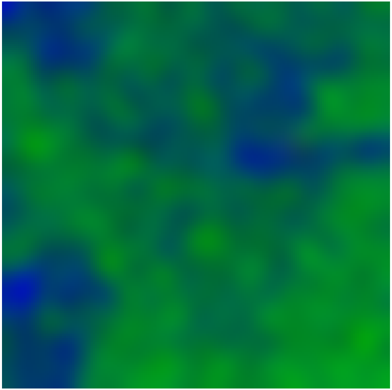

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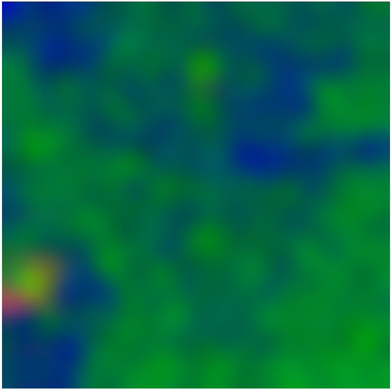

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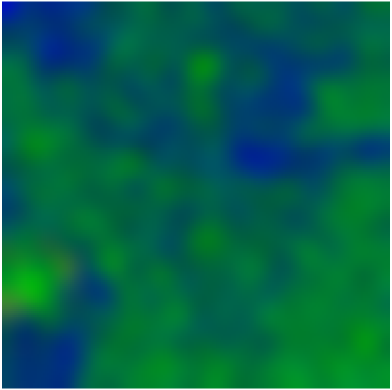

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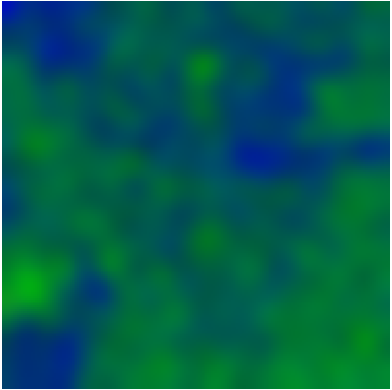

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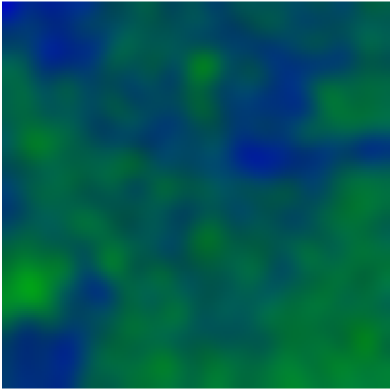

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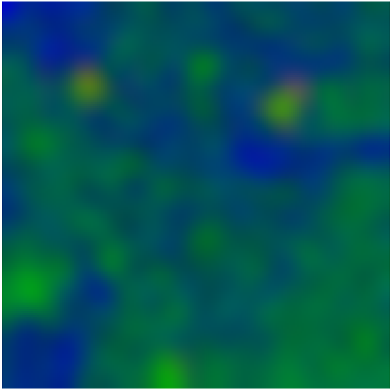

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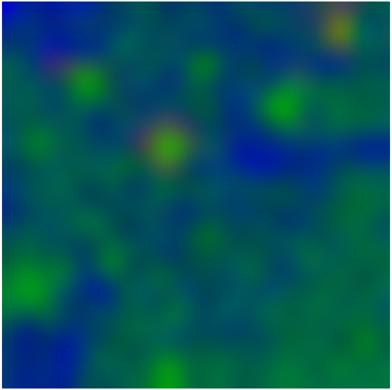

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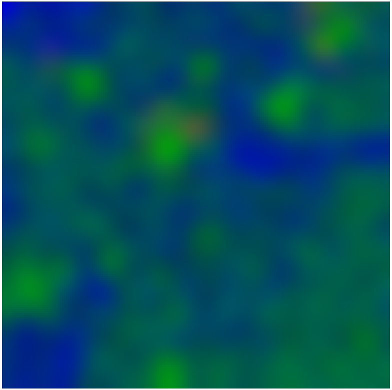

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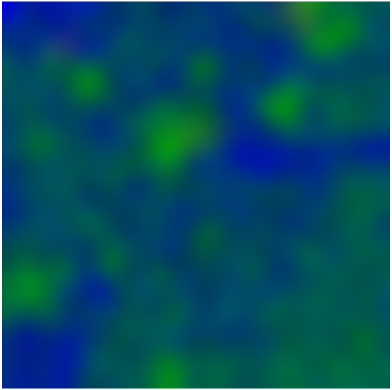

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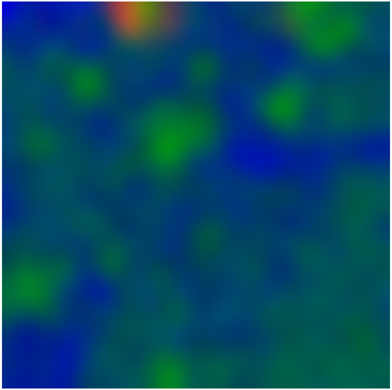

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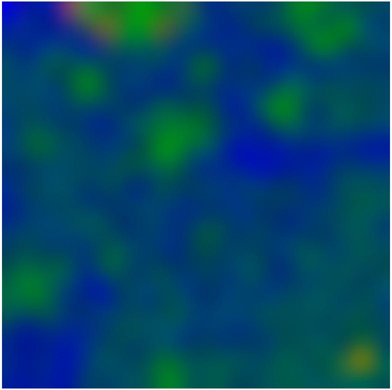

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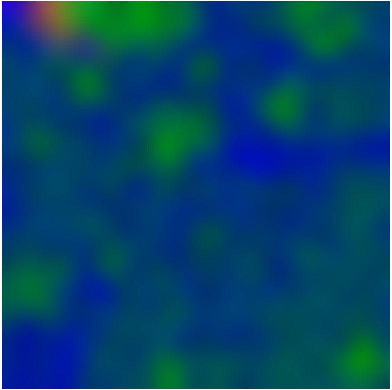

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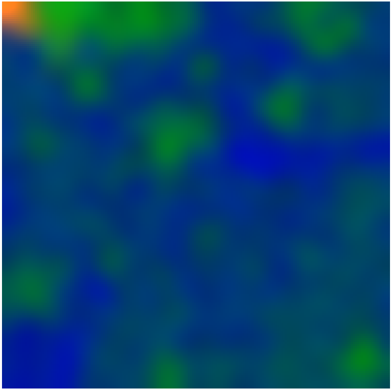

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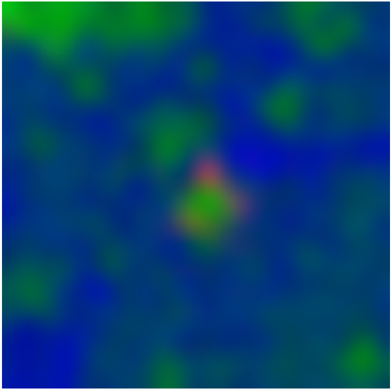

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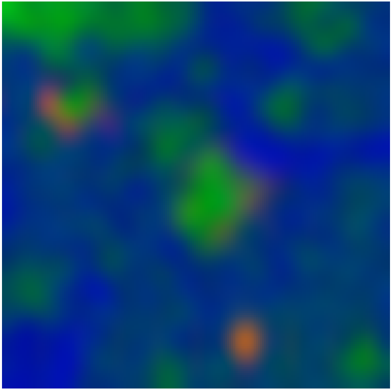

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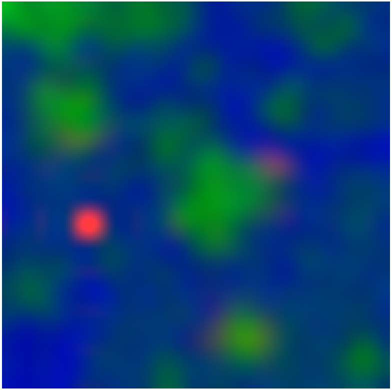

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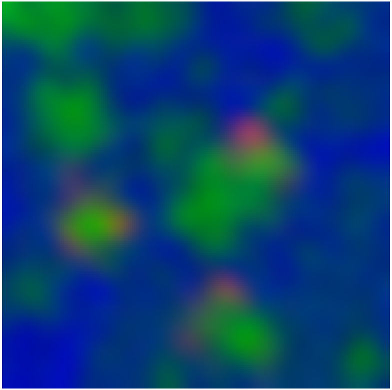

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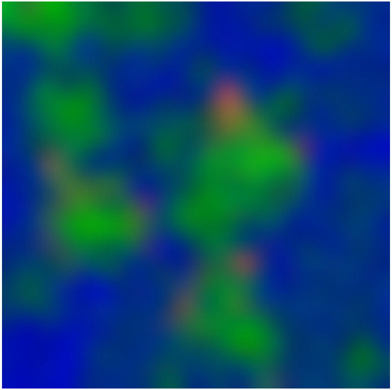

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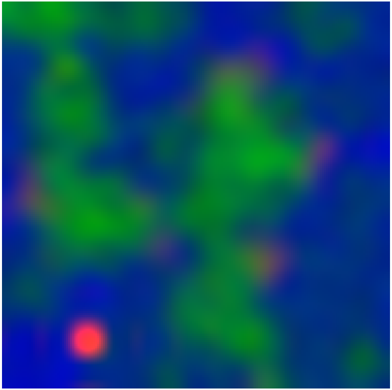

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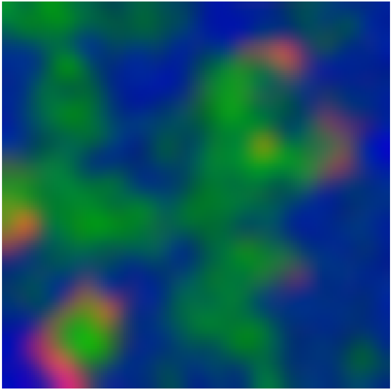

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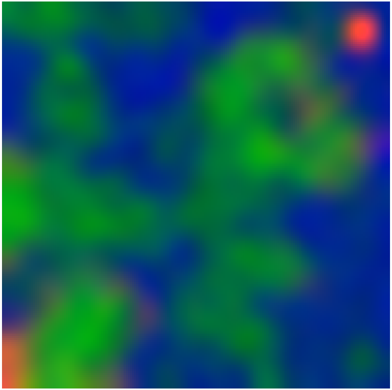

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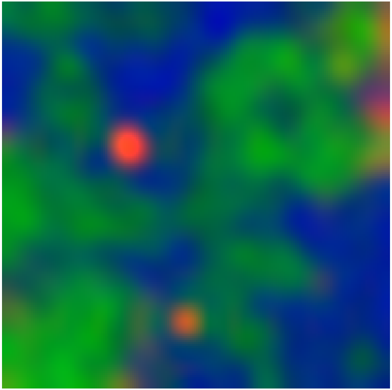

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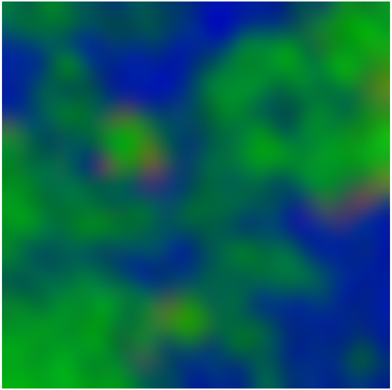

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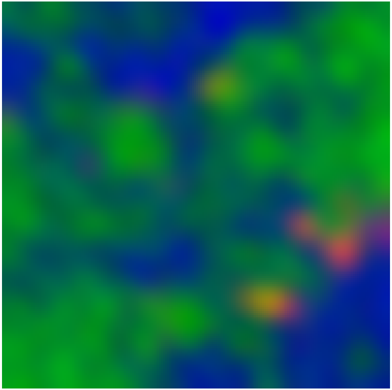

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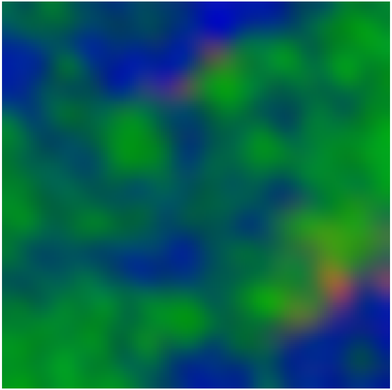

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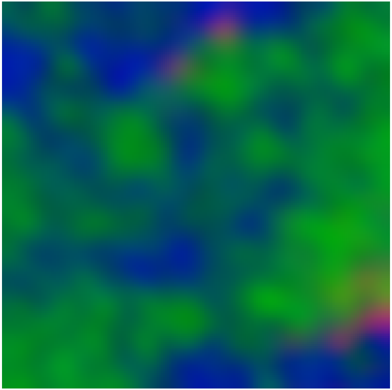

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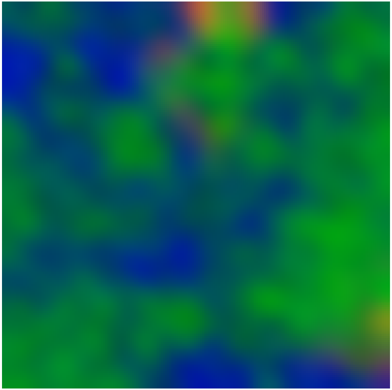

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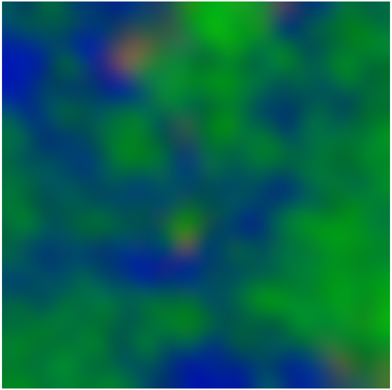

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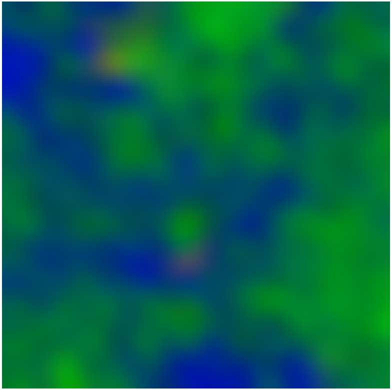

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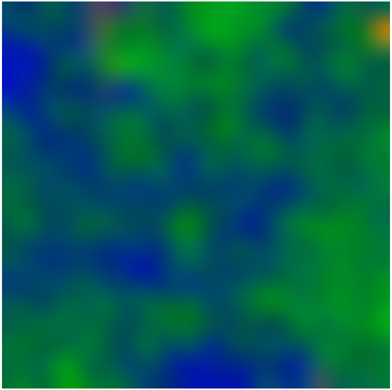

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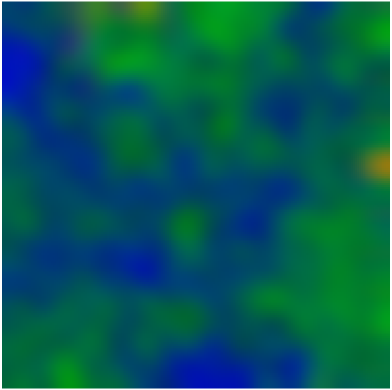

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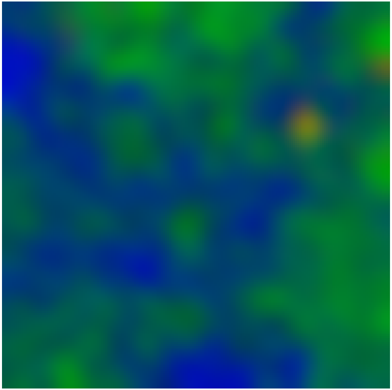

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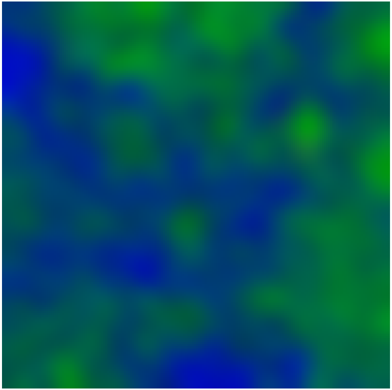

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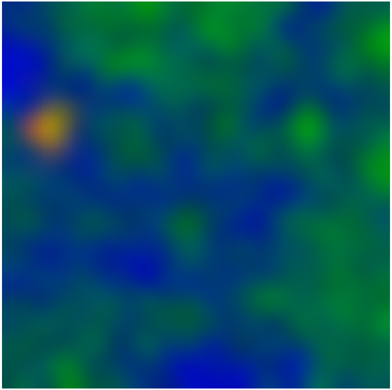

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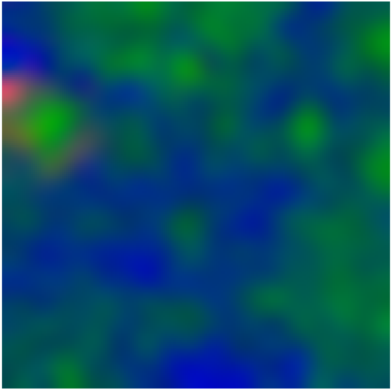

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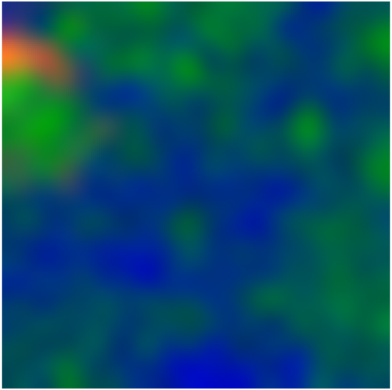

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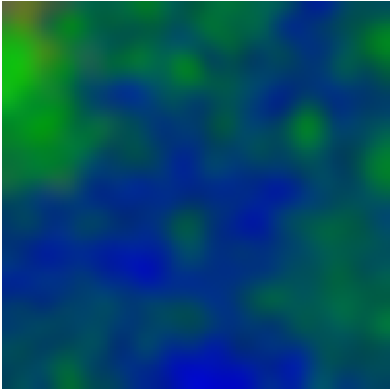

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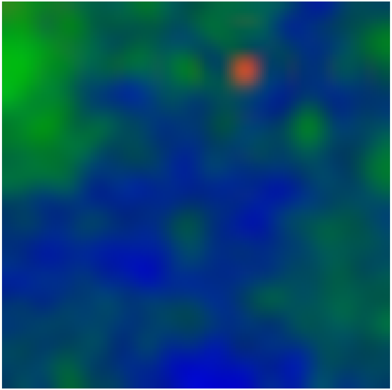

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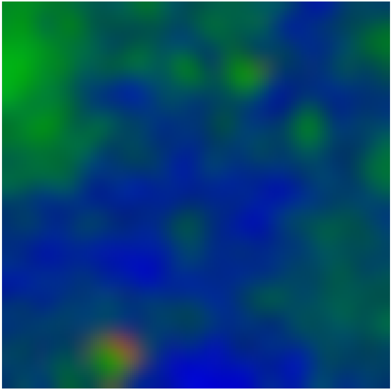

Quiescent

Active

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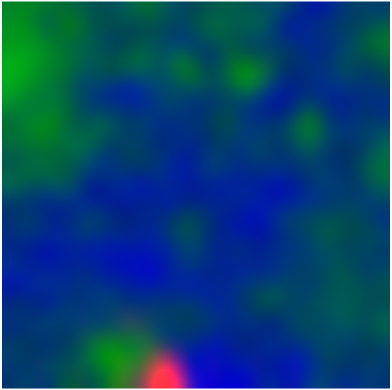

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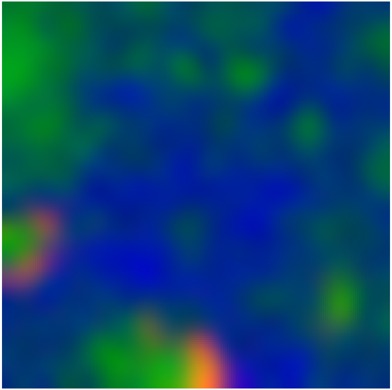

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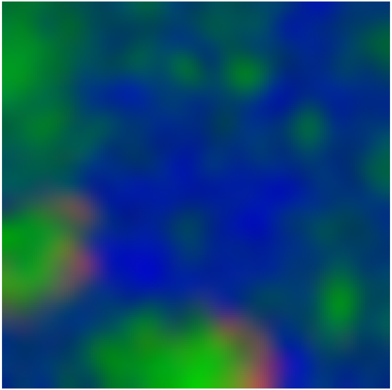

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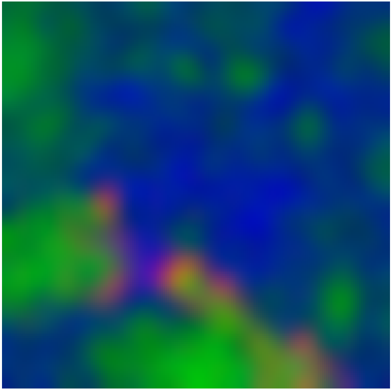

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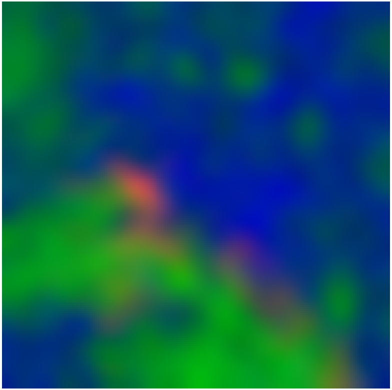

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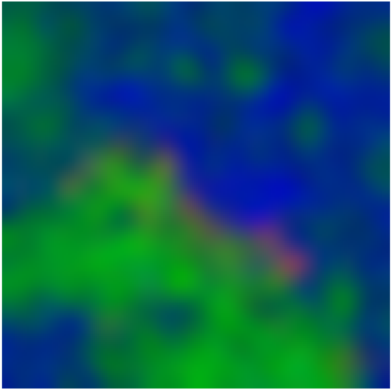

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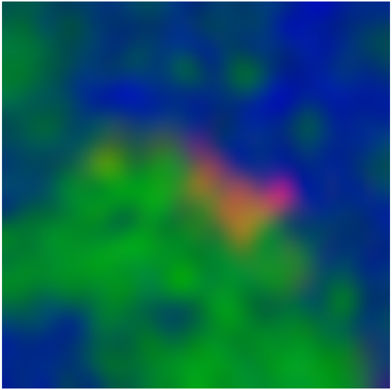

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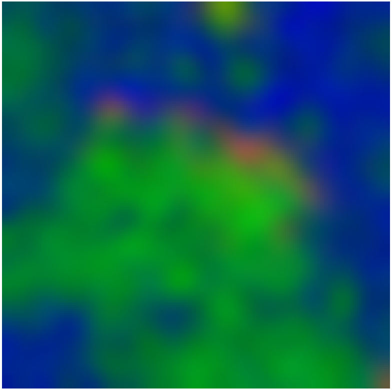

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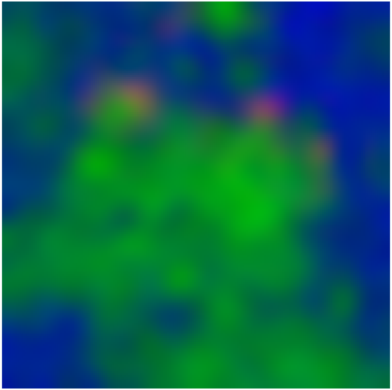

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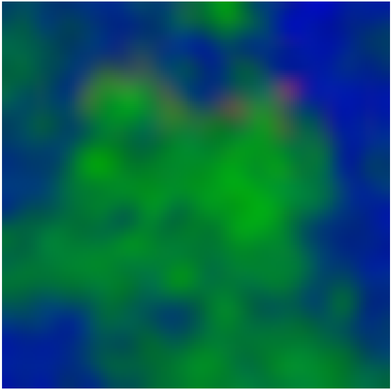

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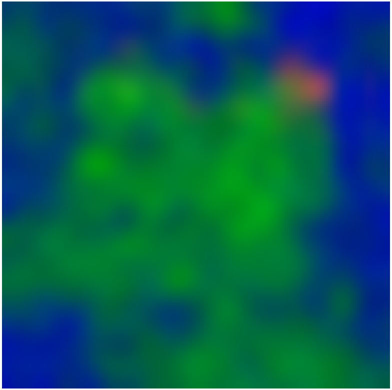

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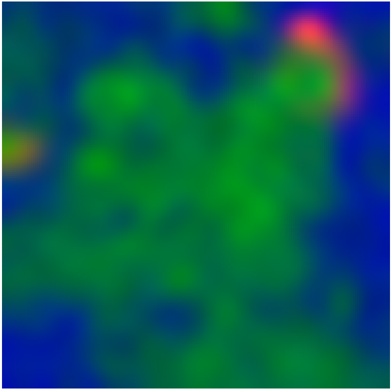

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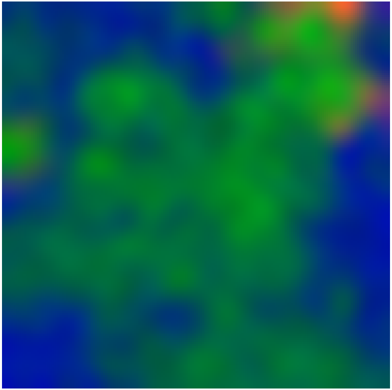

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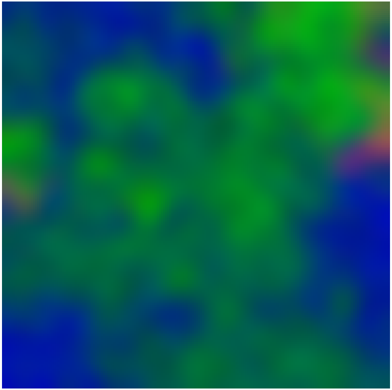

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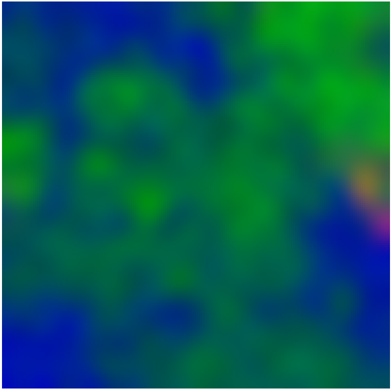

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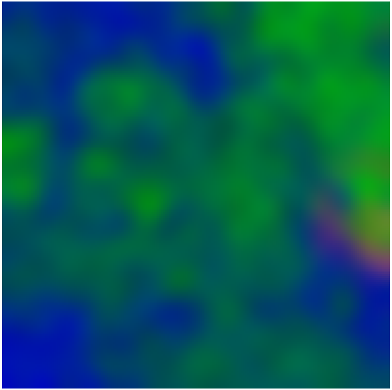

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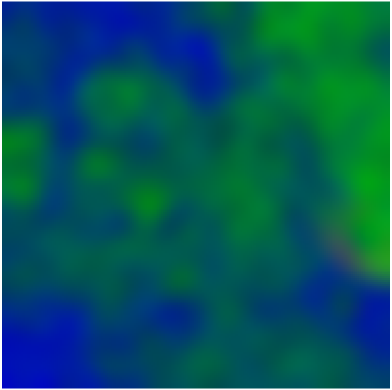

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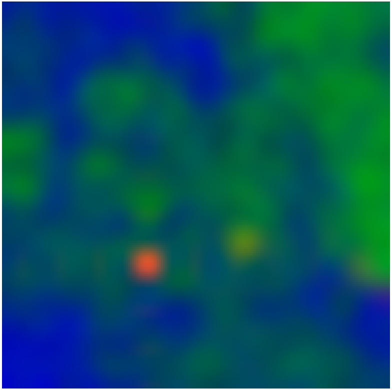

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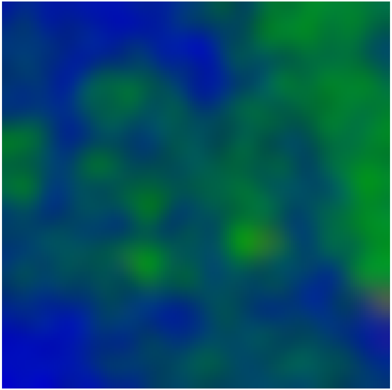

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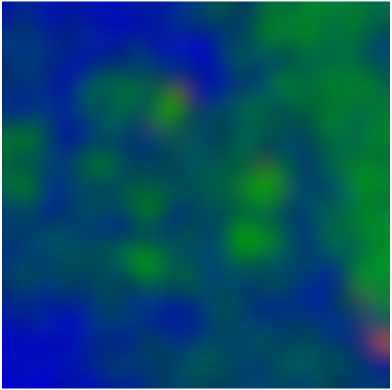

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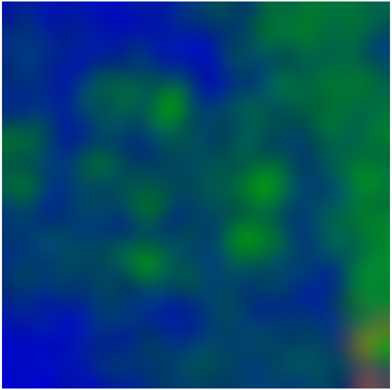

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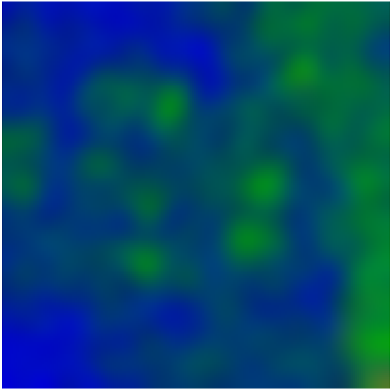

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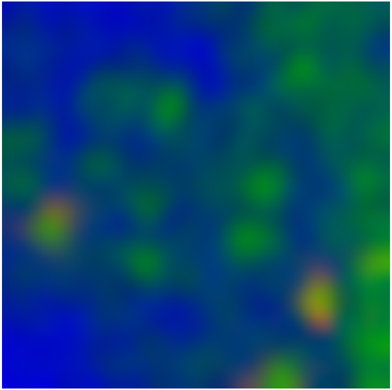

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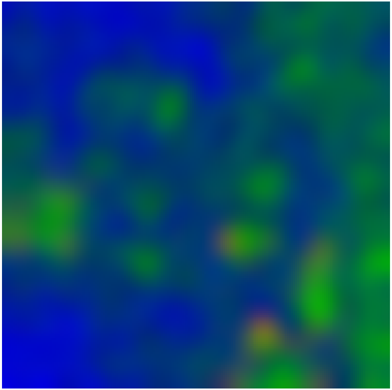

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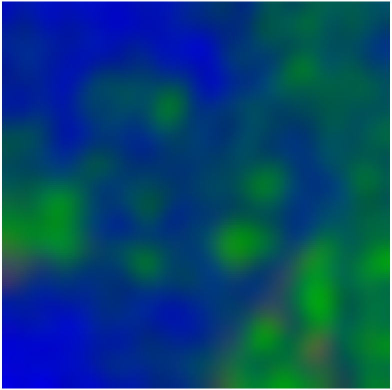

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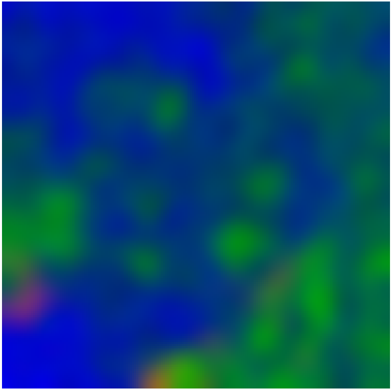

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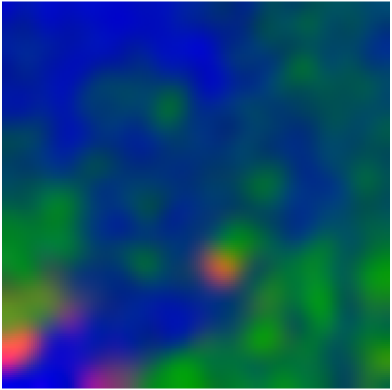

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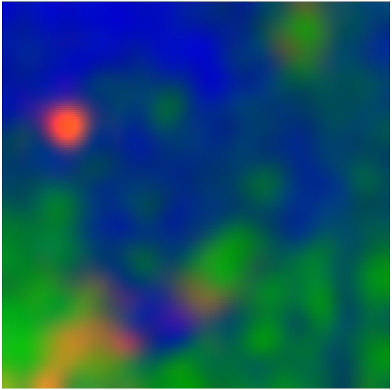

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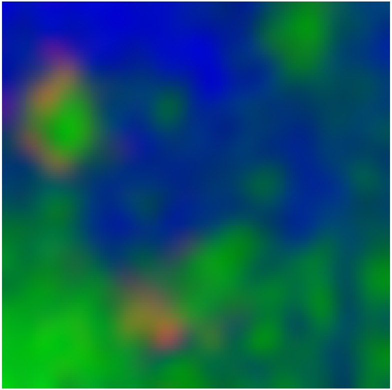

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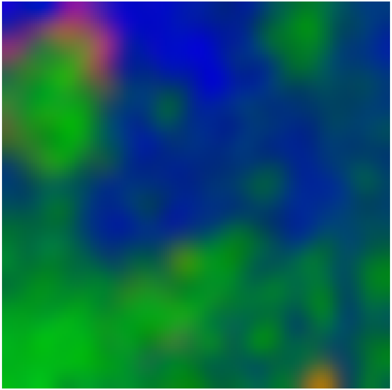

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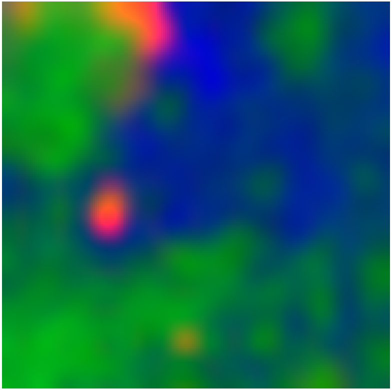

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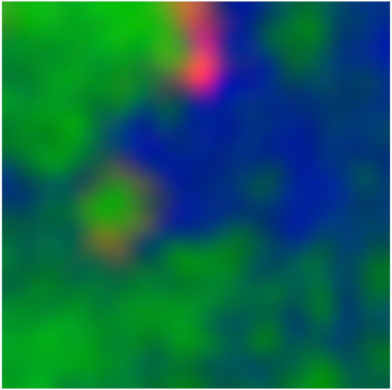

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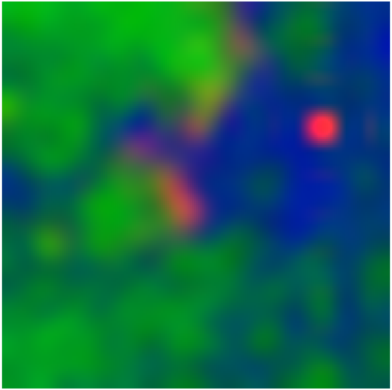

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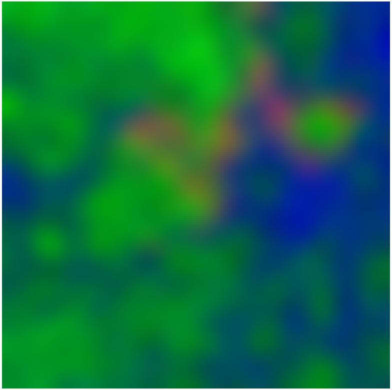

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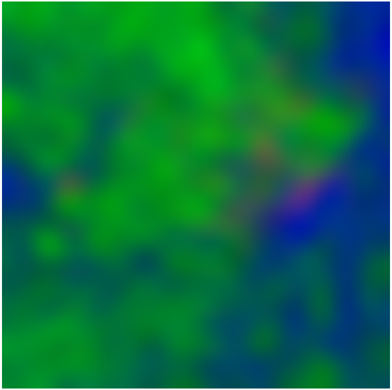

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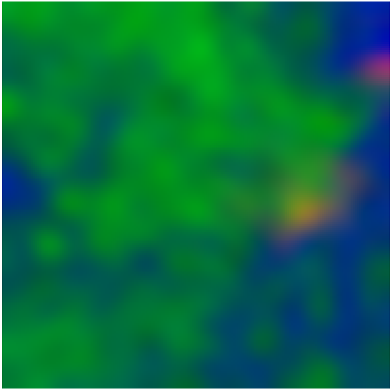

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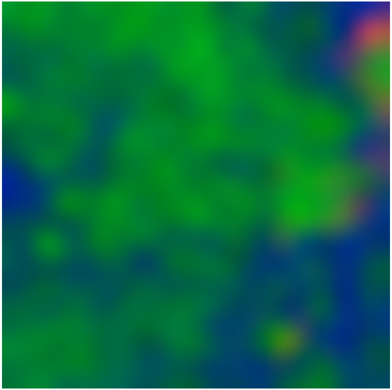

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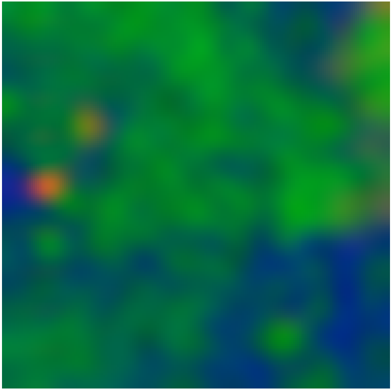

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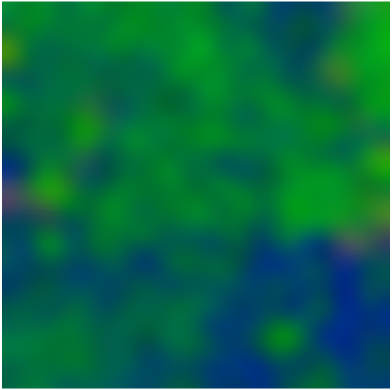

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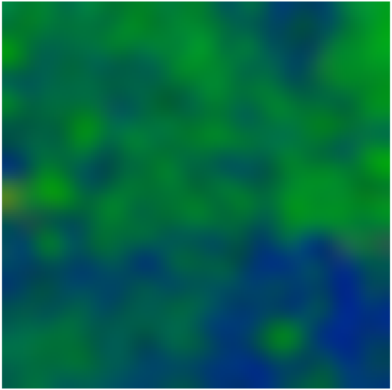

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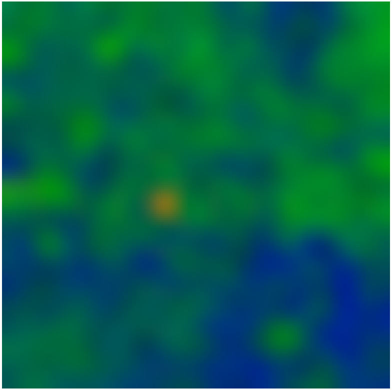

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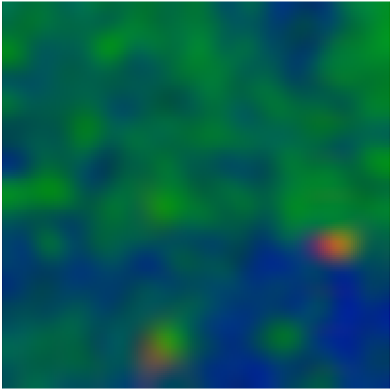

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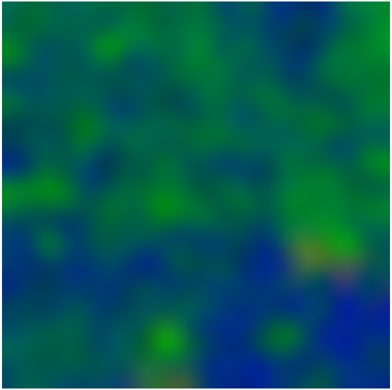

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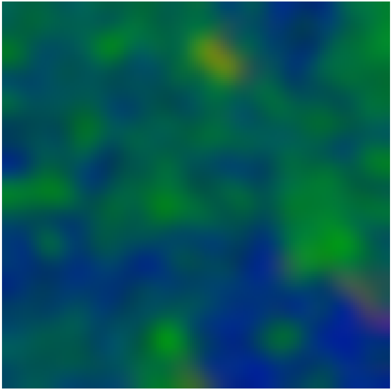

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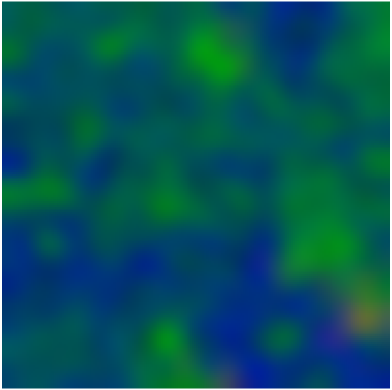

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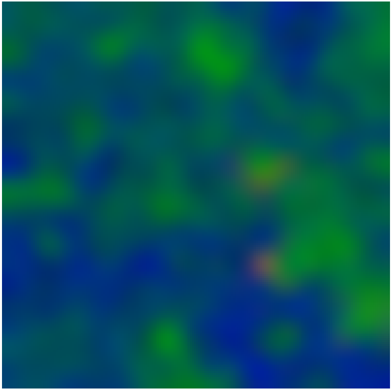

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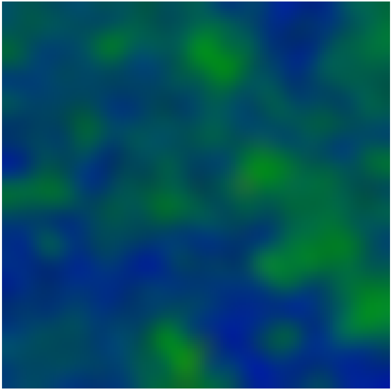

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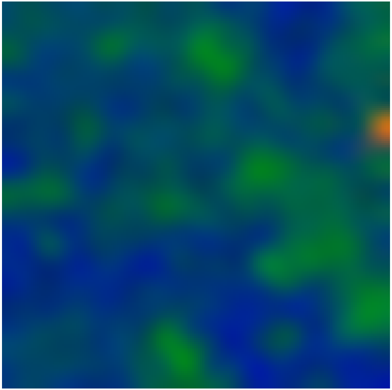

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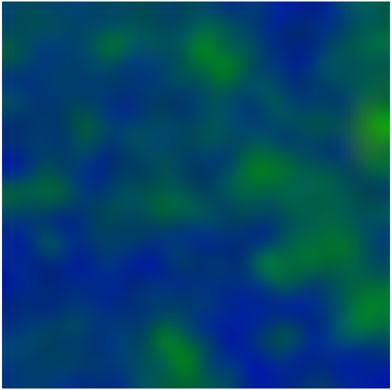

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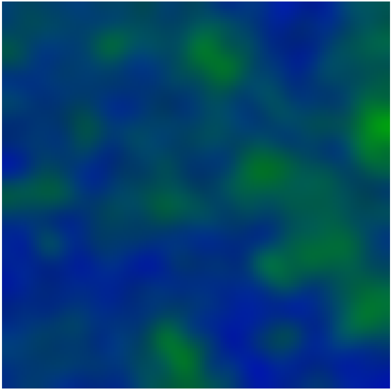

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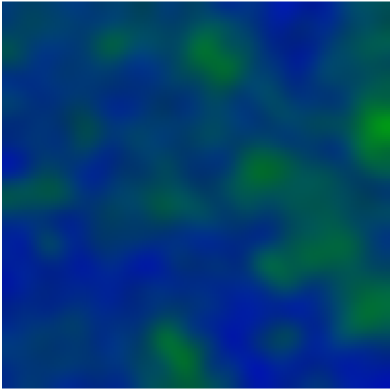

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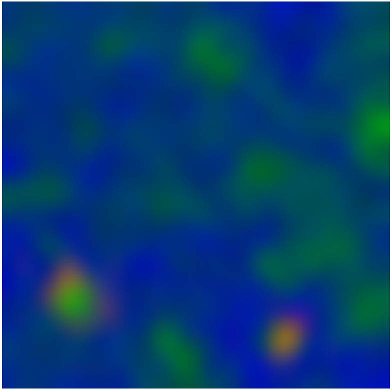

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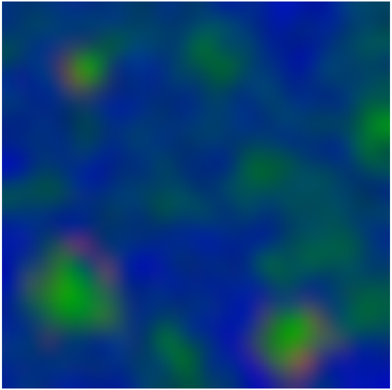

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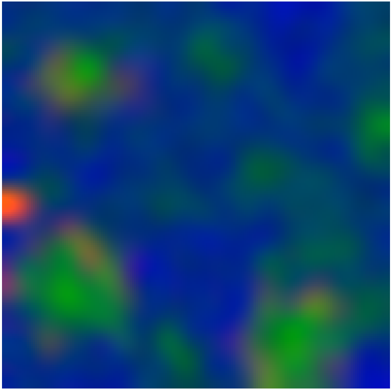

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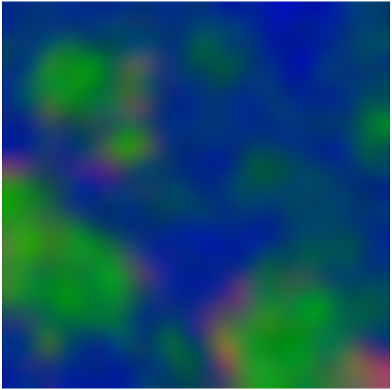

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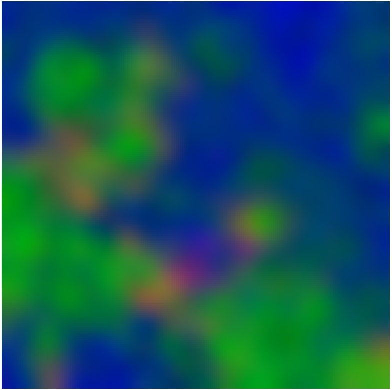

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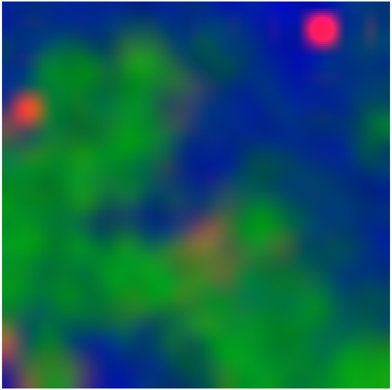

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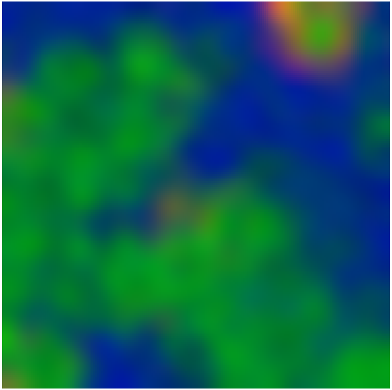

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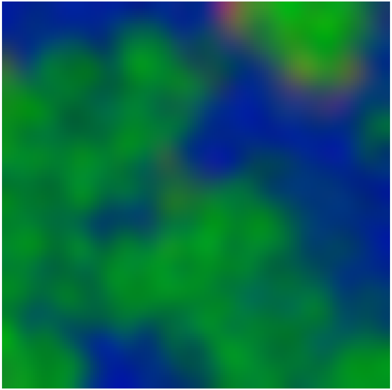

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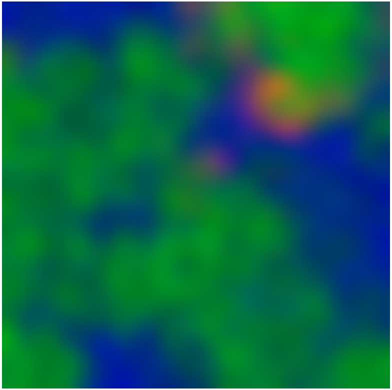

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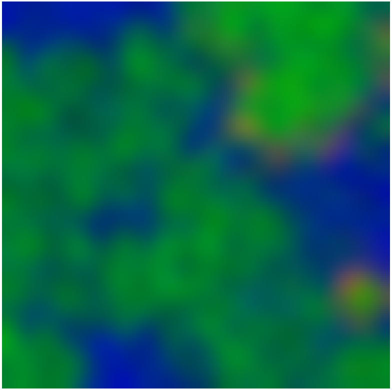

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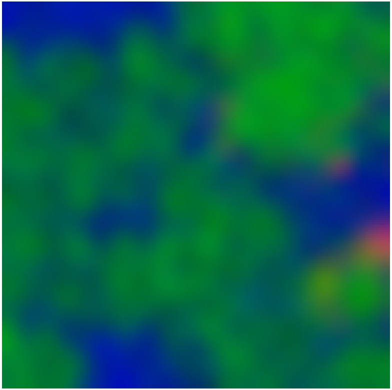
Refractory

Stochastic 3-state model recapitulates retinal waves

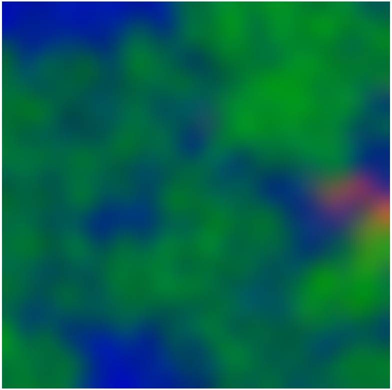


Quiescent

Active

Refractory

Stochastic 3-state model recapitulates retinal waves



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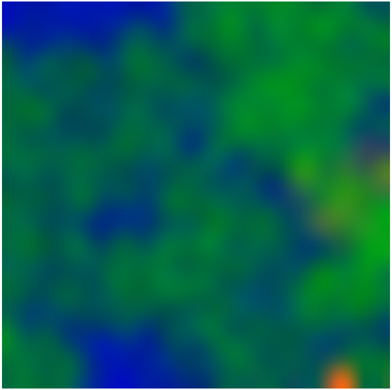

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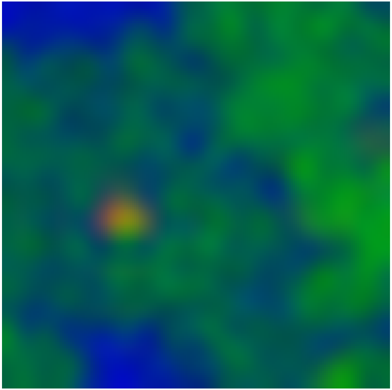

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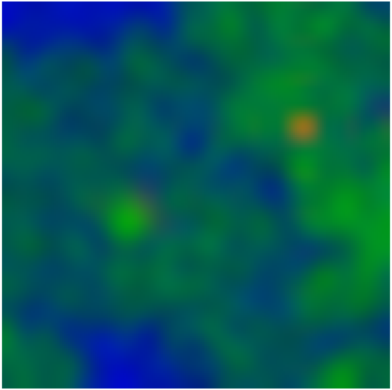

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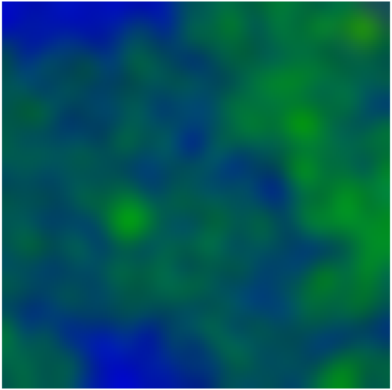

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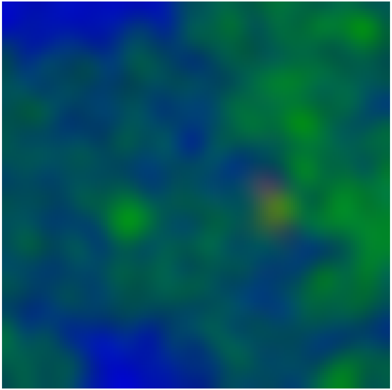
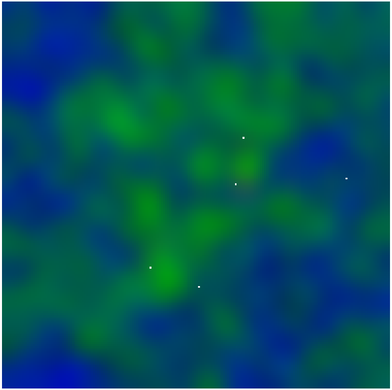


Quiescent

Active

Refractory

Cox process assumption: spike rates $\propto$ I field



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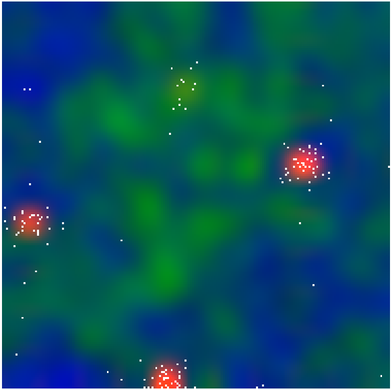

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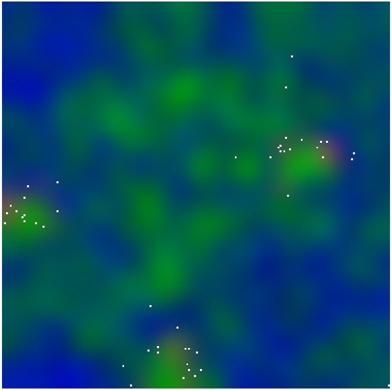

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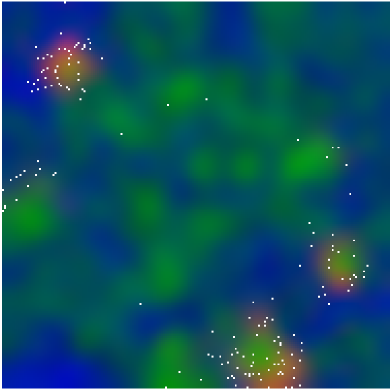

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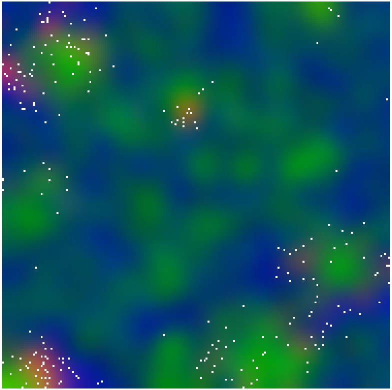

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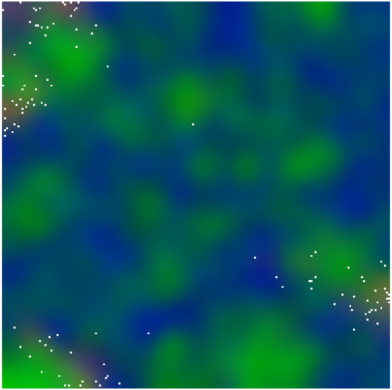

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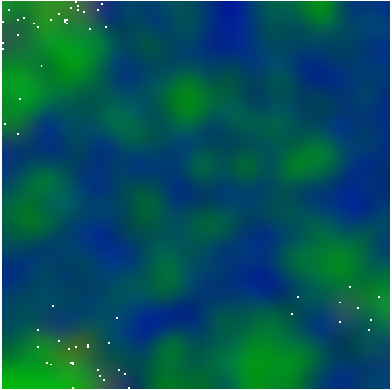

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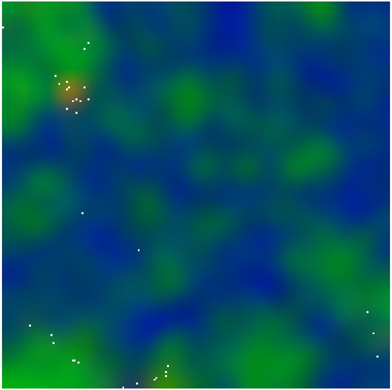

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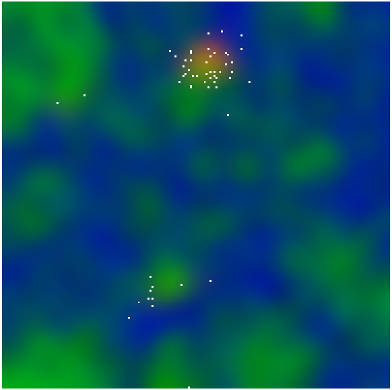

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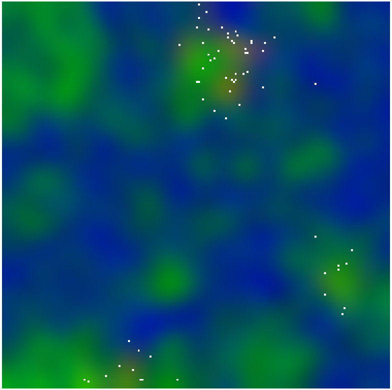

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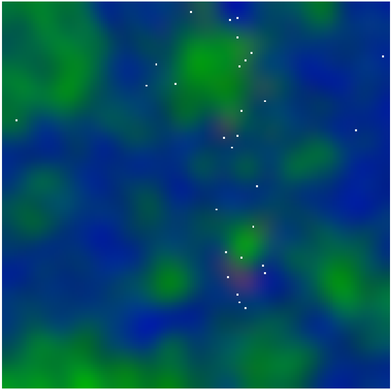

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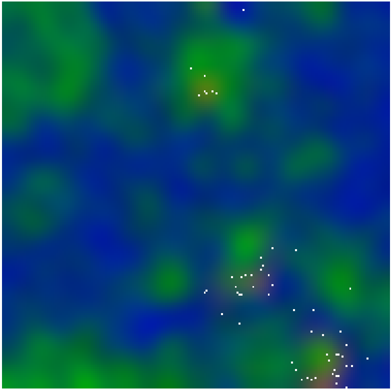

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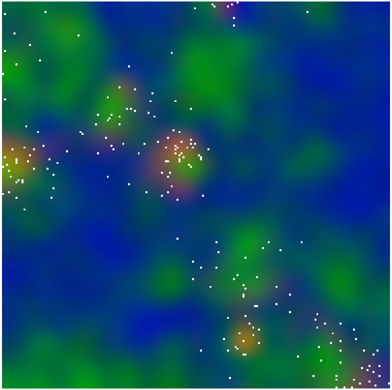

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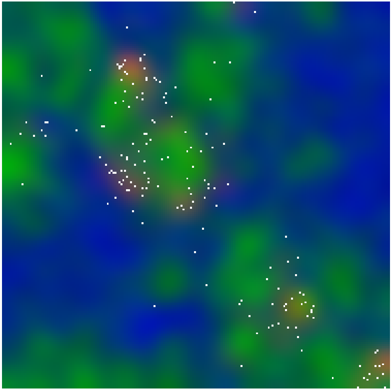

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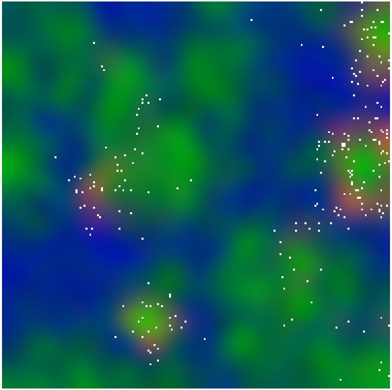

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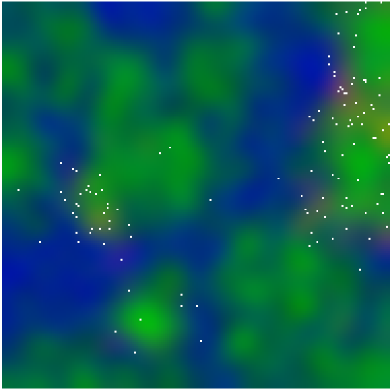

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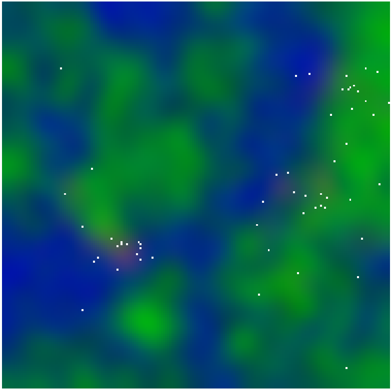

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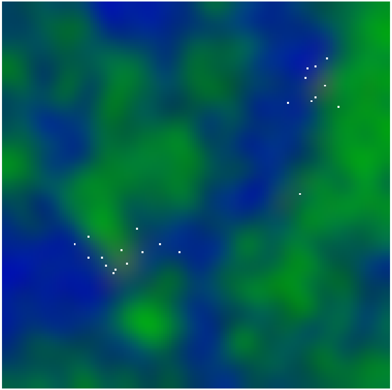

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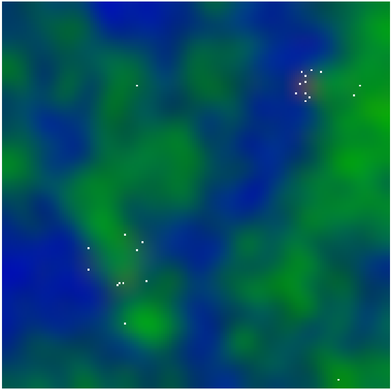

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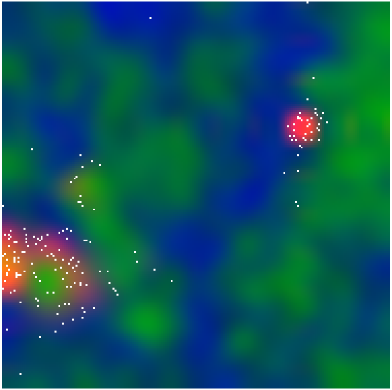

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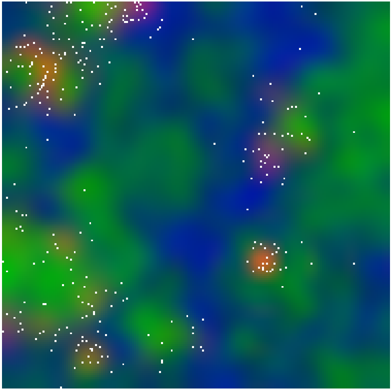

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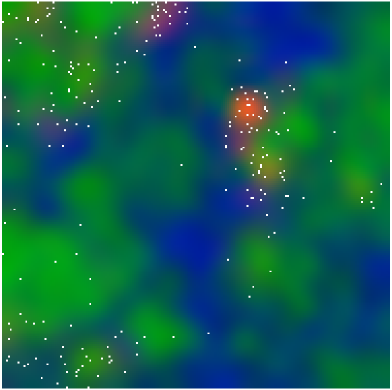

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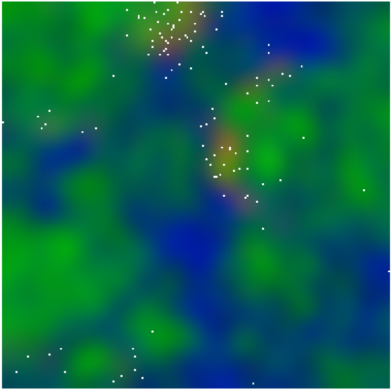
Refractory

Cox process assumption: spike rates $\propto I$ field



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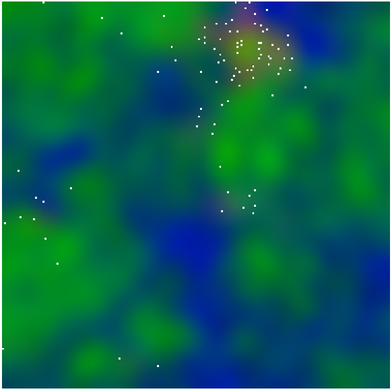
Refractory

Cox process assumption: spike rates ∝ I field



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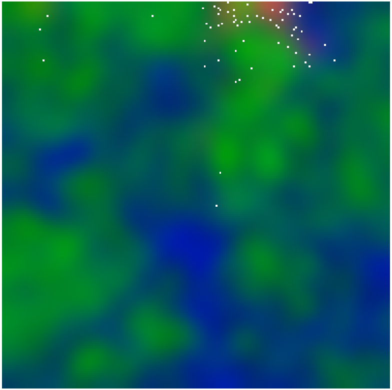

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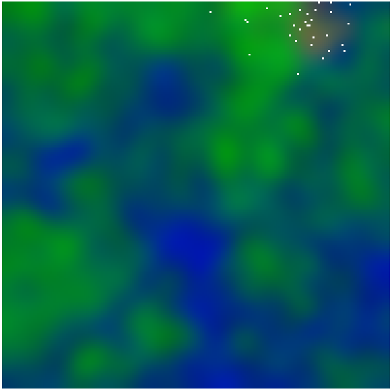

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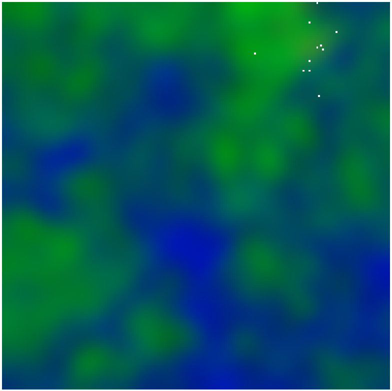

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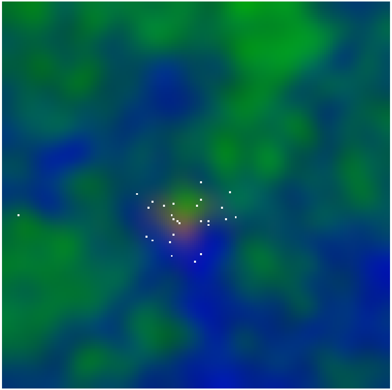

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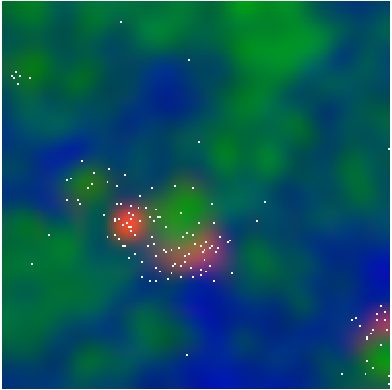

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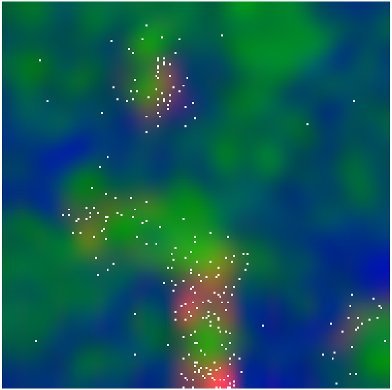

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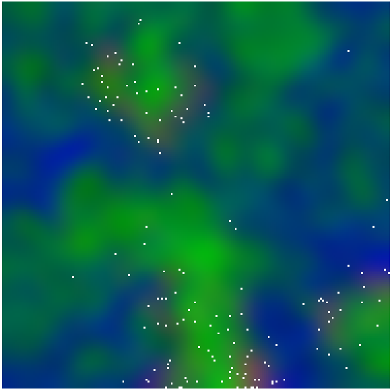

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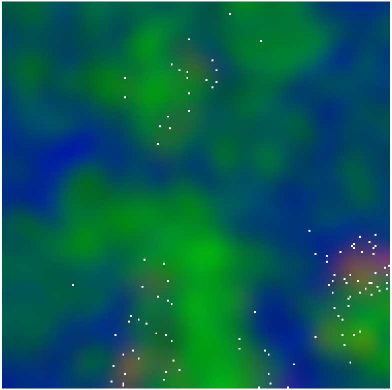

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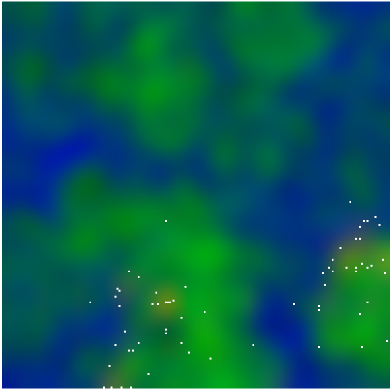

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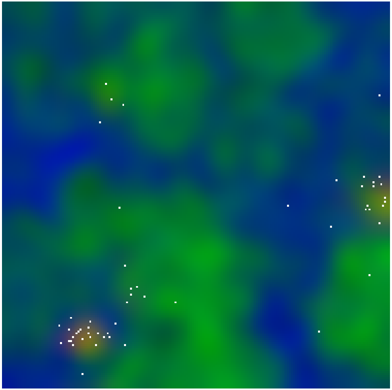

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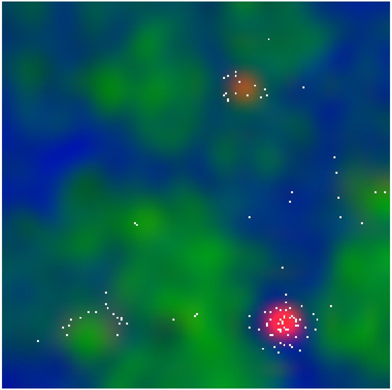

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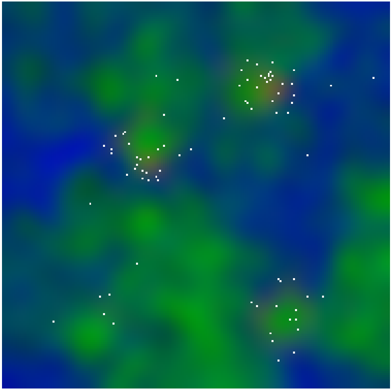

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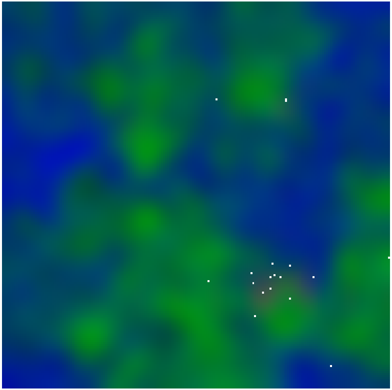

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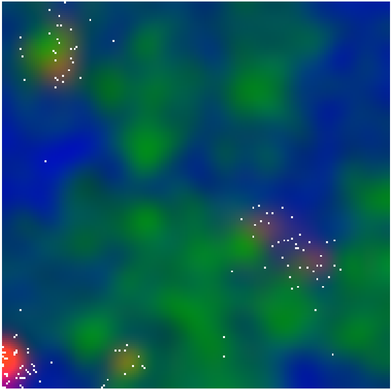

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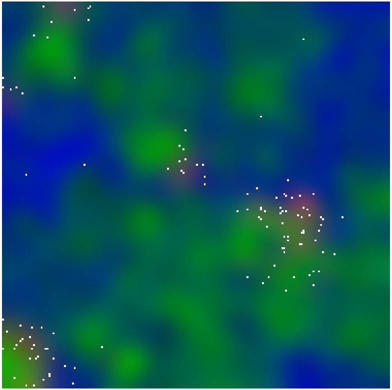

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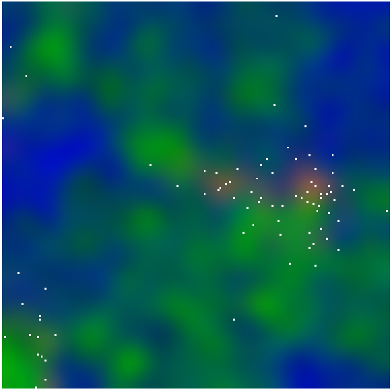

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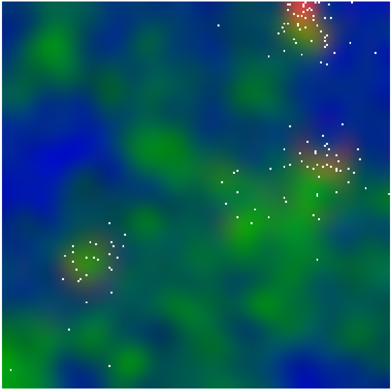

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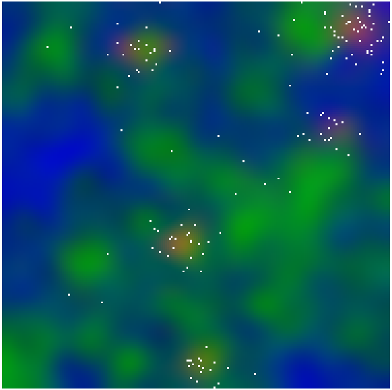

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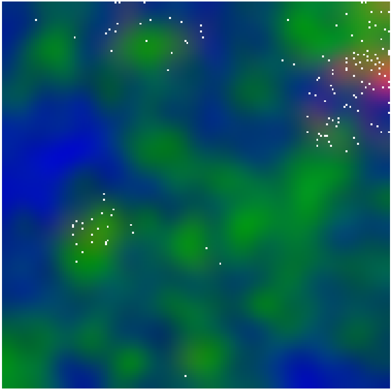

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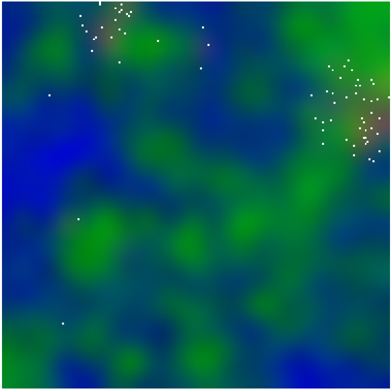

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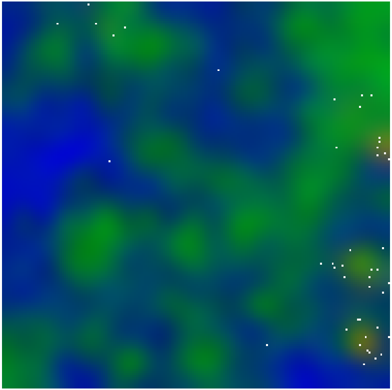

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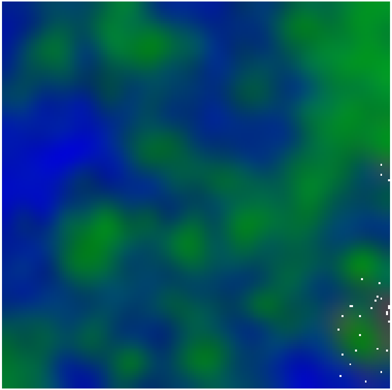

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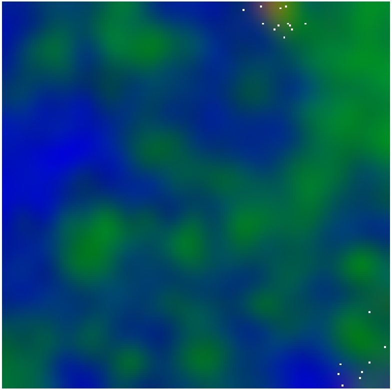

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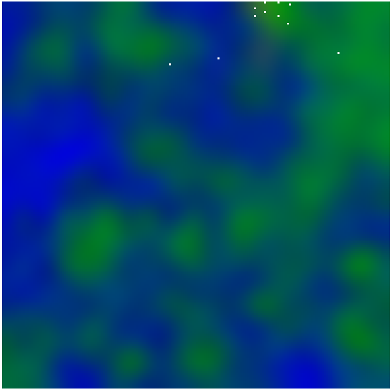

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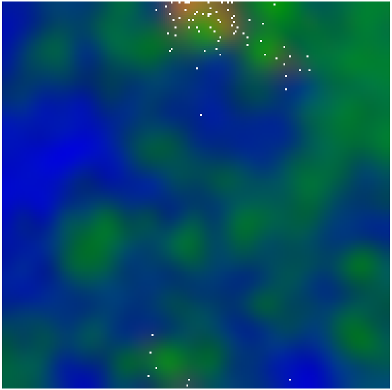

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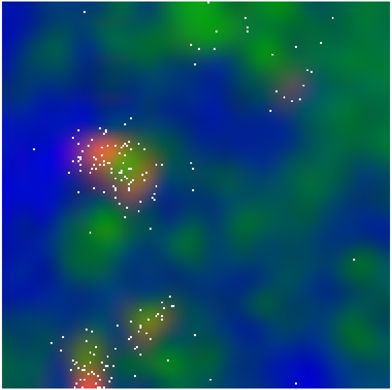

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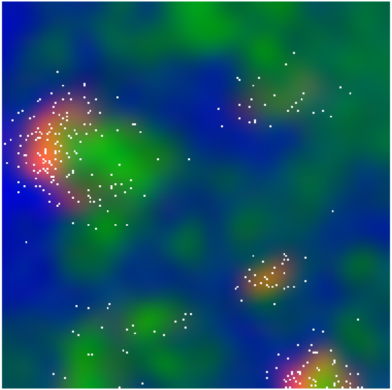

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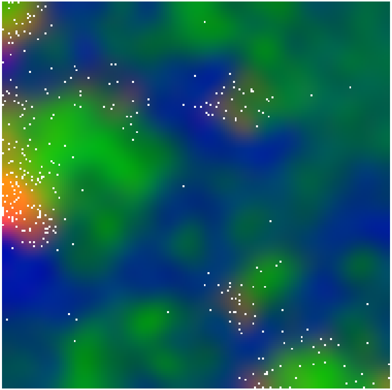

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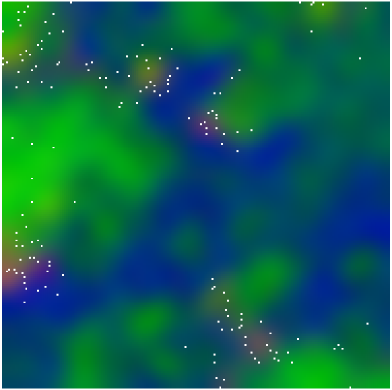

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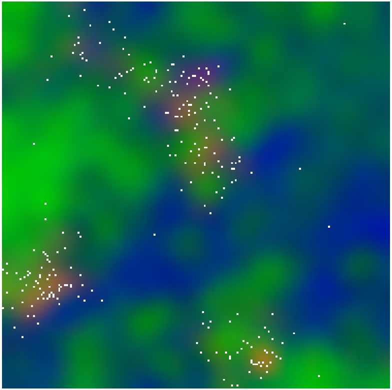

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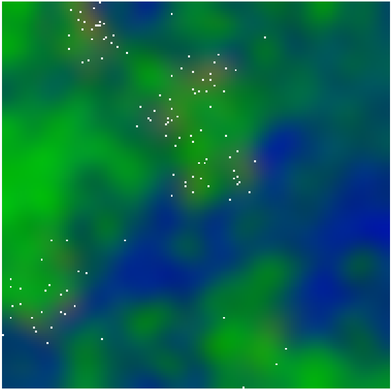

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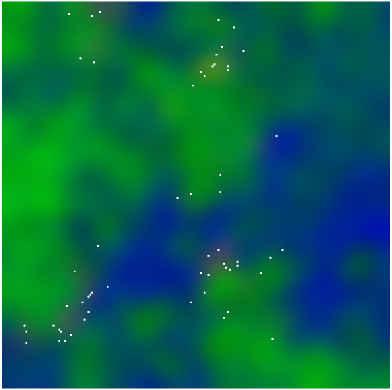
Cox process assumption: spike rates $\propto$ I field



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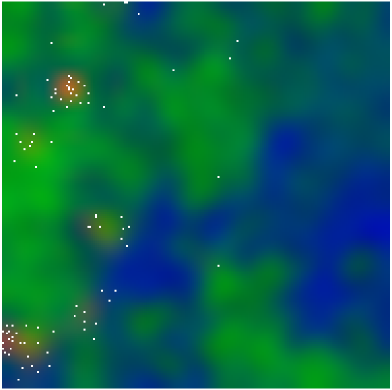
Active

Refractory

Cox process assumption: spike rates $\propto$ I field



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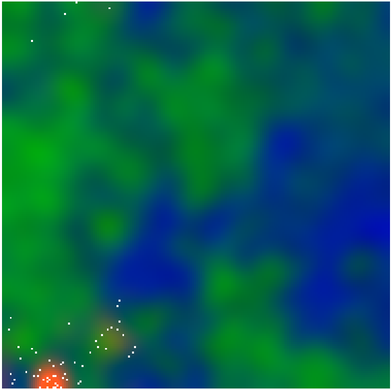
Cox process assumption: spike rates $\propto I$ field



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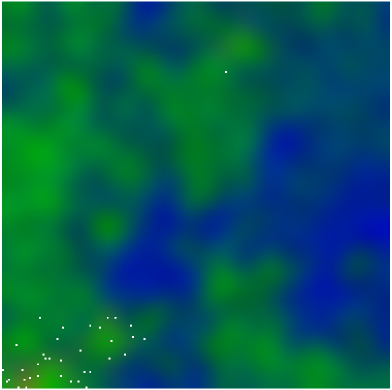

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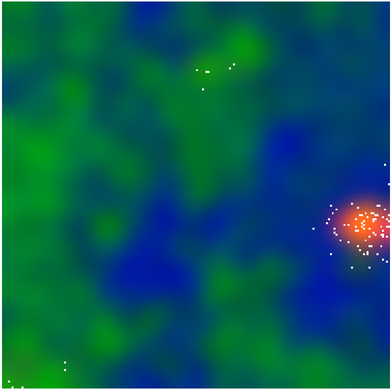

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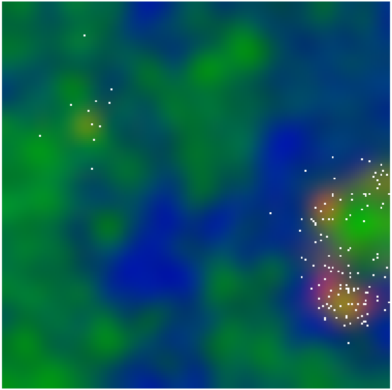

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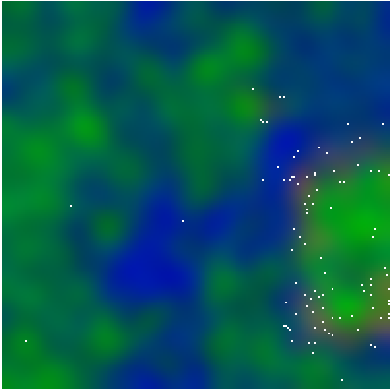

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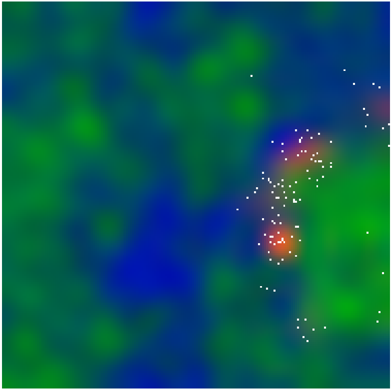

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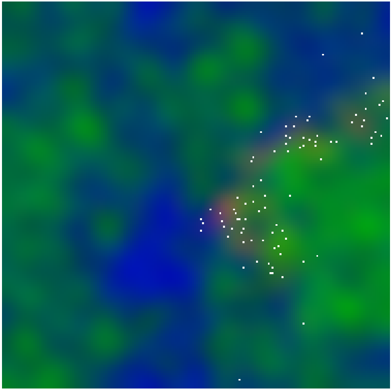

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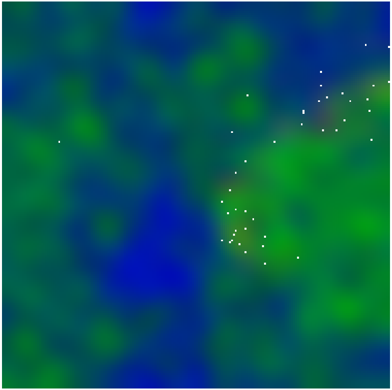

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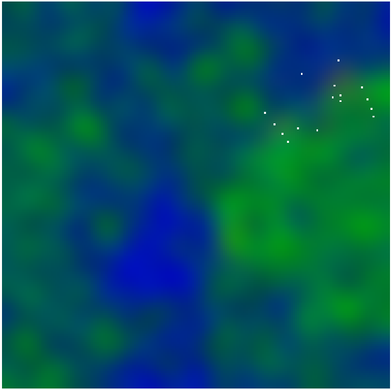

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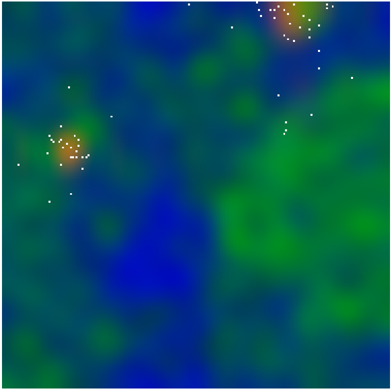

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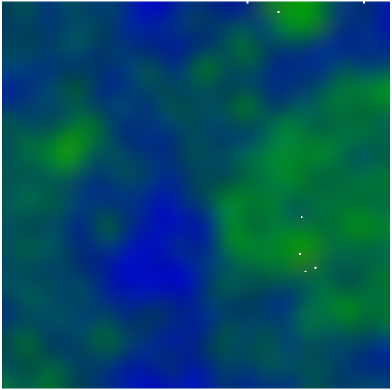

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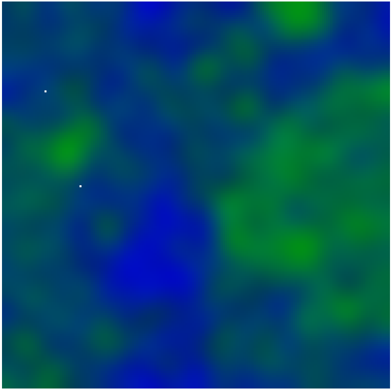

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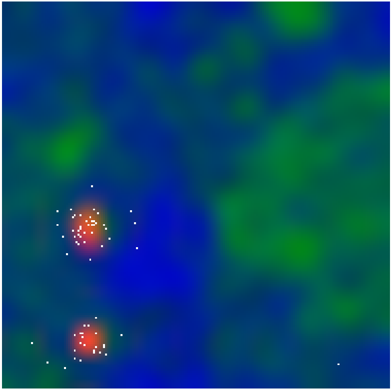

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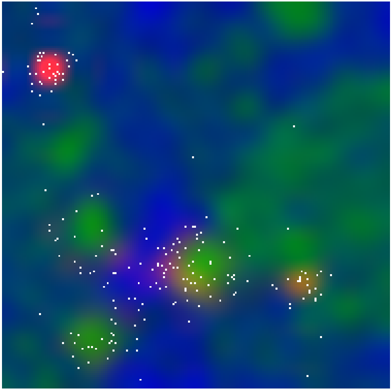

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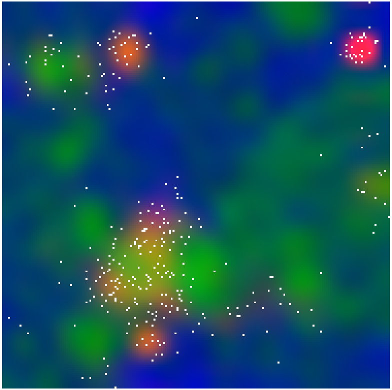

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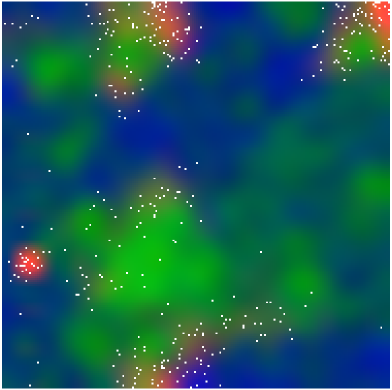

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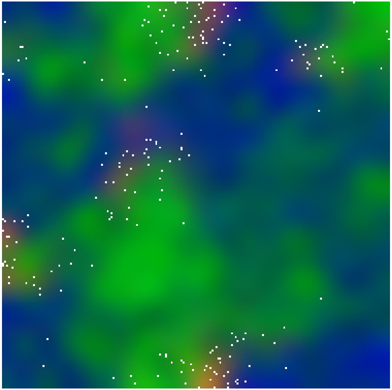

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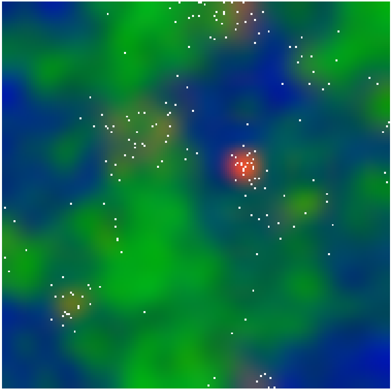

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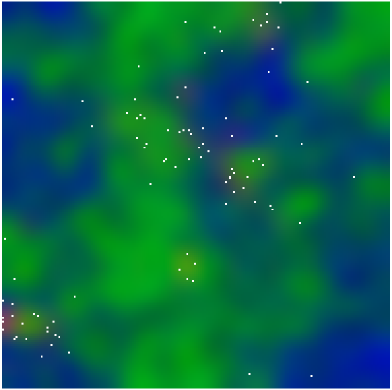

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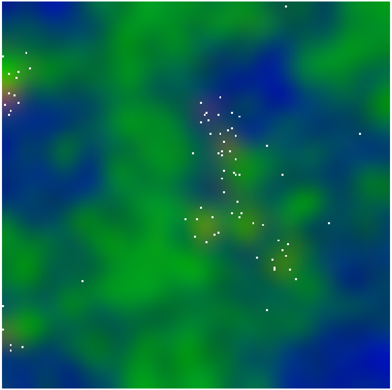

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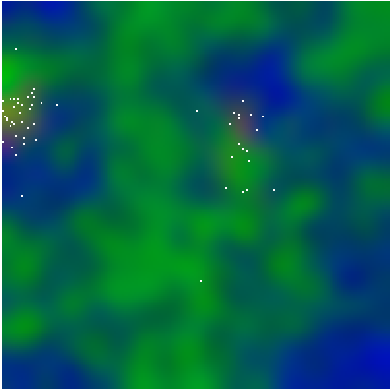

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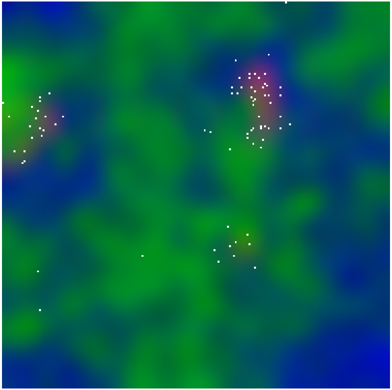

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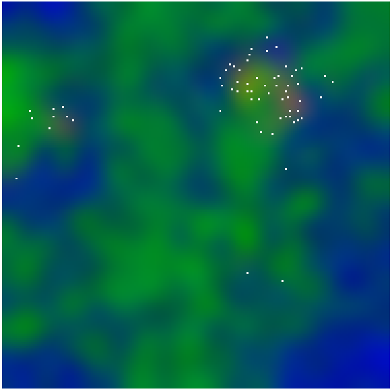

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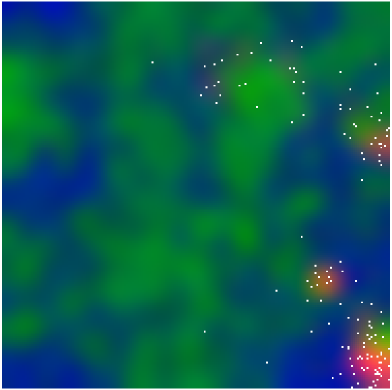

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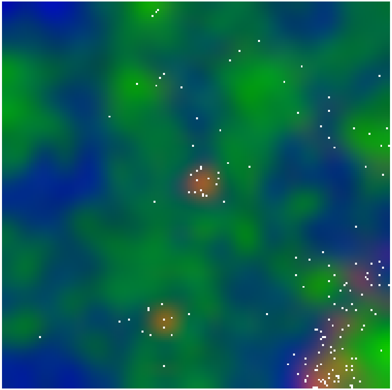

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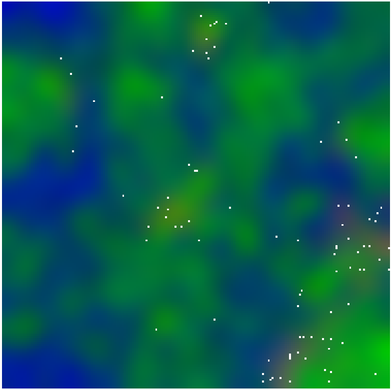

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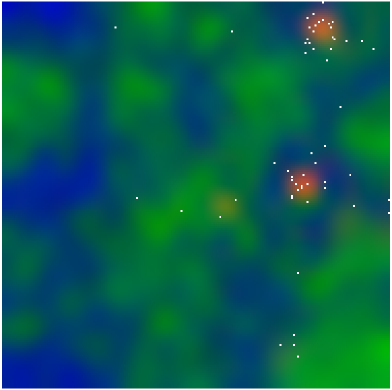

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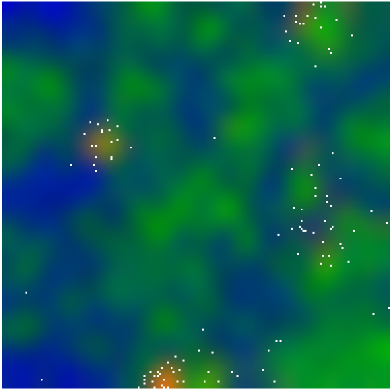

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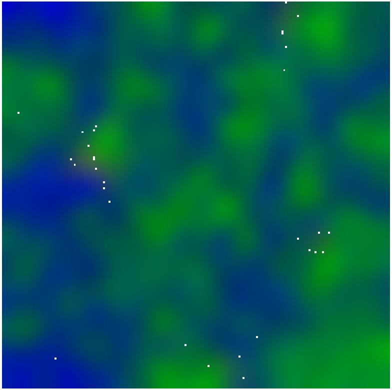

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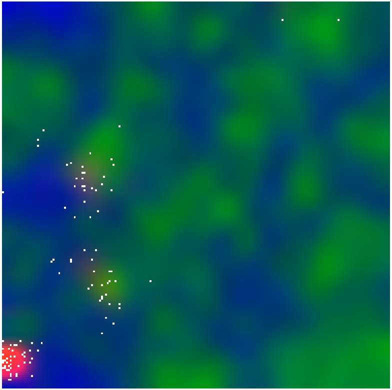

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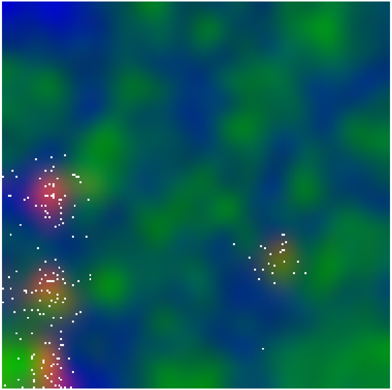

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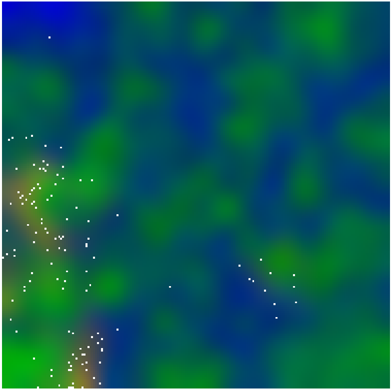

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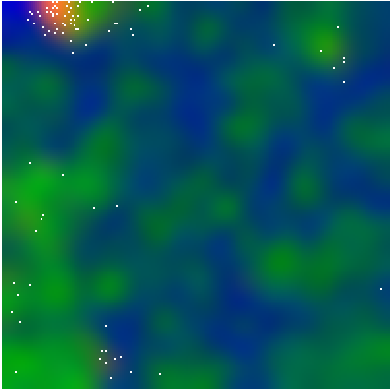

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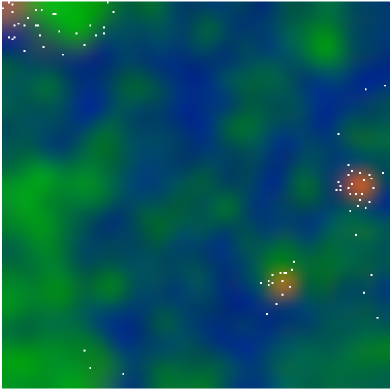

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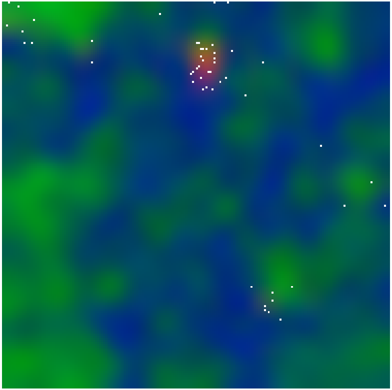

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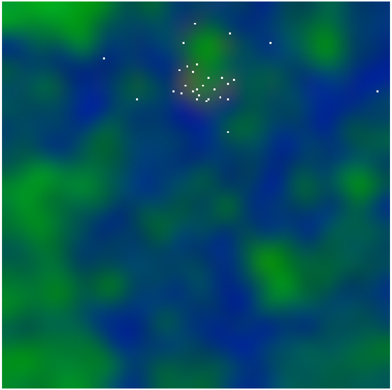

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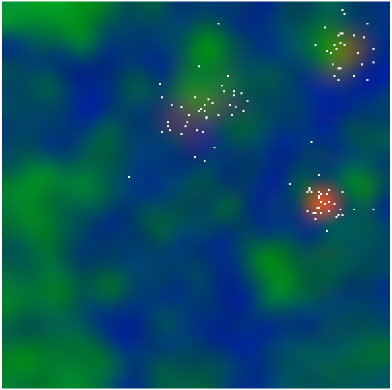

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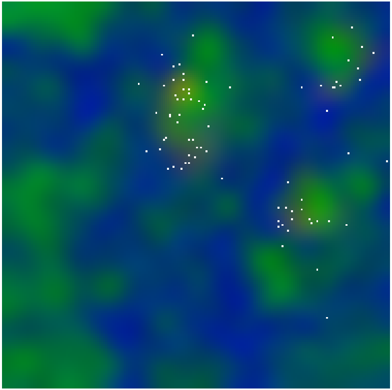

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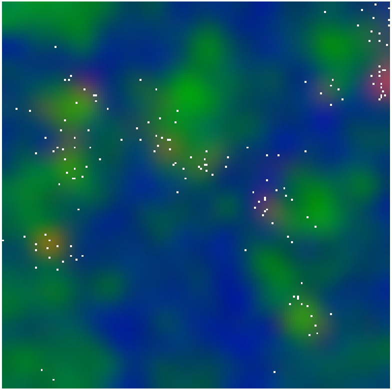

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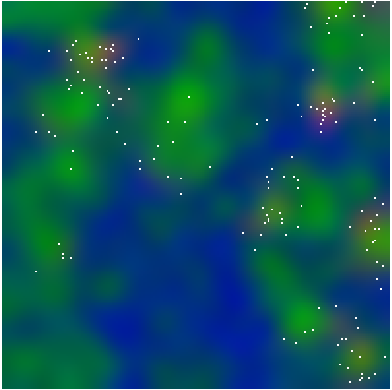

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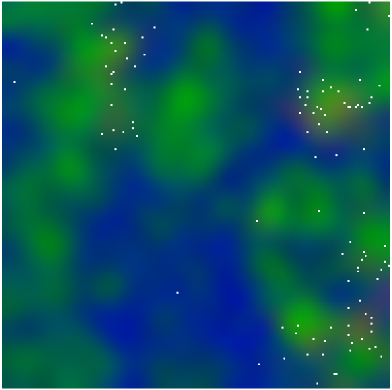

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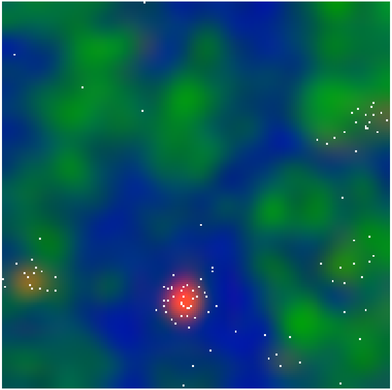

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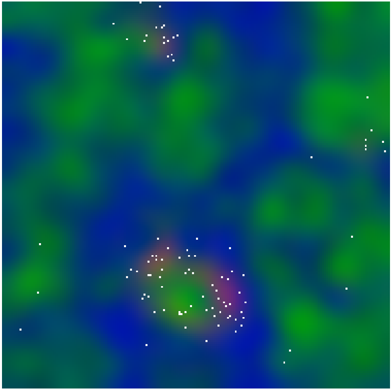

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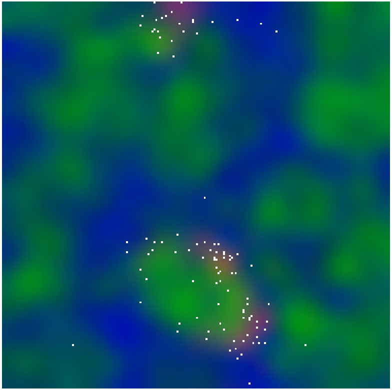

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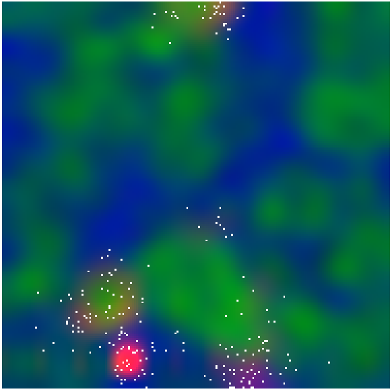

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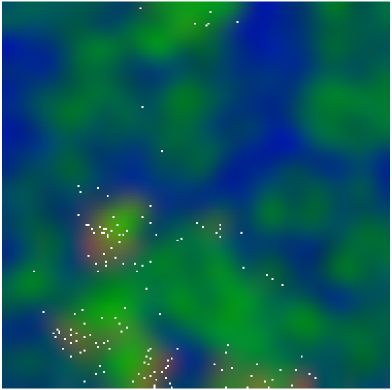

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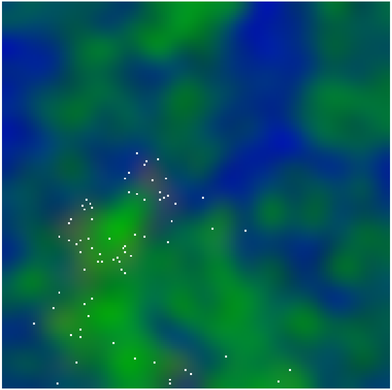

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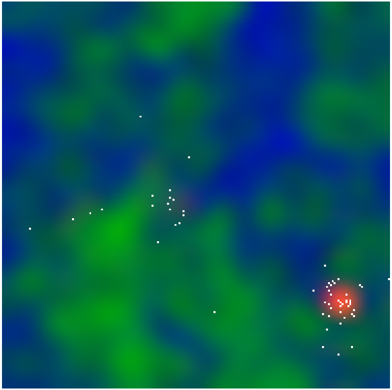

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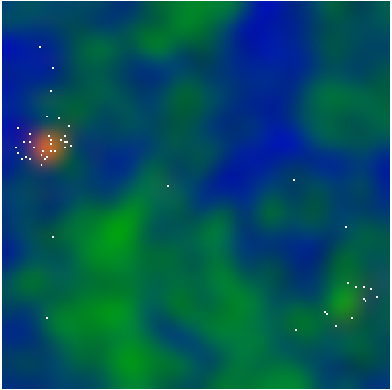

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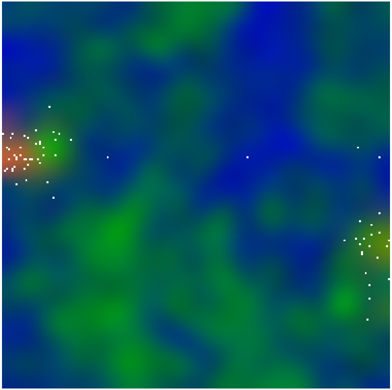

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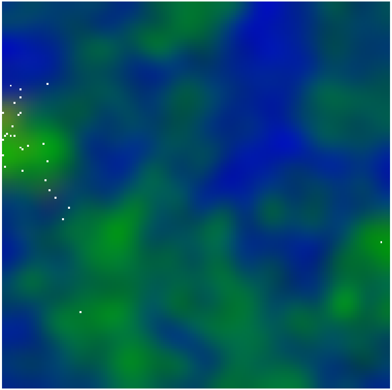

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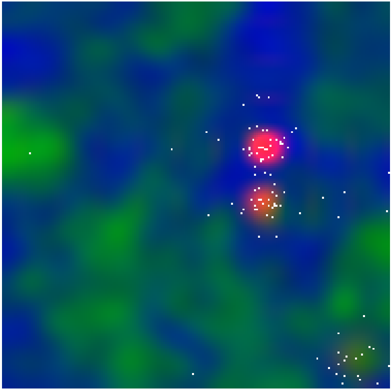

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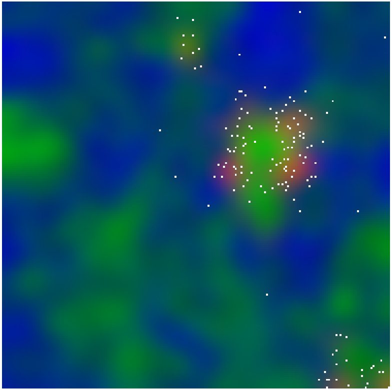

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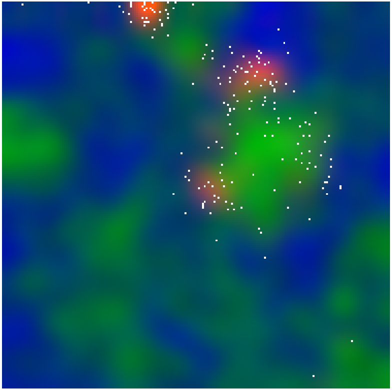

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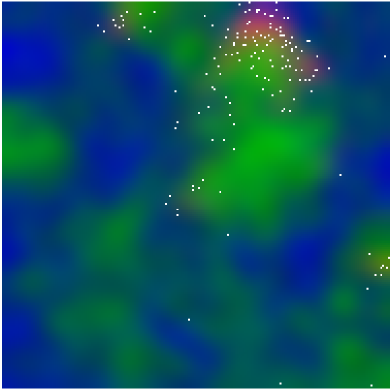

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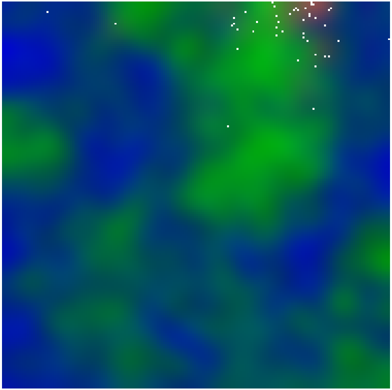

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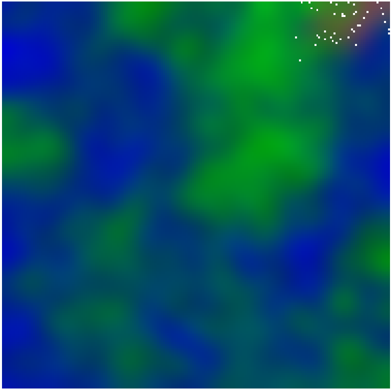

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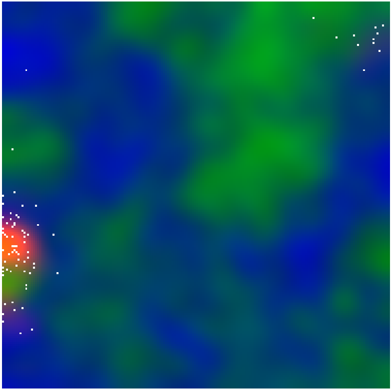

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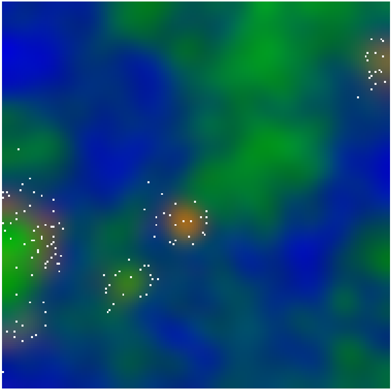

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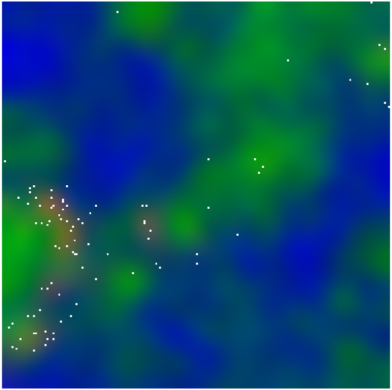

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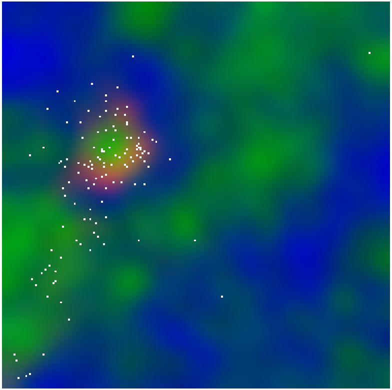
Cox process assumption: spike rates $\propto$ I field



Quiescent

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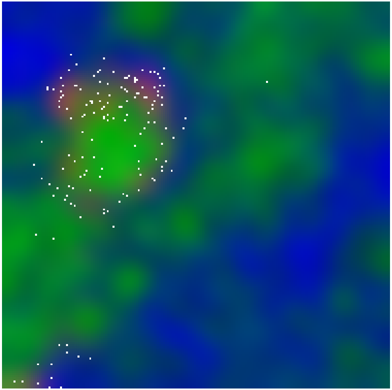

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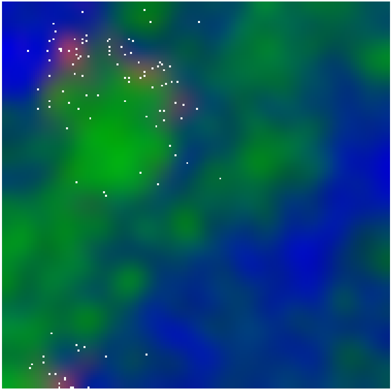

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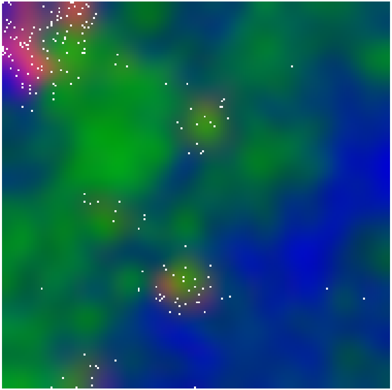

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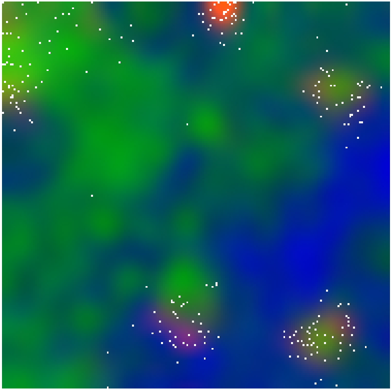

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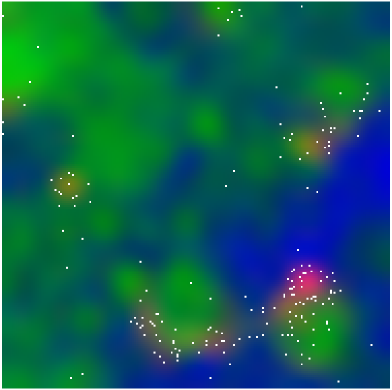

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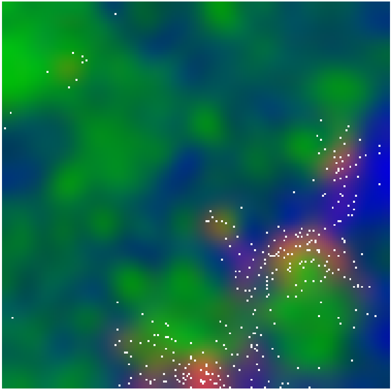

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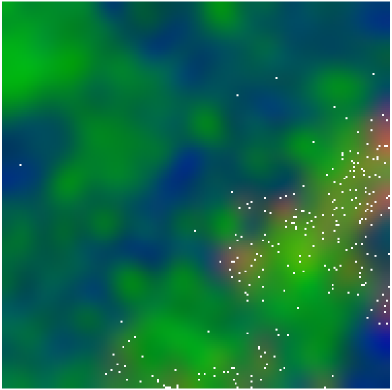

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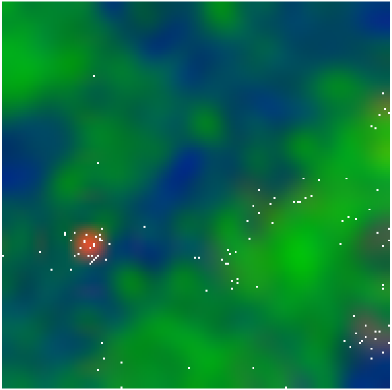

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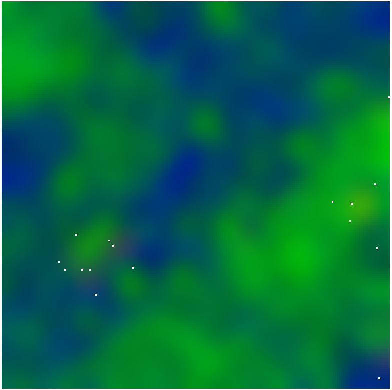

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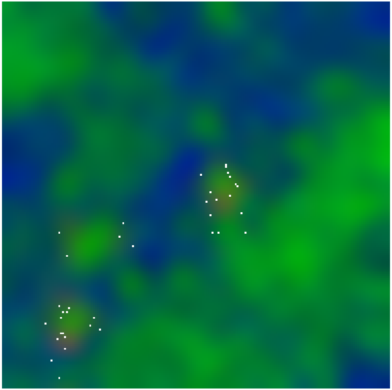

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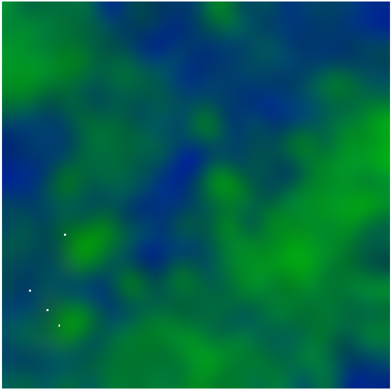

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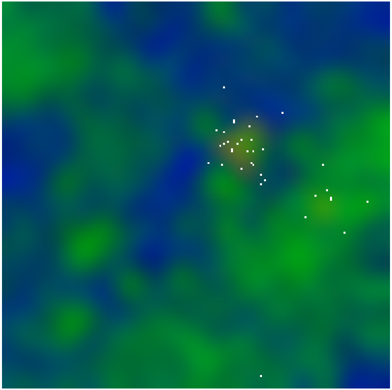

Quiescent

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Refractory

State-space model: 3-state moment-closure equations

Means:

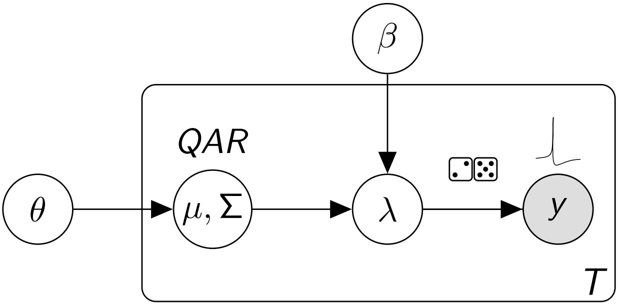
$$\partial_t \langle Q \rangle = r_{rq} - r_{qa} \qquad r_{qa} = \rho_q \langle Q \rangle + \rho_e \langle Q \cdot f[A] \rangle$$
$$\partial_t \langle A \rangle = r_{qa} - r_{ar} \qquad r_{ar} = \rho_a \langle A \rangle$$
$$\partial_t \langle R \rangle = r_{ar} - r_{rq} \qquad r_{rq} = \rho_r \langle R \rangle$$

Covariance:

- Deterministic evolution given by Jacobian of mean
- Noise contribution is:

$$\Sigma_{\text{noise}}(Q, A, R) = \begin{bmatrix} r_{qa} + r_{rq} & -r_{qa} & -r_{rq} \\ -r_{qa} & r_{qa} + r_{ar} & -r_{ar} \\ -r_{rq} & -r_{ar} & r_{ar} + r_{qa} \end{bmatrix}$$

State-space model for inference



θ : *Model parameters*

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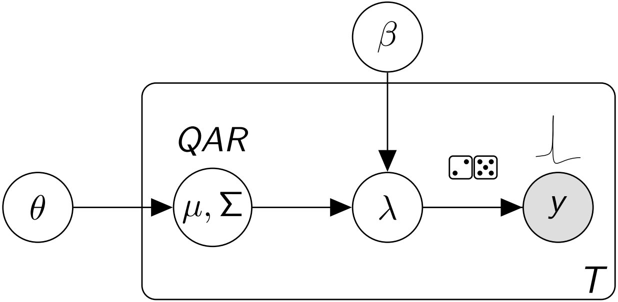

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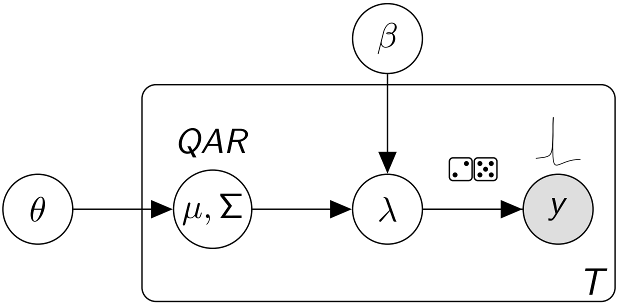

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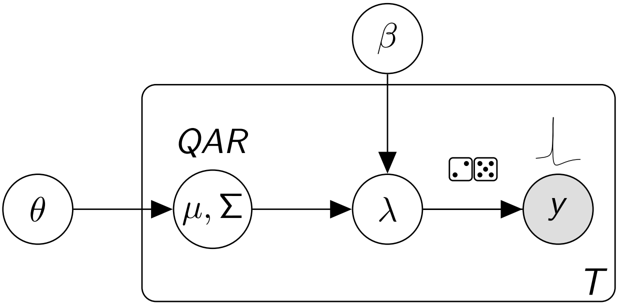

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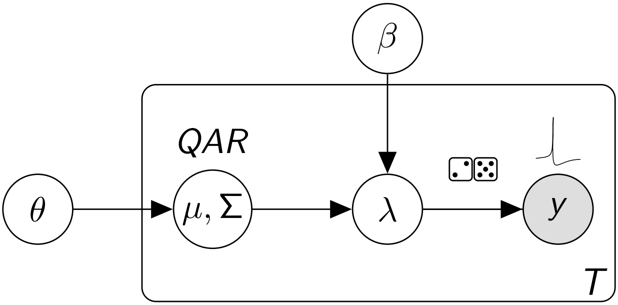

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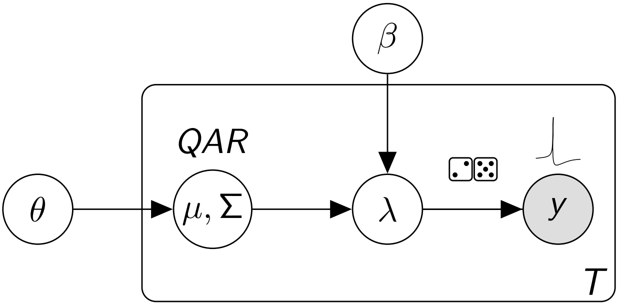

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μ, Σ : QAR **3-state** Gaussian appx.

β : *Observation model*

λ : Ganglion Cell firing **intensity**

y : **Observed** point-process

T : for all time-points $t \in T$

Infer states by filtering

Discrete: break time into Δt width bins, and let

- n index time-bins
- x be a vector of *latent states*
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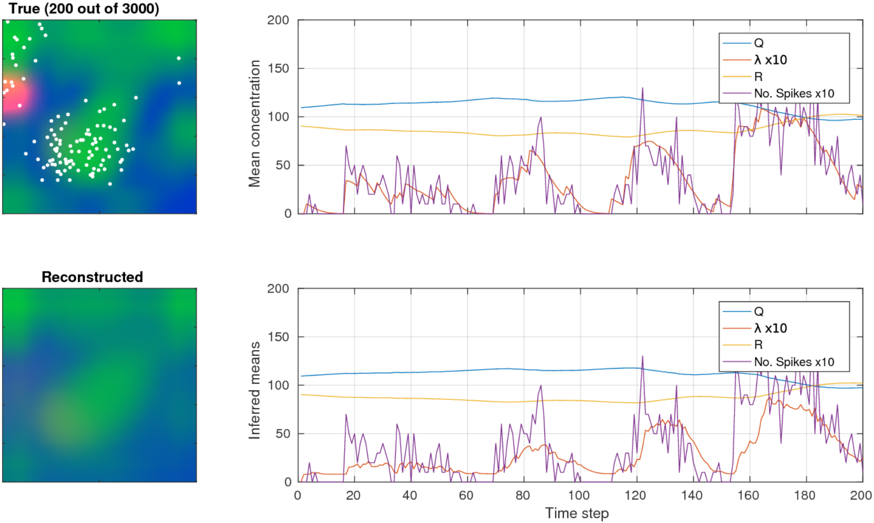
Approximate:

- $\Pr(x) \sim$ multivariate Gaussian
- Poisson likelihood $\Pr(y|x)$ via Laplace approximation

Filtering infers latent intensities from spikes



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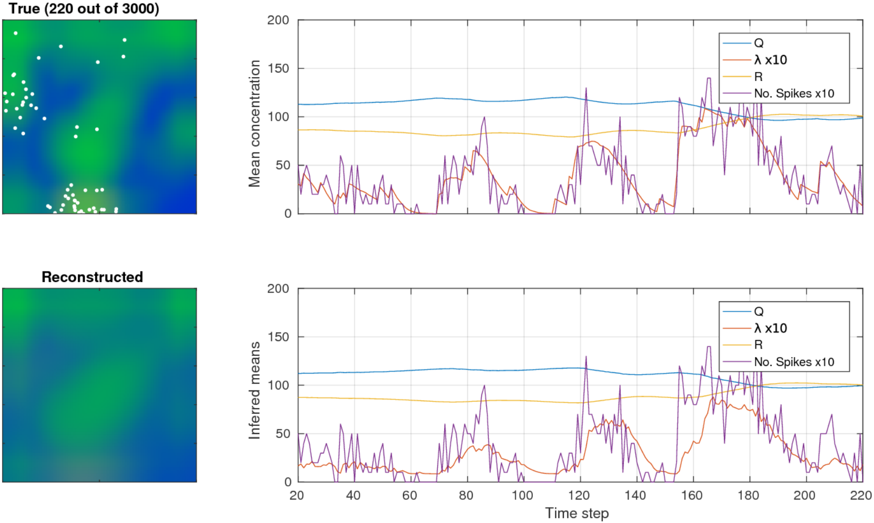

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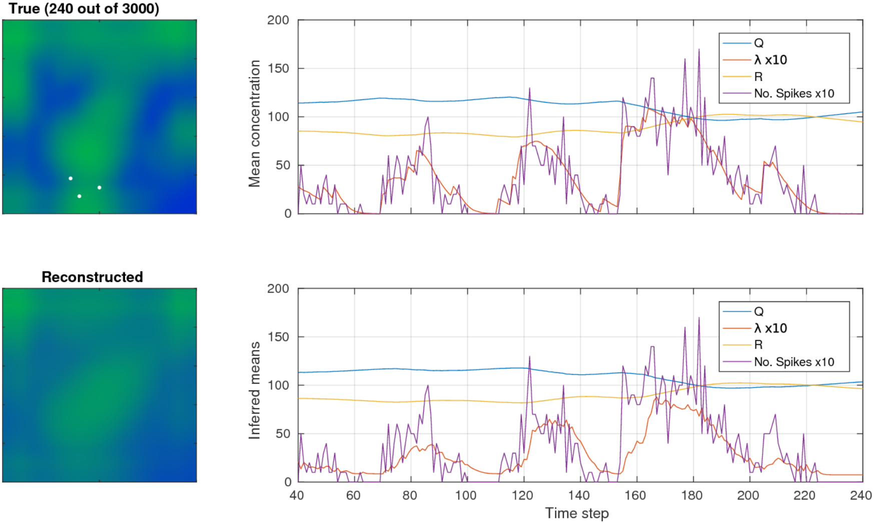

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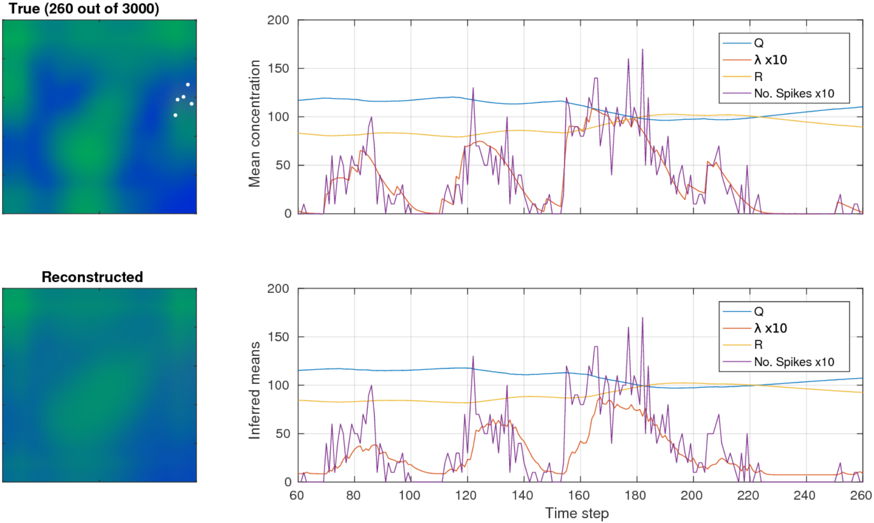

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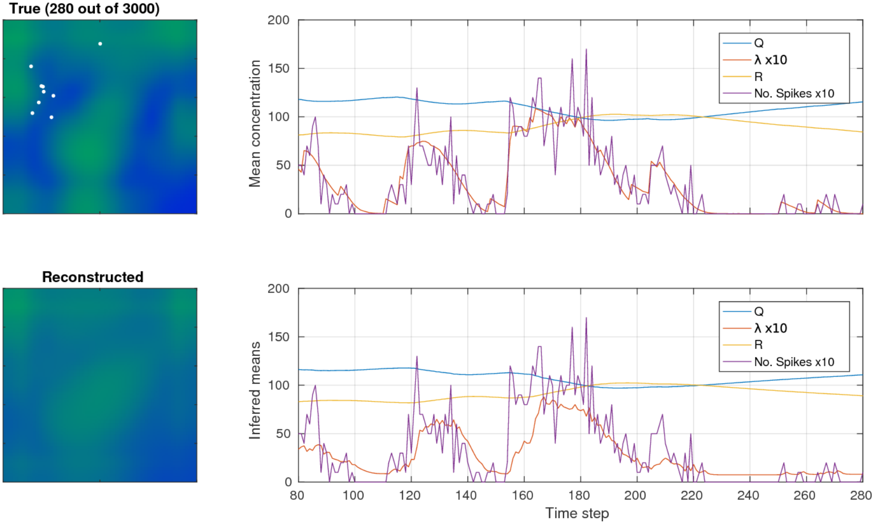

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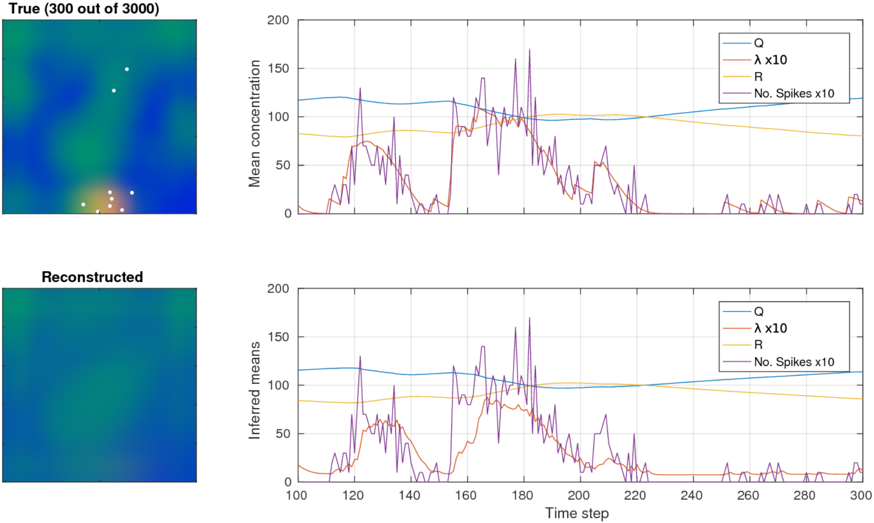

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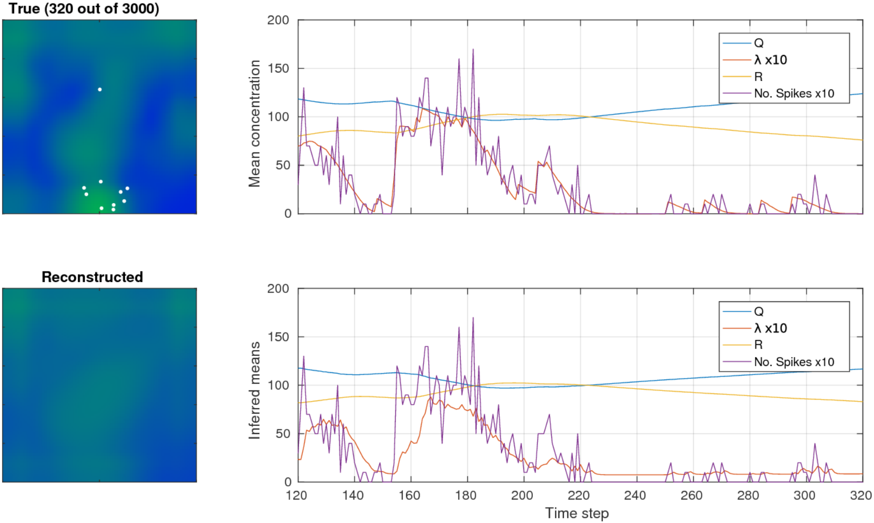

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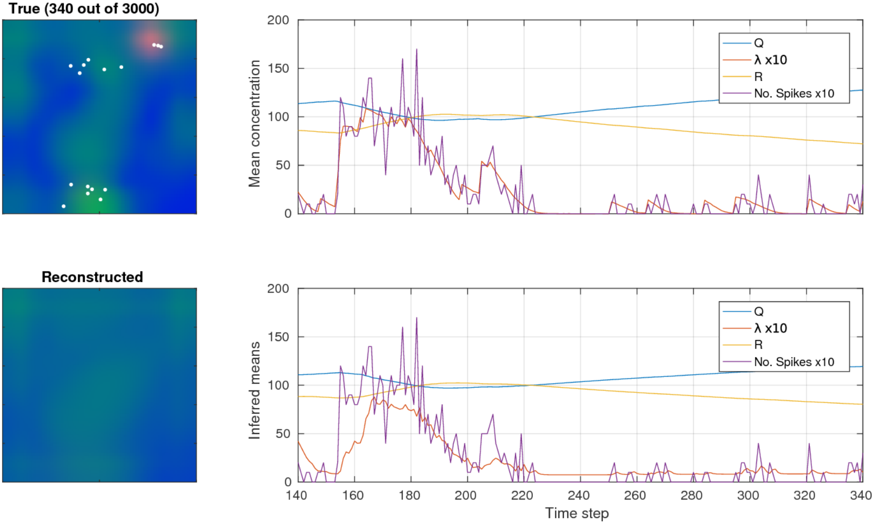

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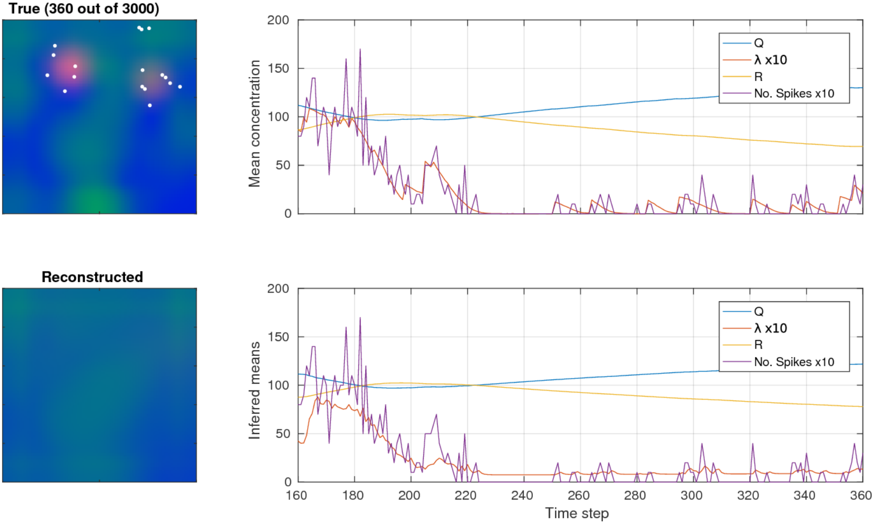

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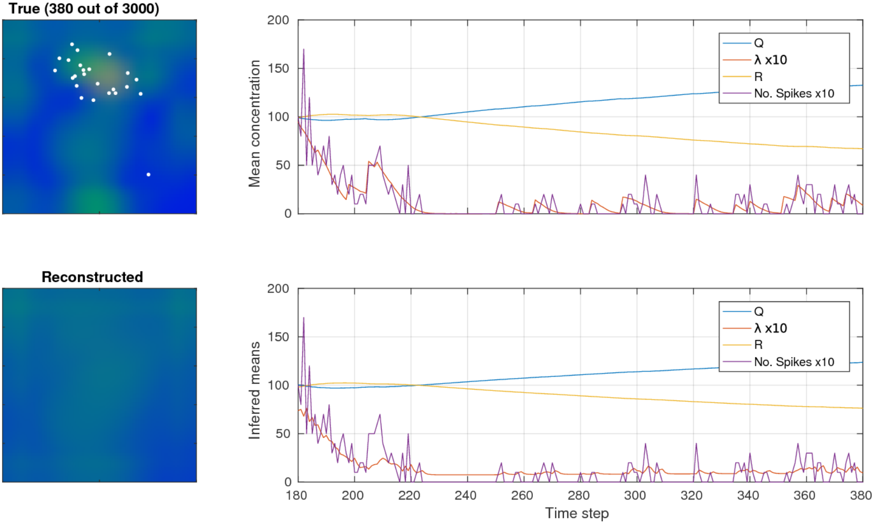

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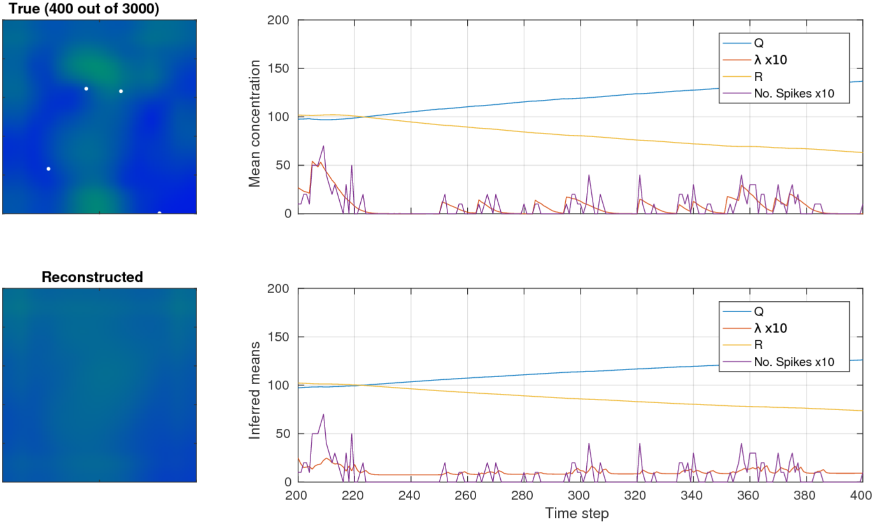

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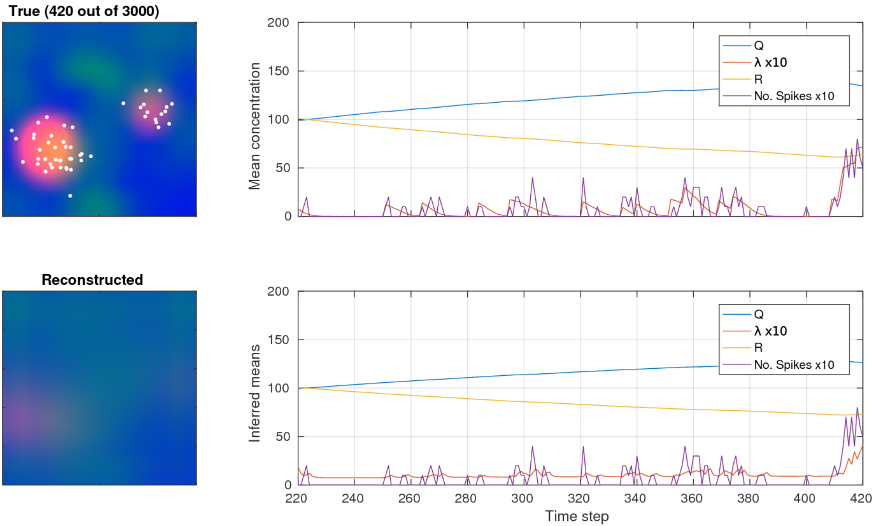

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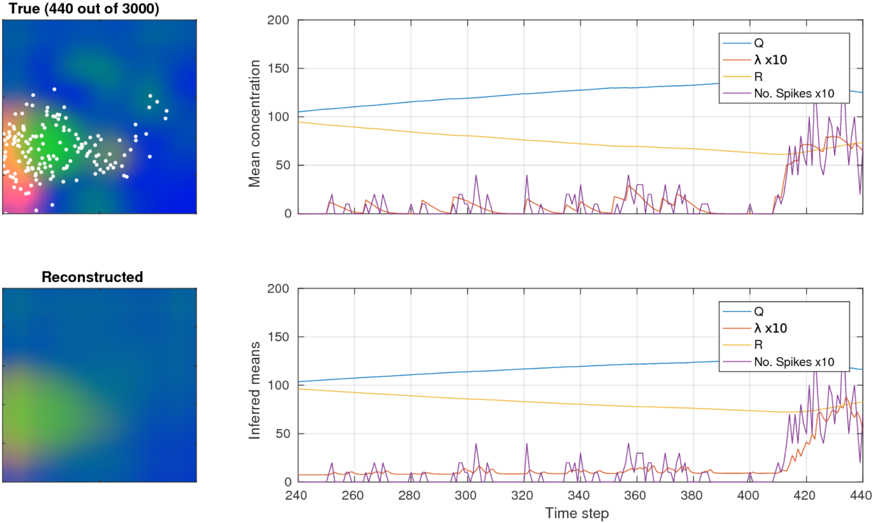

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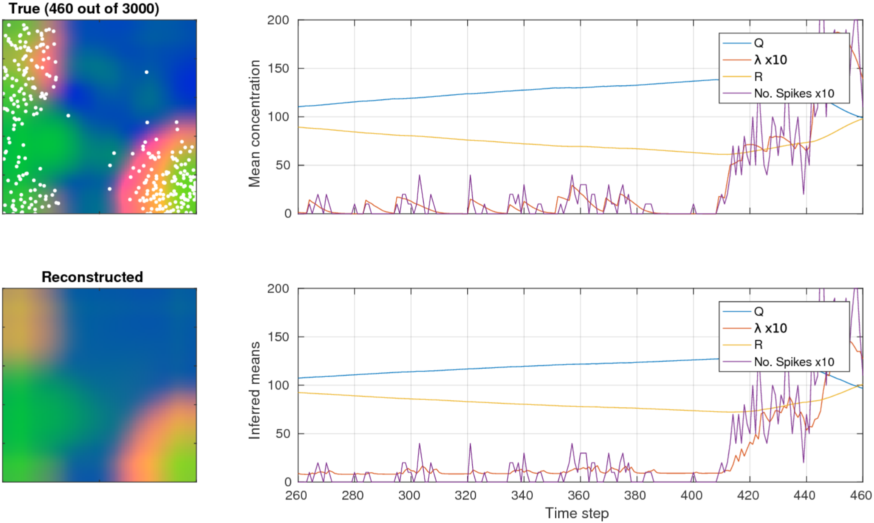

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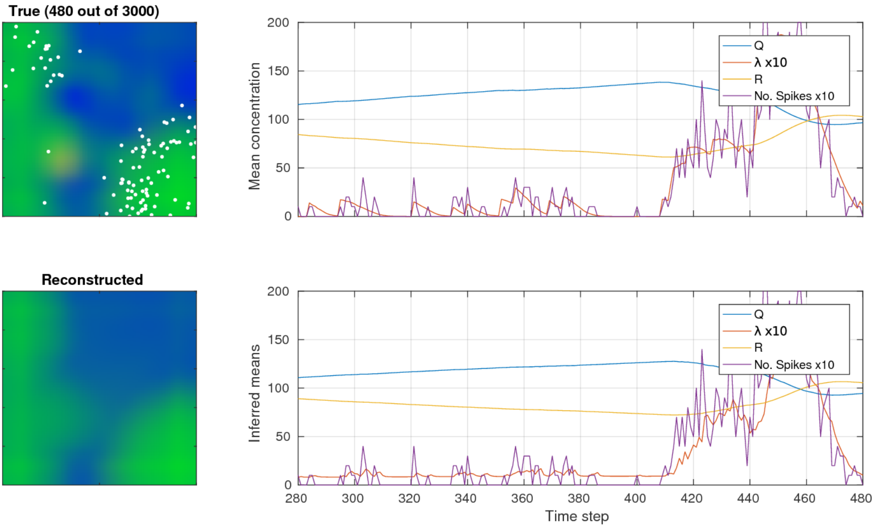

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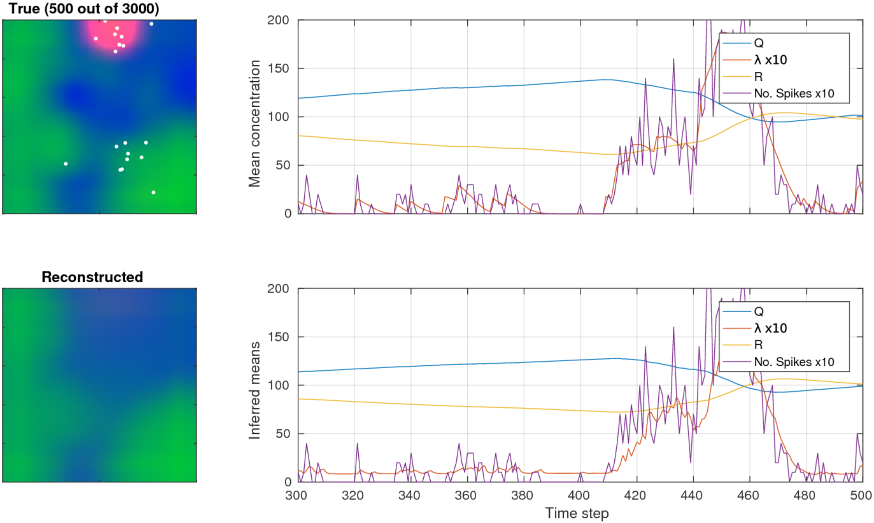

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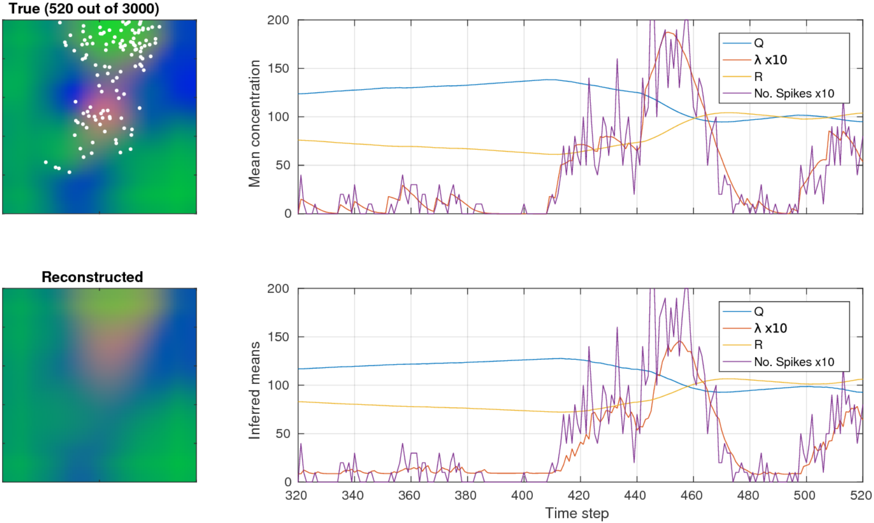

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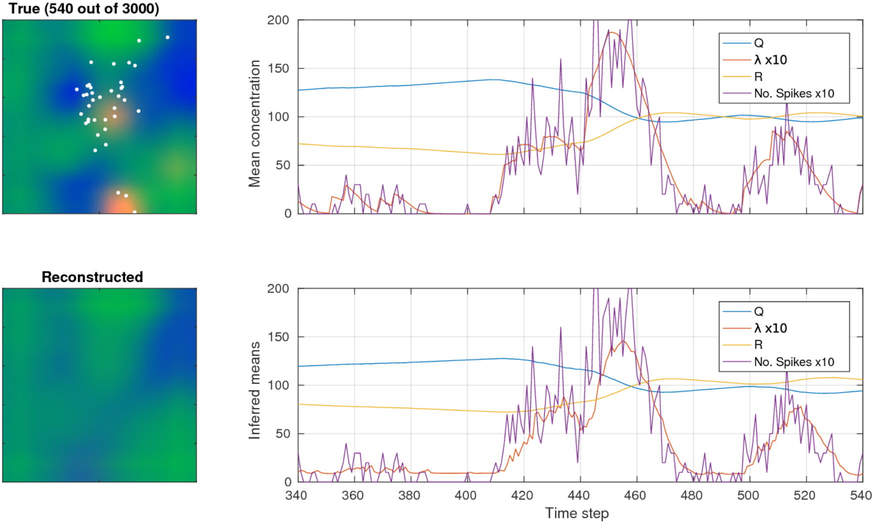

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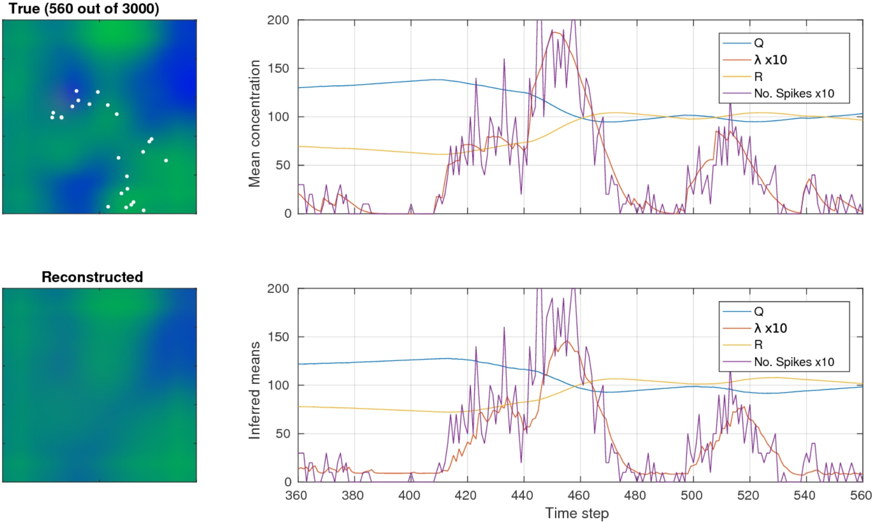

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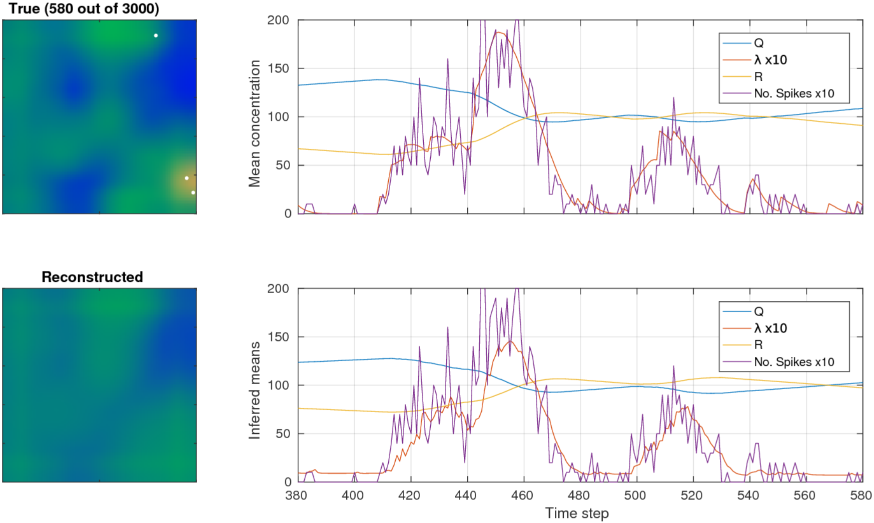

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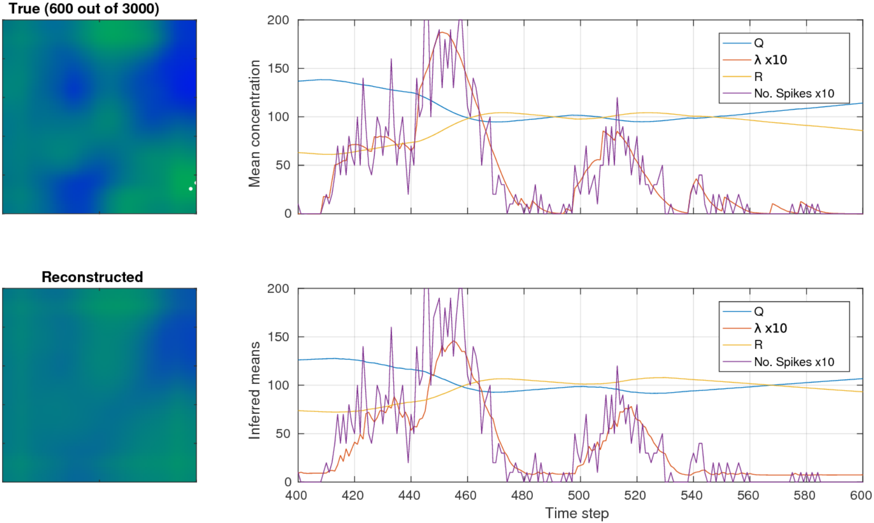

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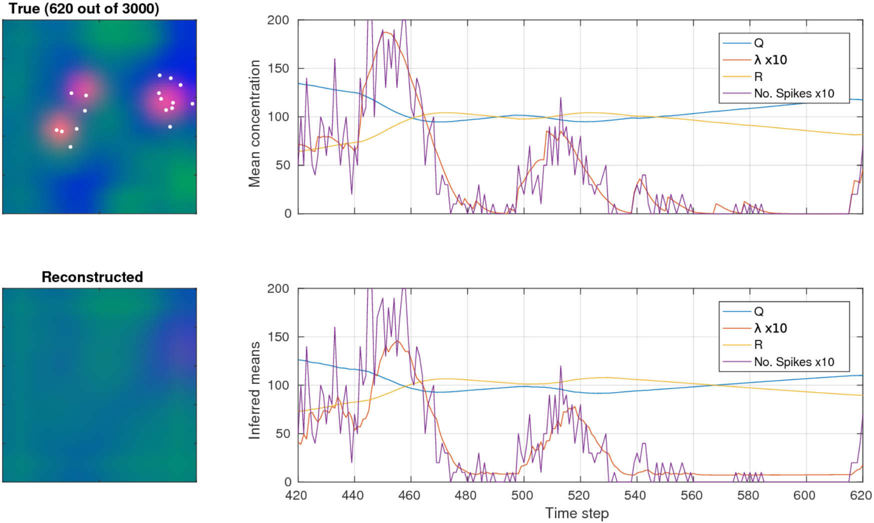

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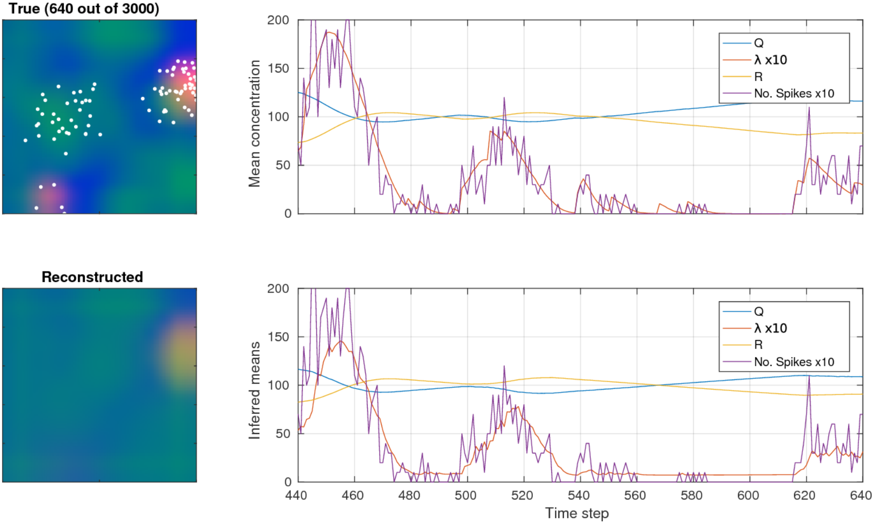

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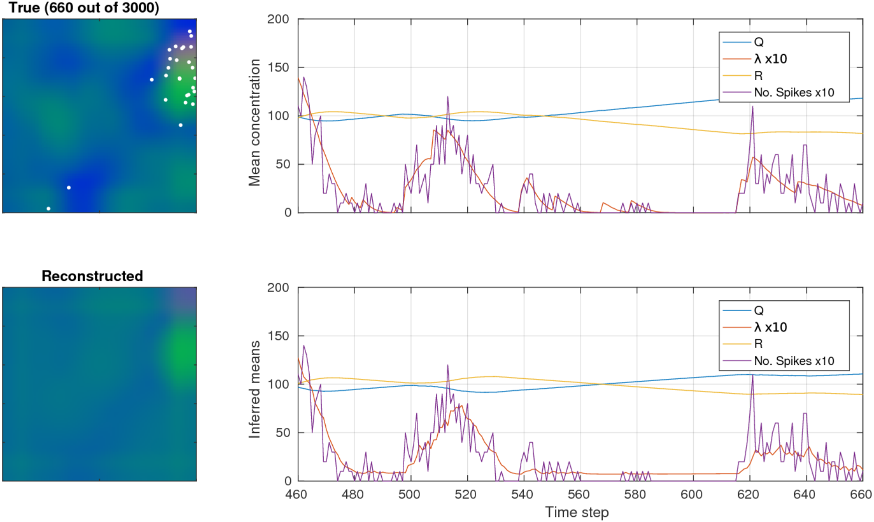

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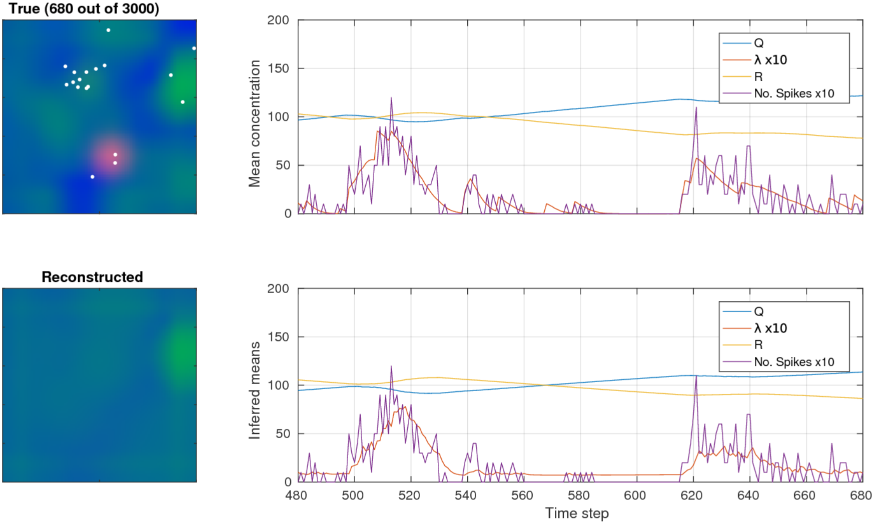

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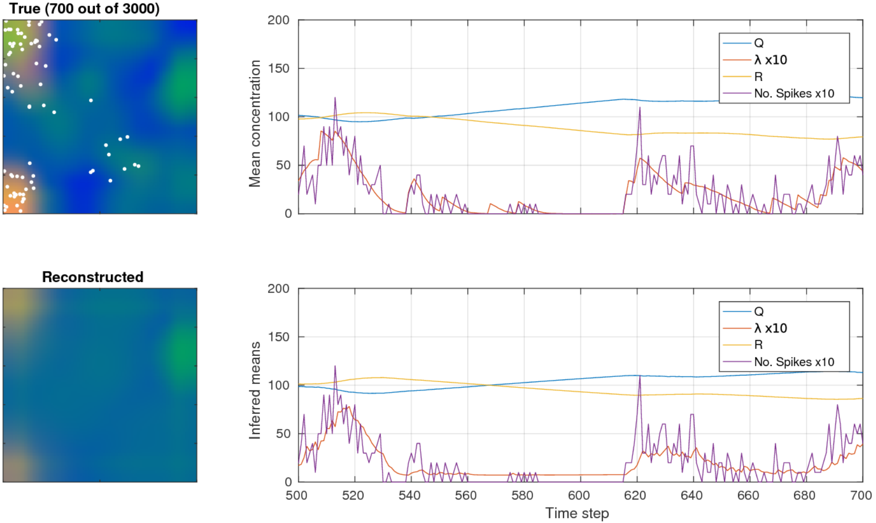

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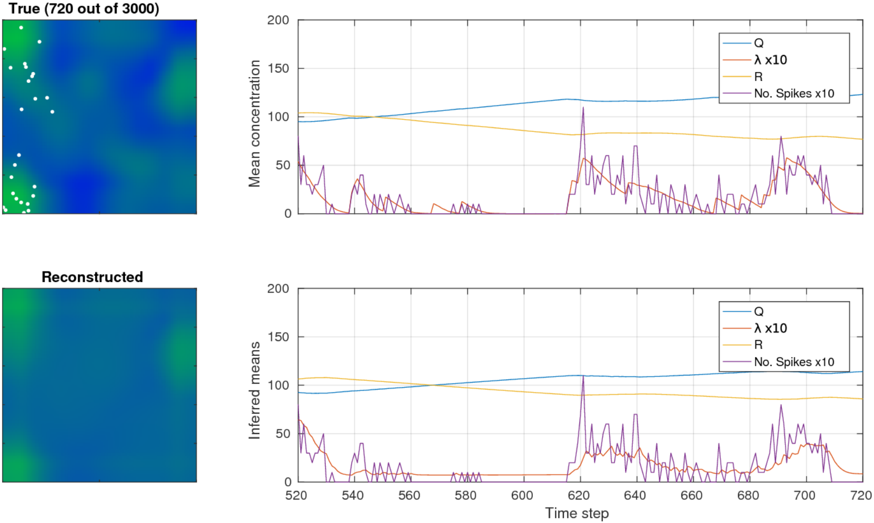

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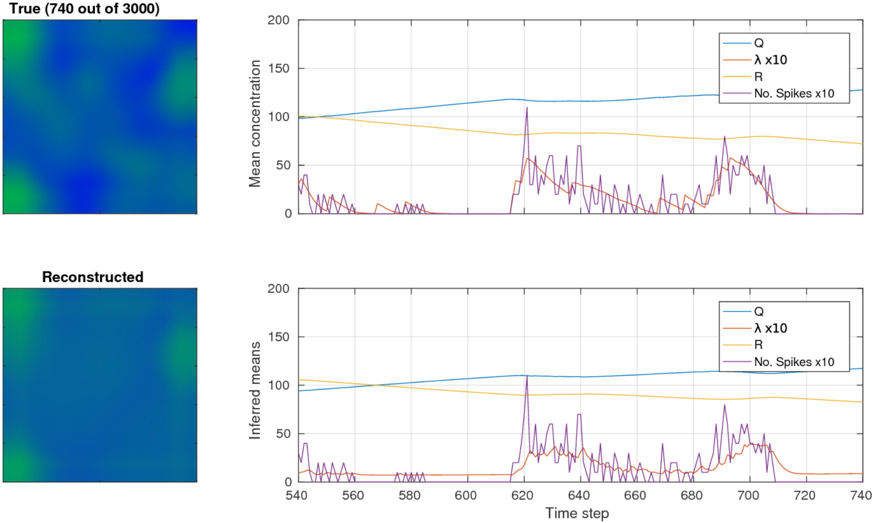

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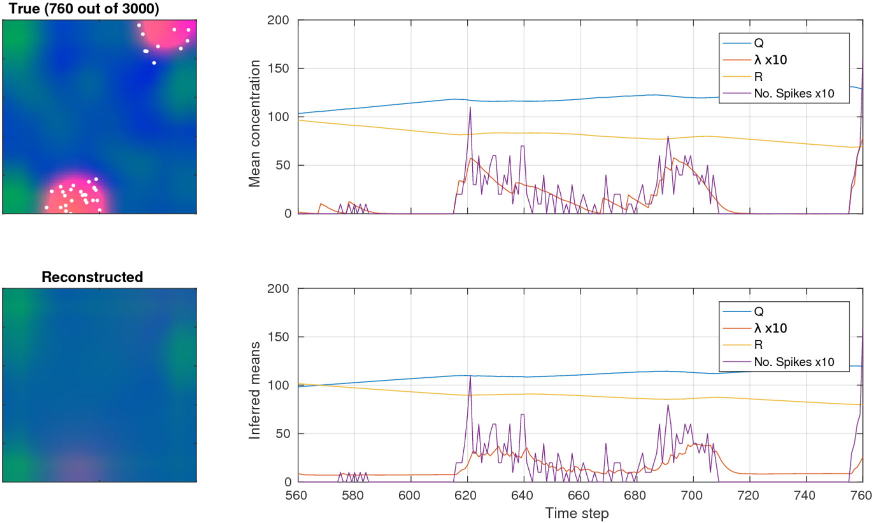

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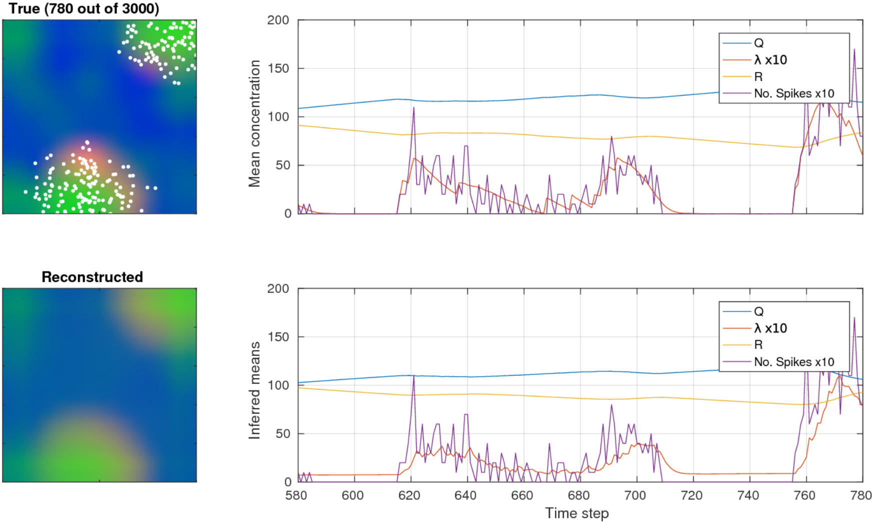

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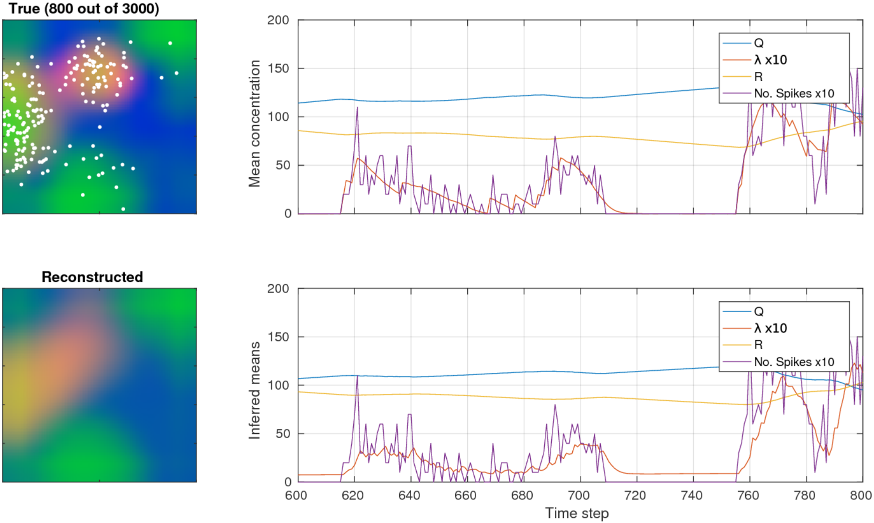

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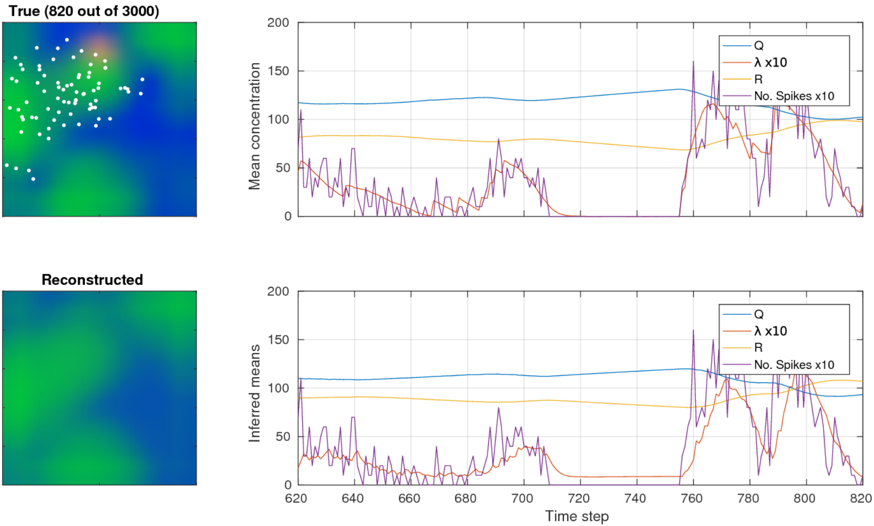

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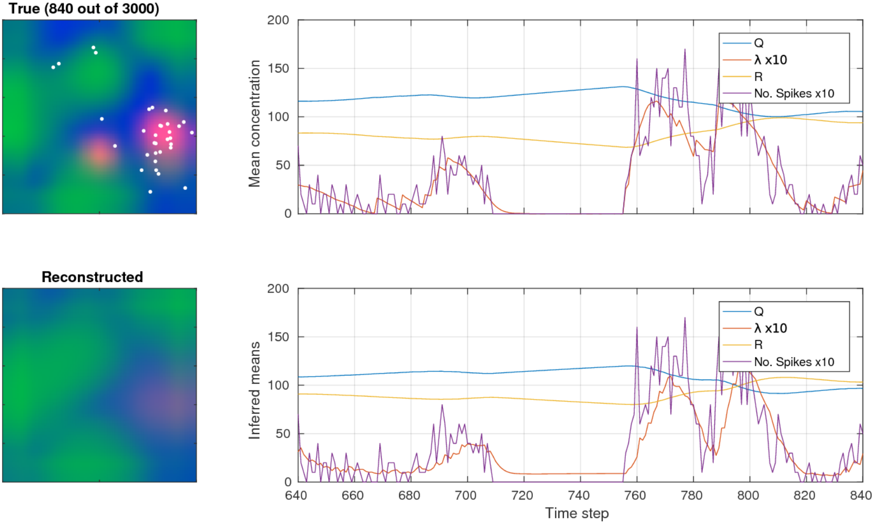

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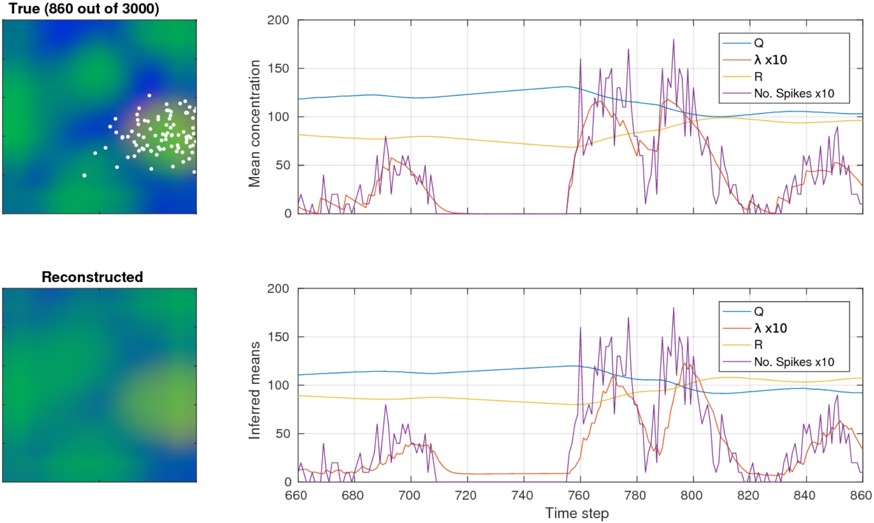

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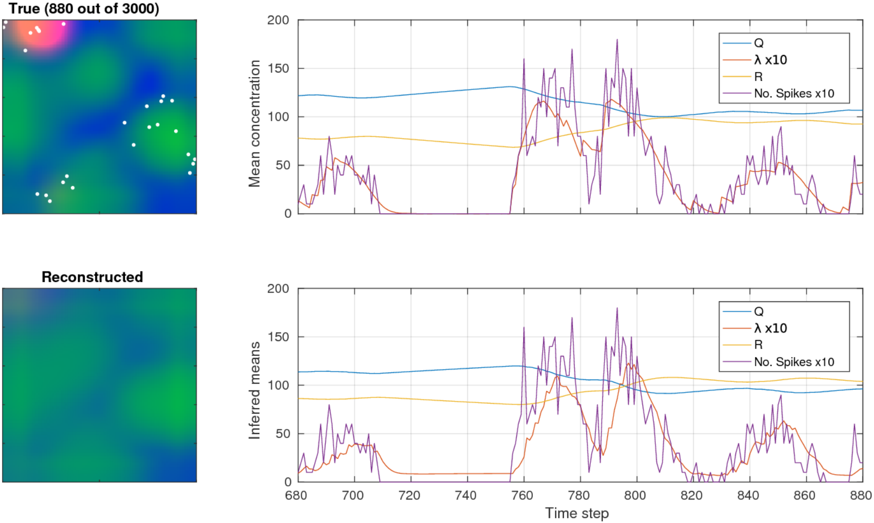

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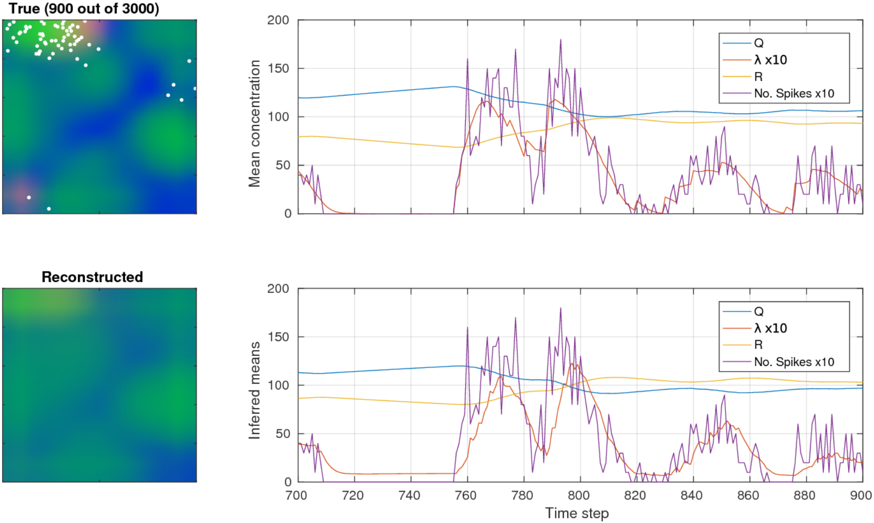
Filtering infers latent intensities from spikes



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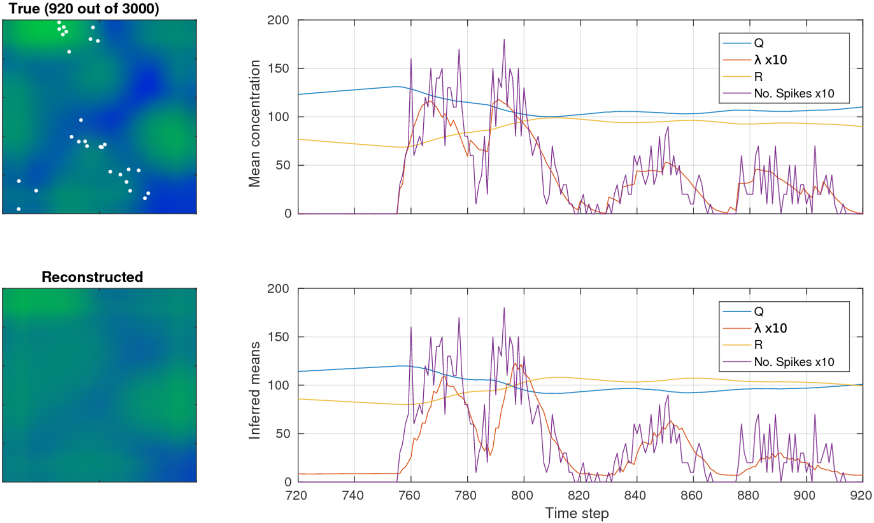

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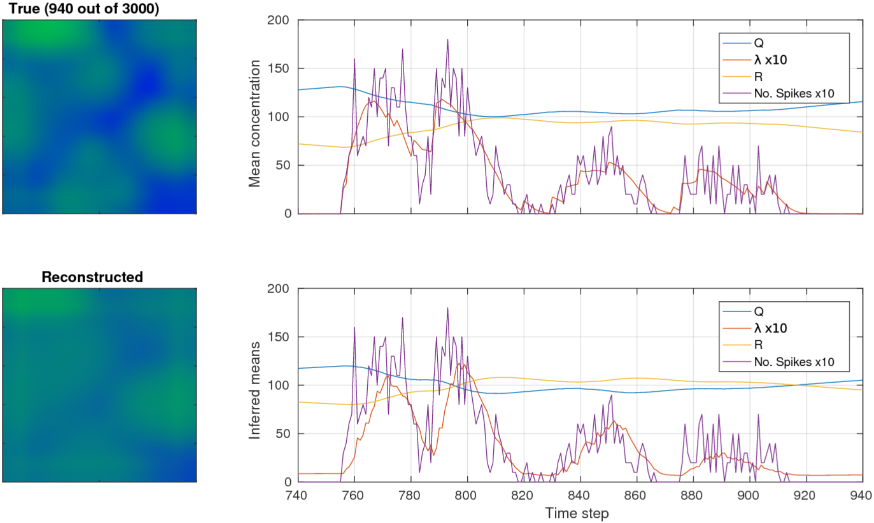

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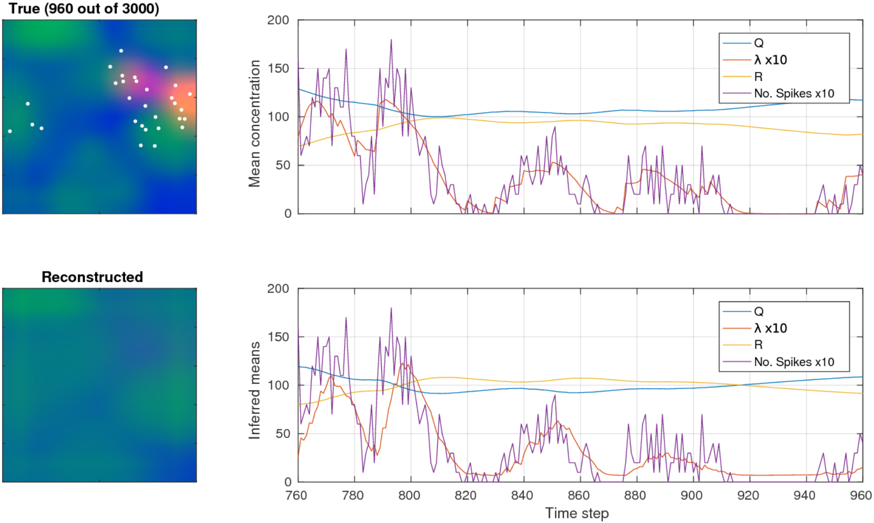

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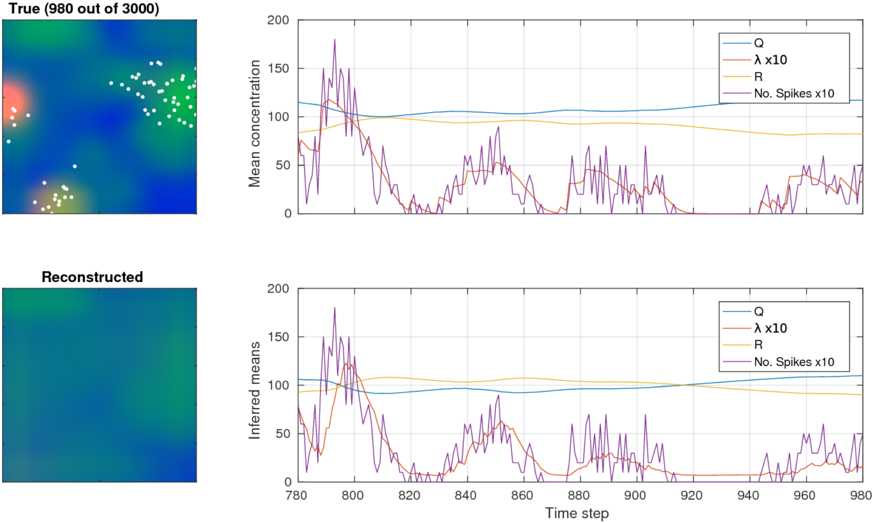

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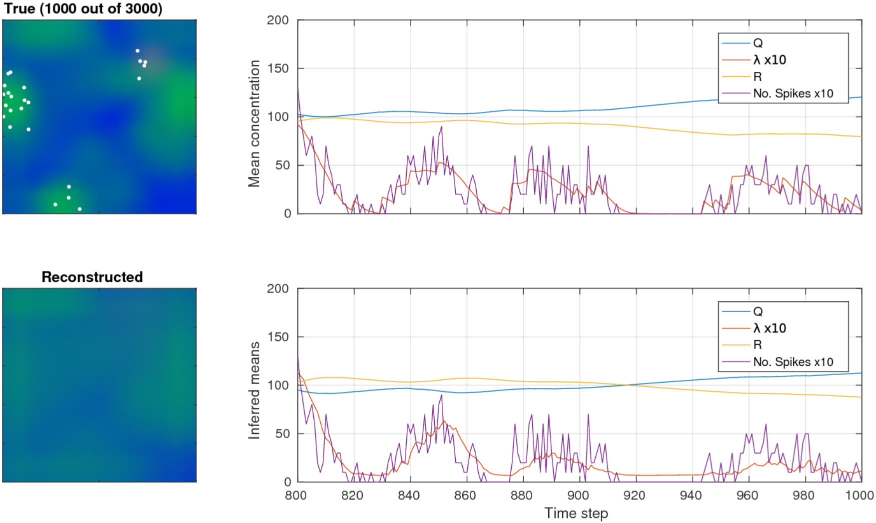

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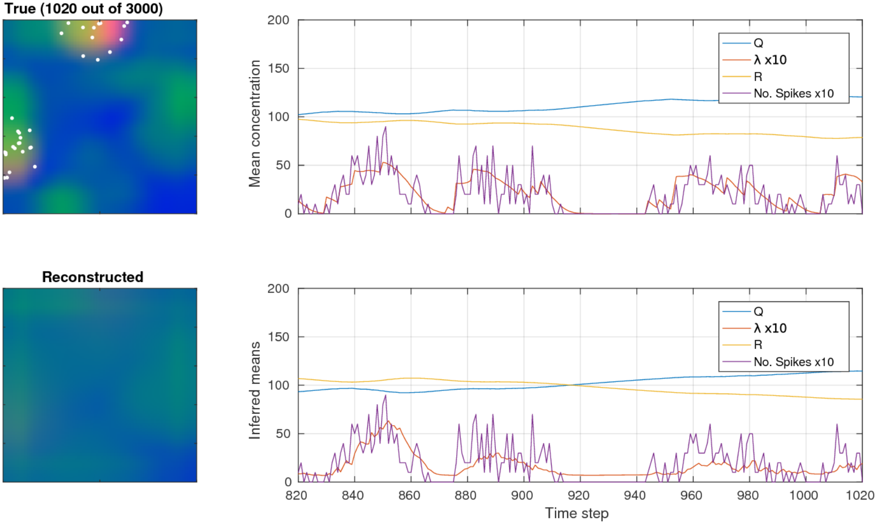

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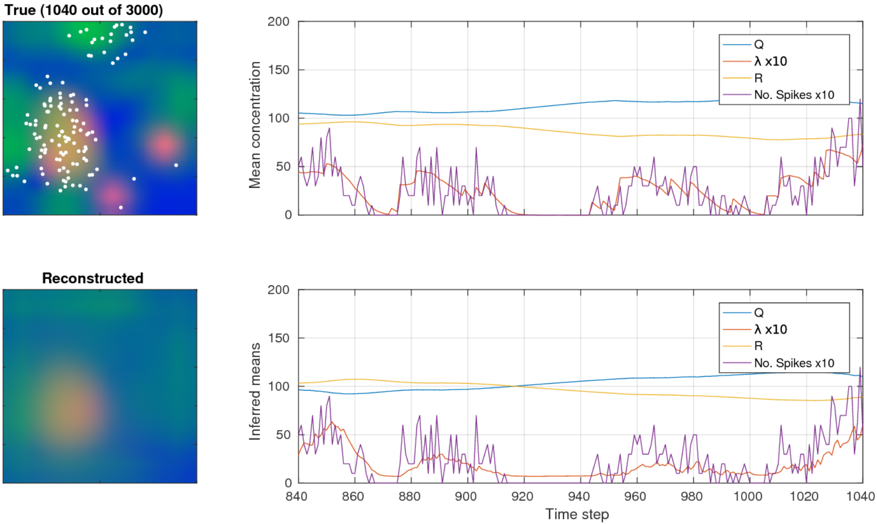

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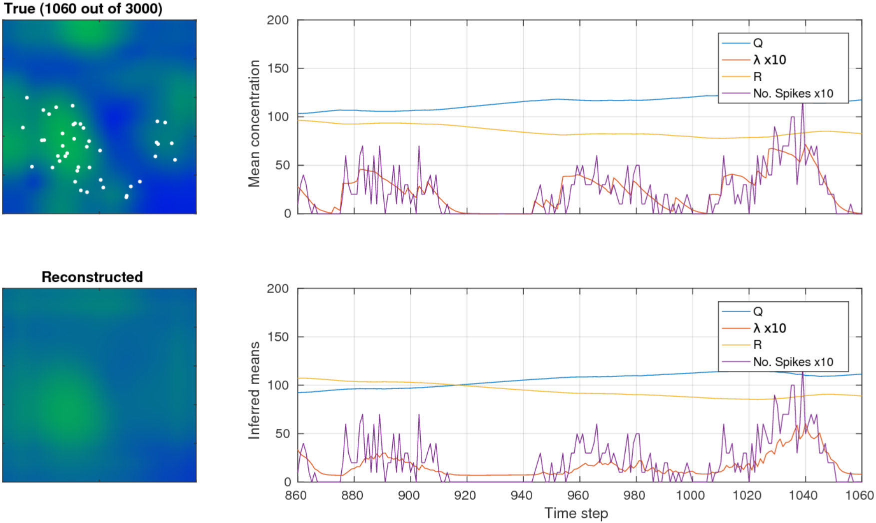

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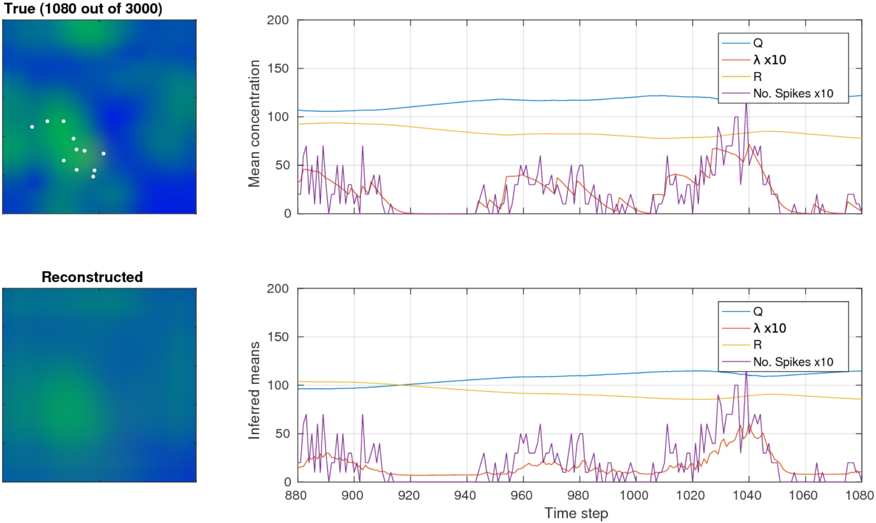

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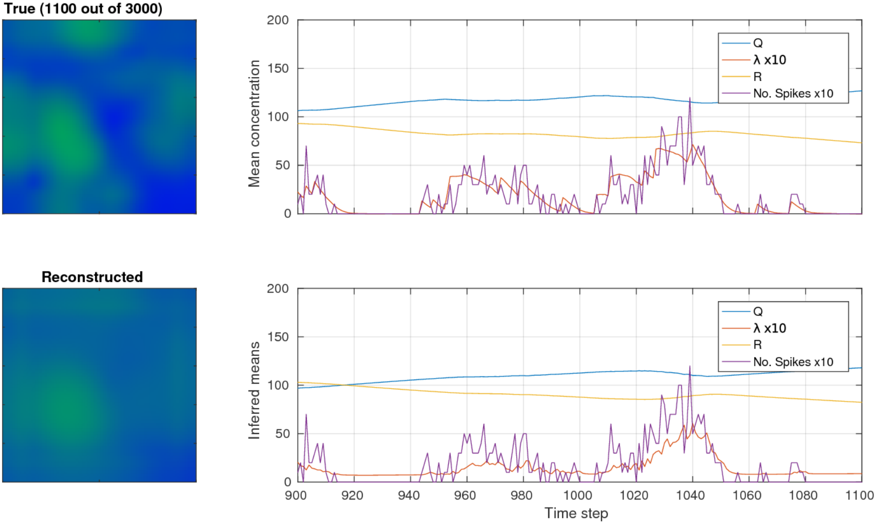
Filtering infers latent intensities from spikes



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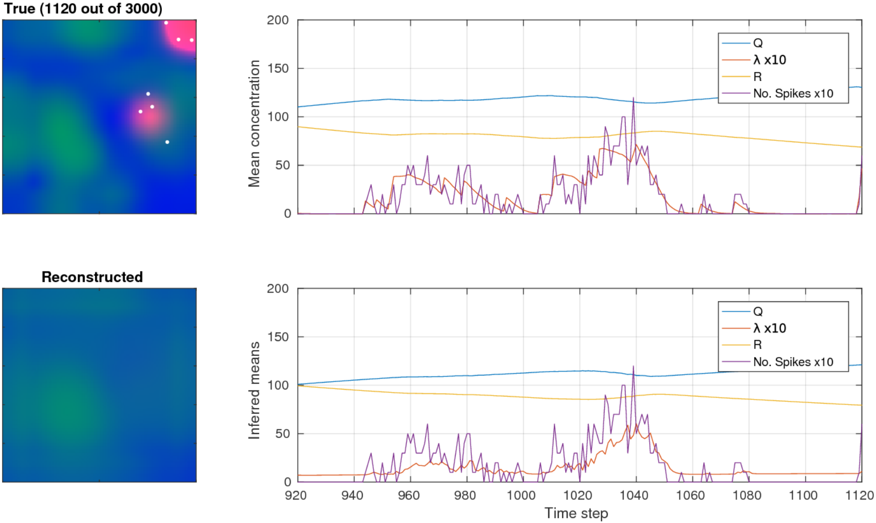

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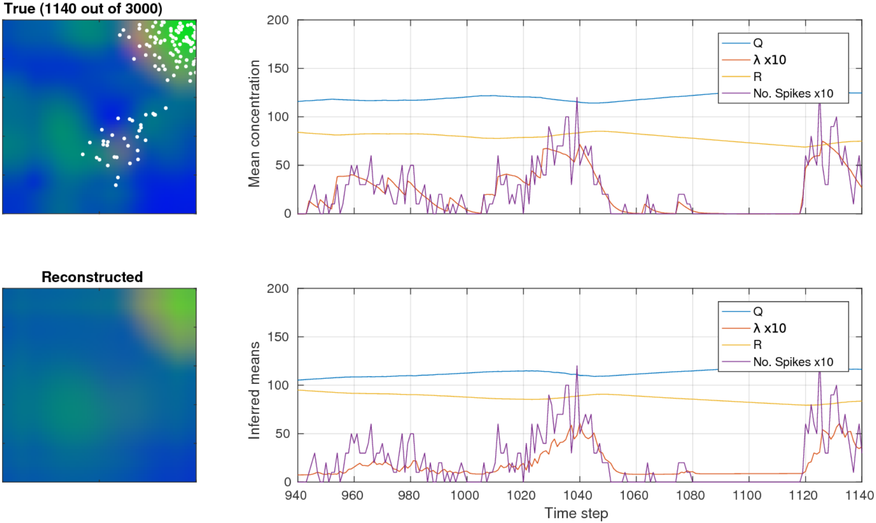

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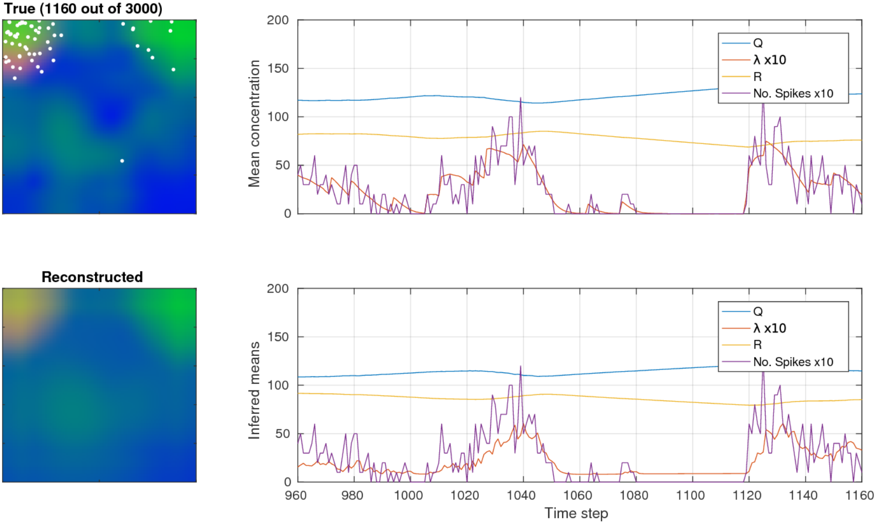

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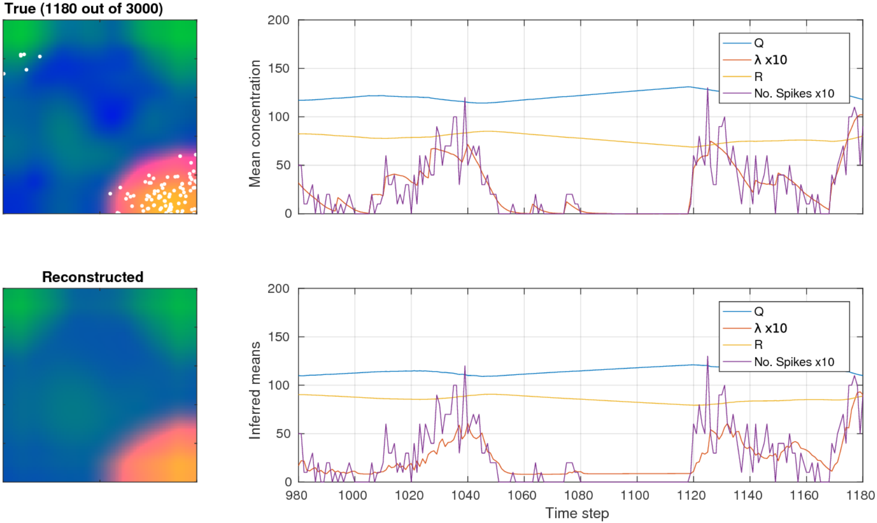

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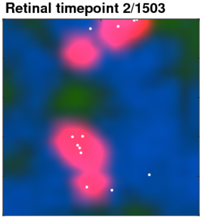
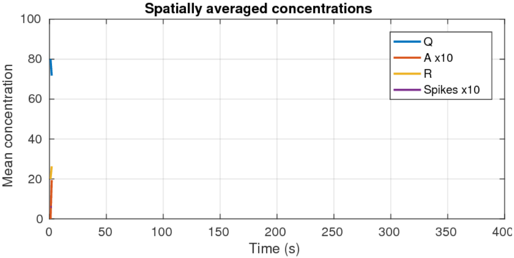
Filtering infers latent intensities from spiking data

P6 mouse retina; 20× real-time





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(Due to non-identifiability of observation model, concentrations reflect arbitrary units)

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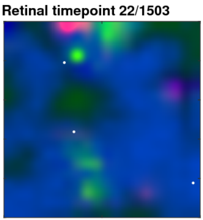

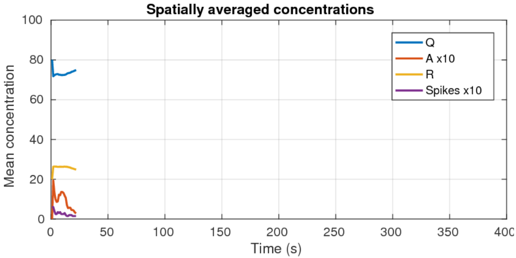

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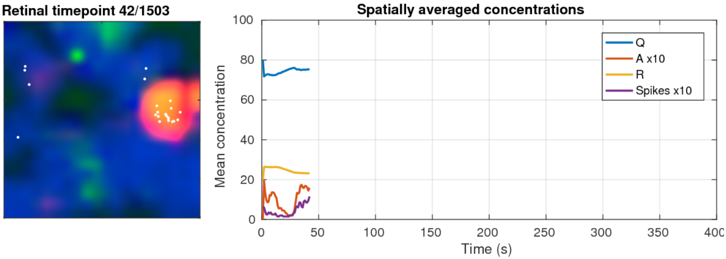

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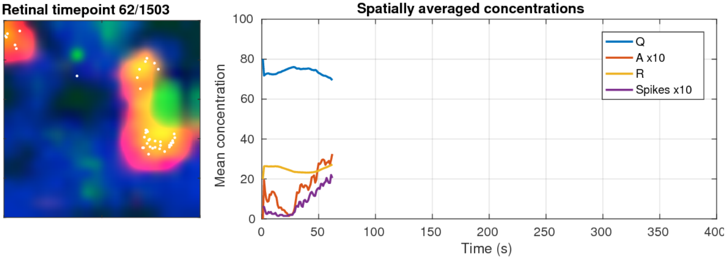

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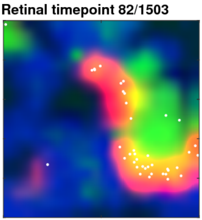

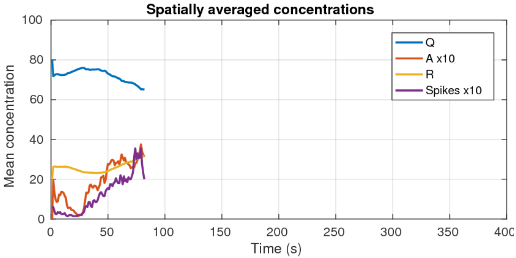

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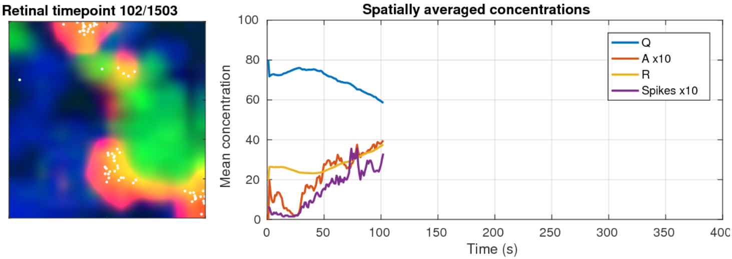

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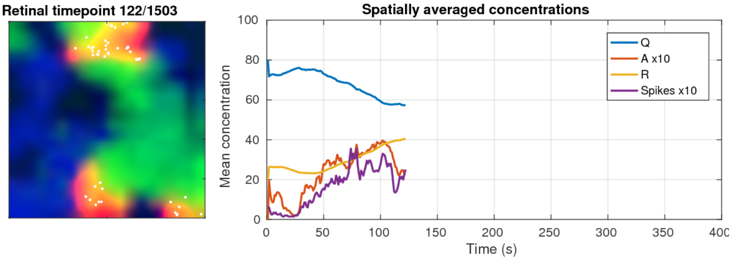

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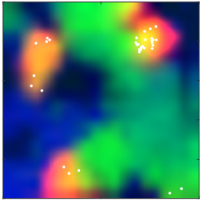

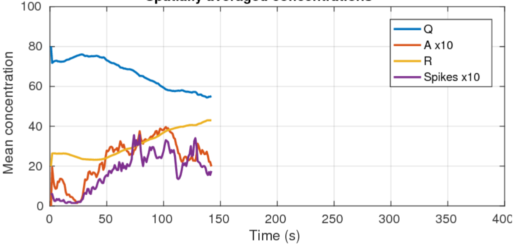

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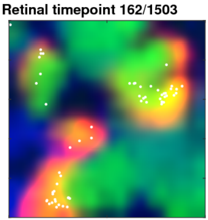

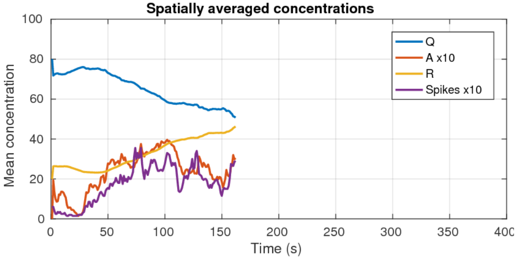

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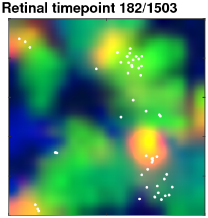

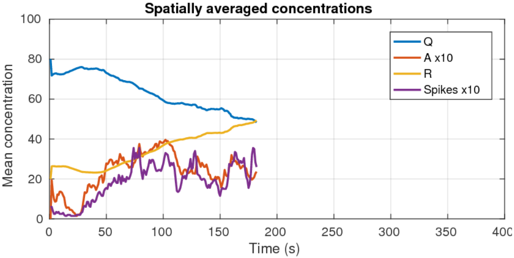

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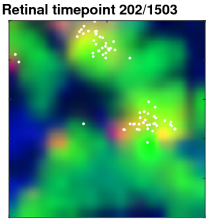

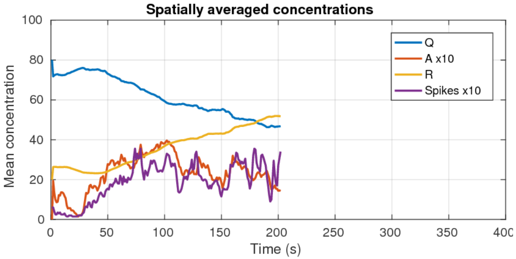

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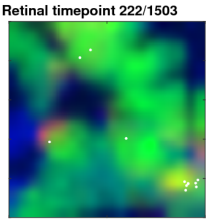

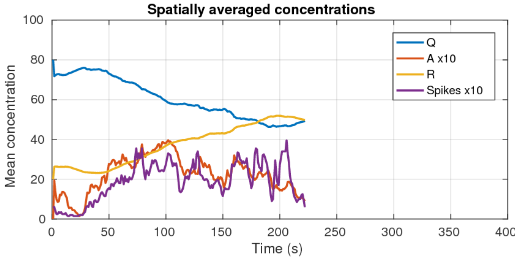

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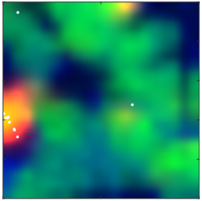

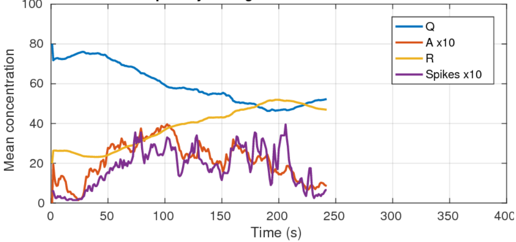

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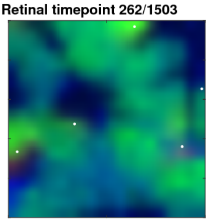

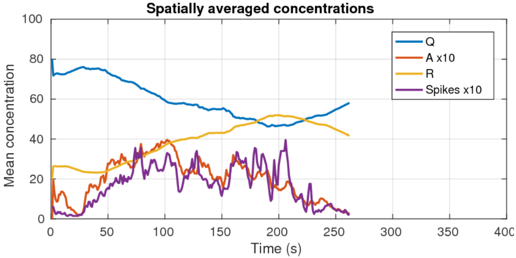

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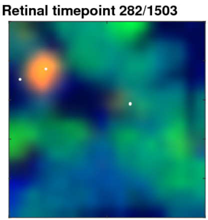

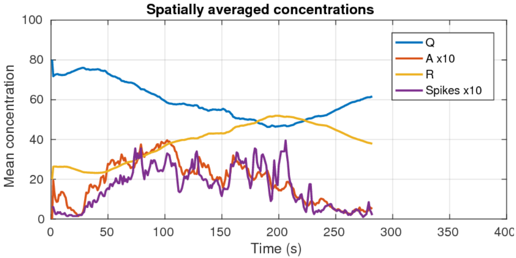

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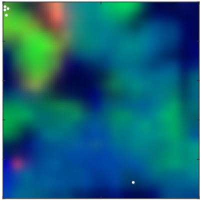

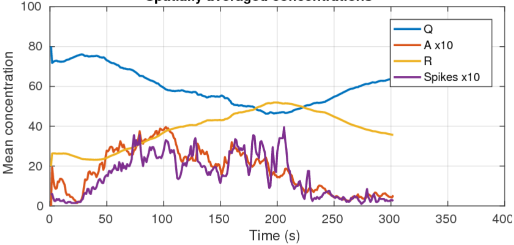

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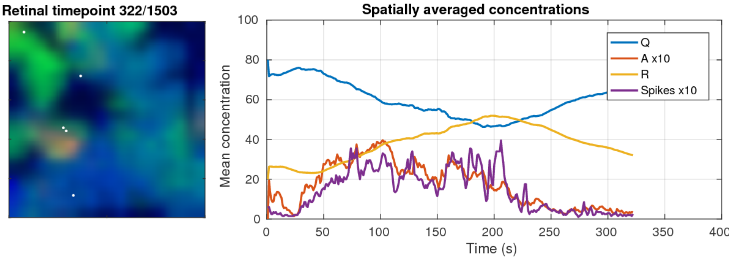

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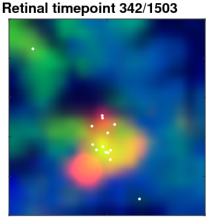

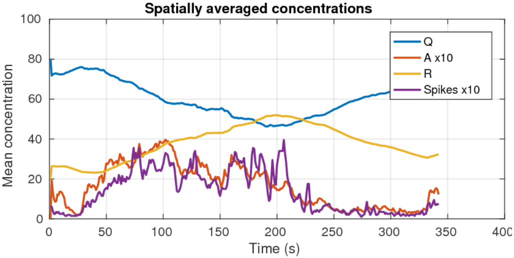

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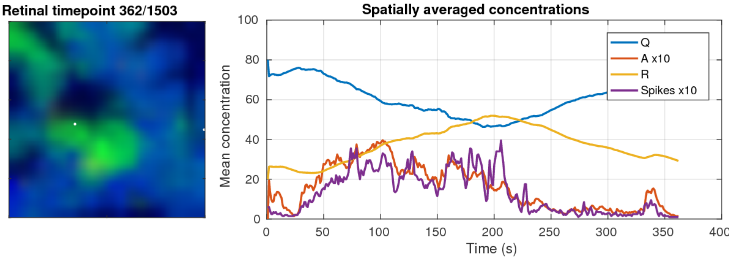

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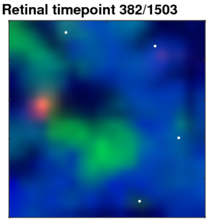

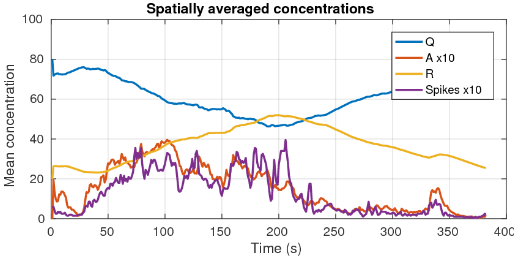

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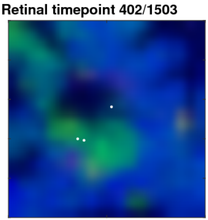

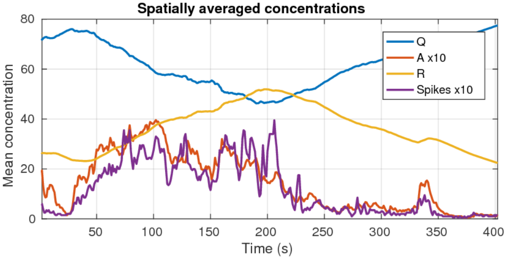

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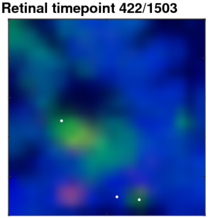

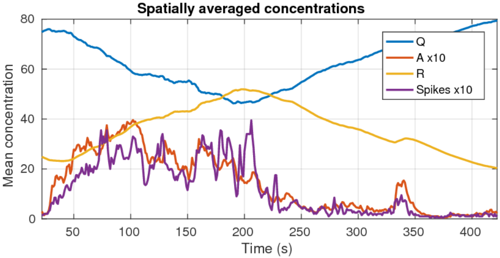

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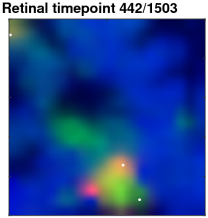

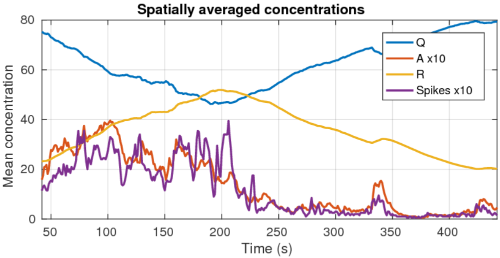

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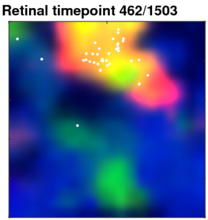

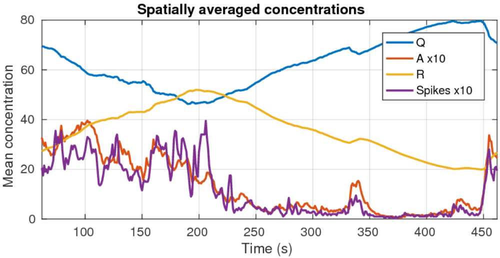

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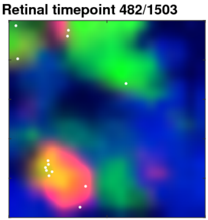
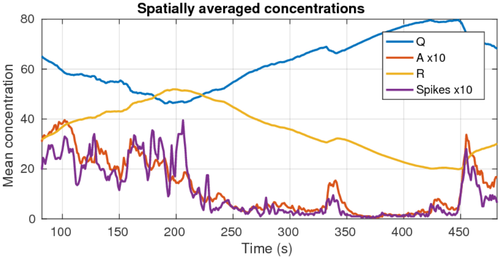
Filtering infers latent intensities from spiking data

P6 mouse retina; 20× real-time





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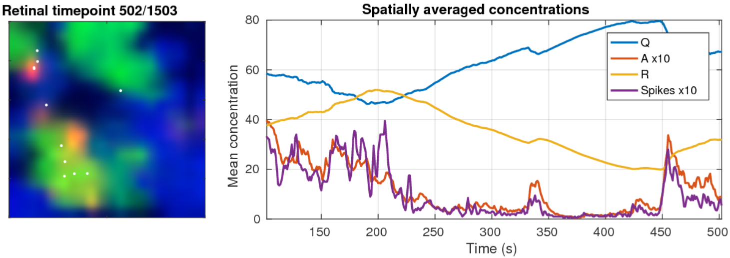

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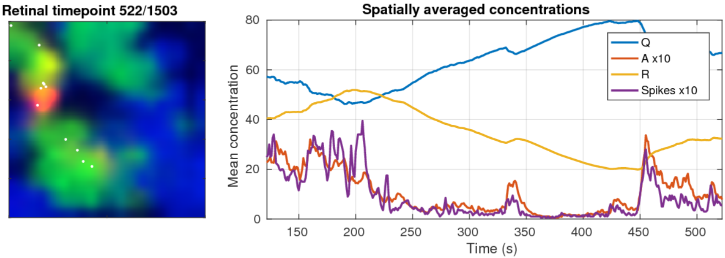

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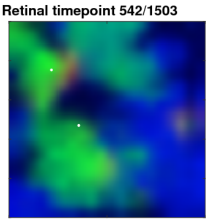

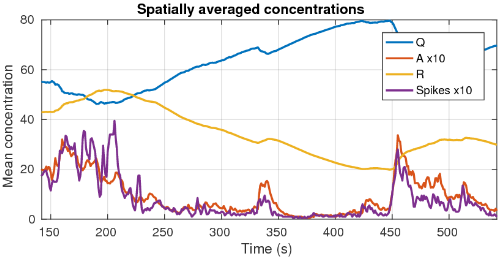

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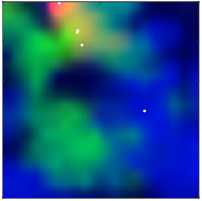

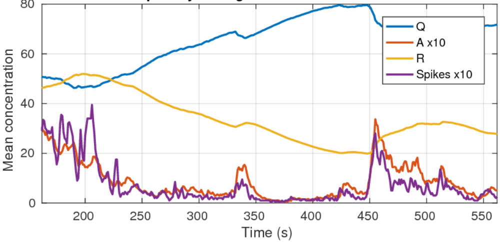

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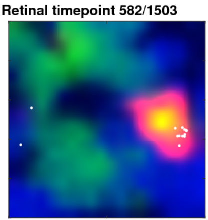

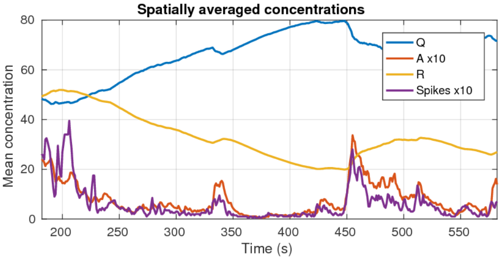

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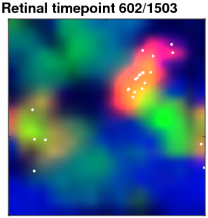

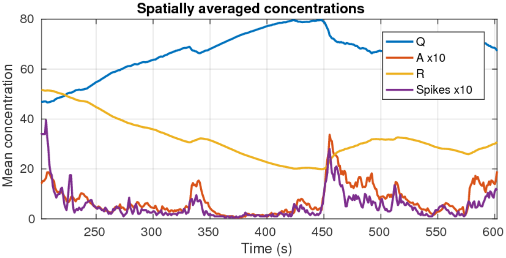

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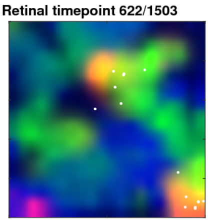

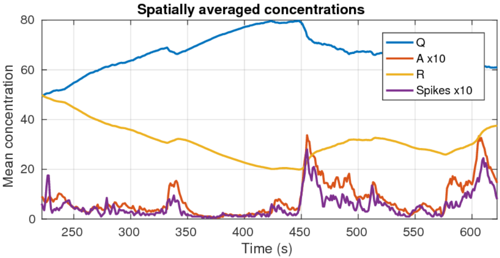

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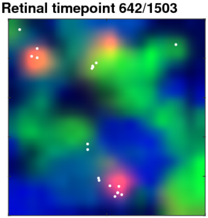

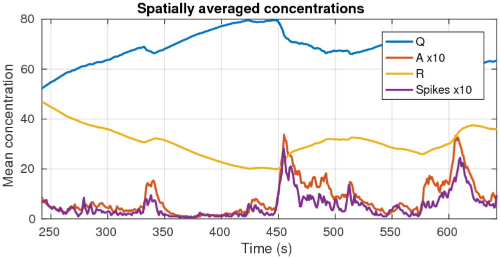

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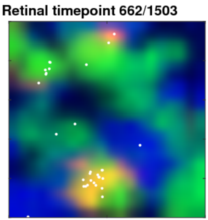

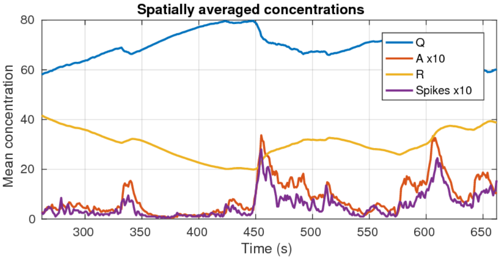

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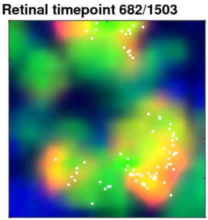

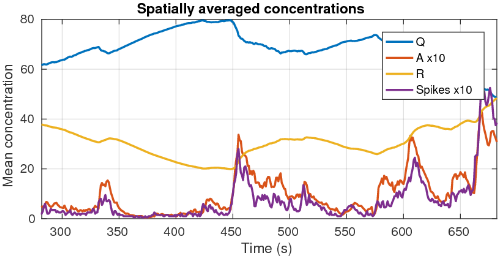

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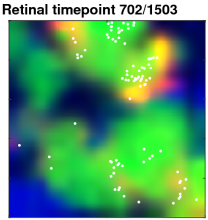

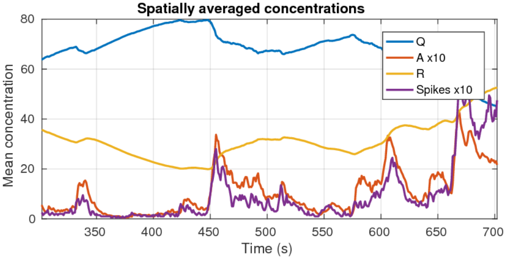

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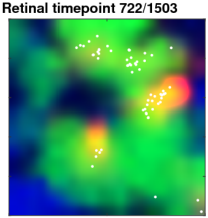

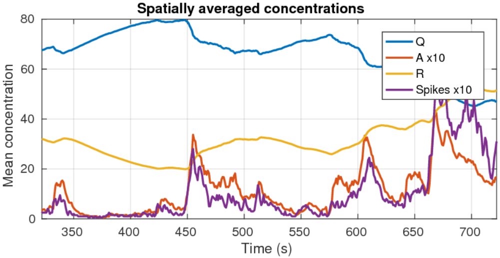

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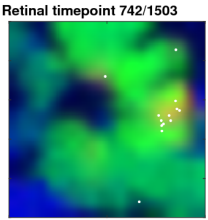

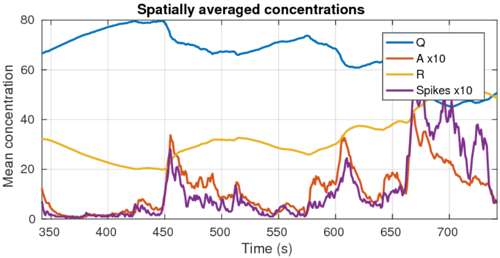

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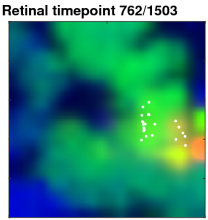

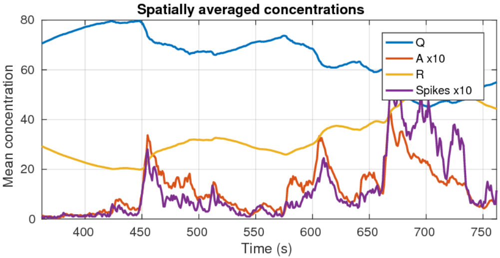

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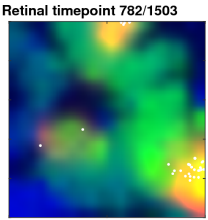

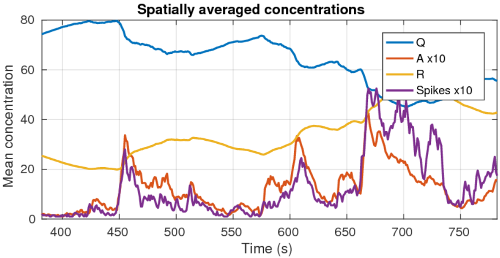

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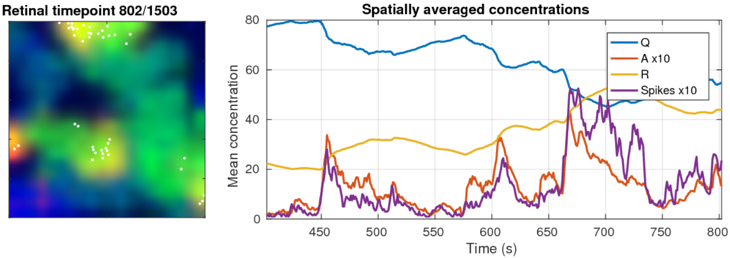

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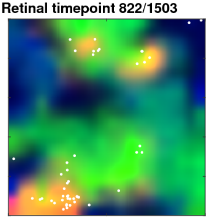

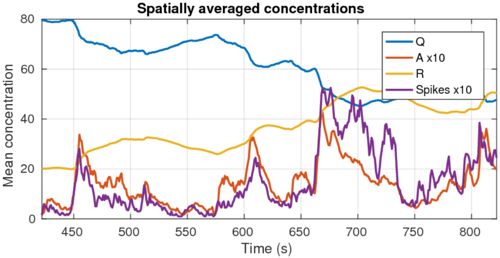

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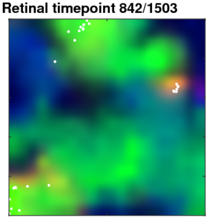

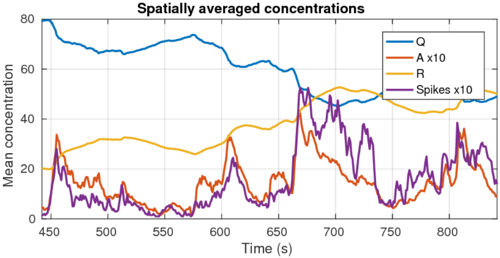

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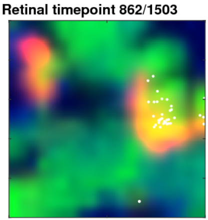

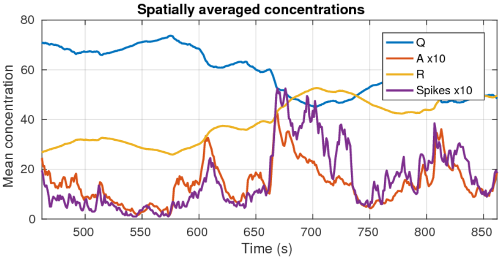

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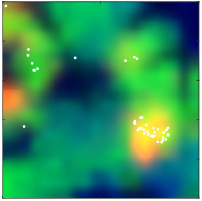

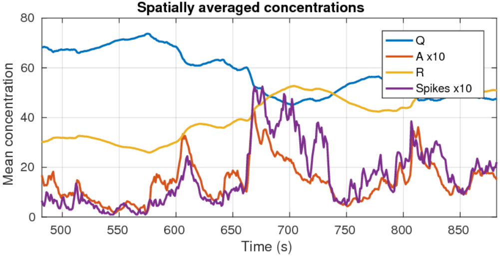

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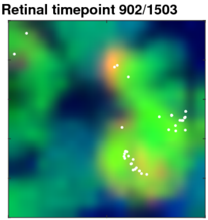

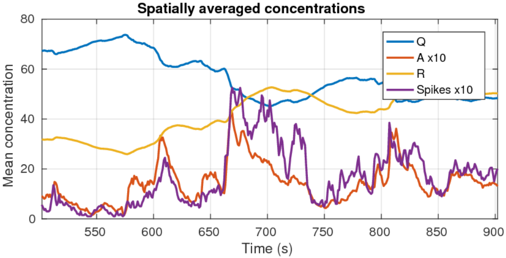

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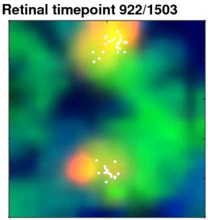

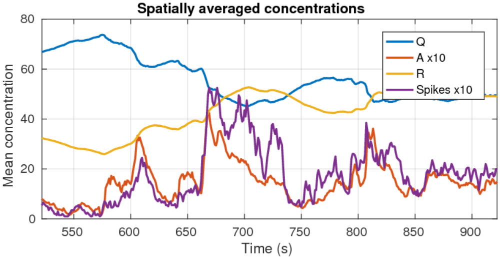

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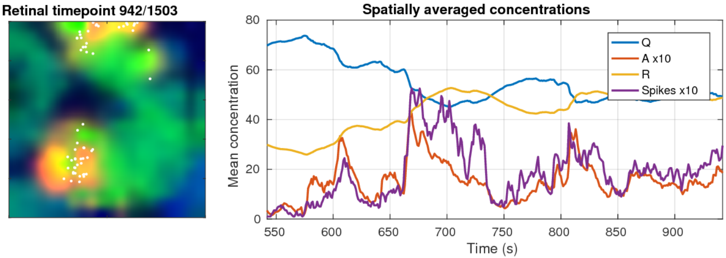

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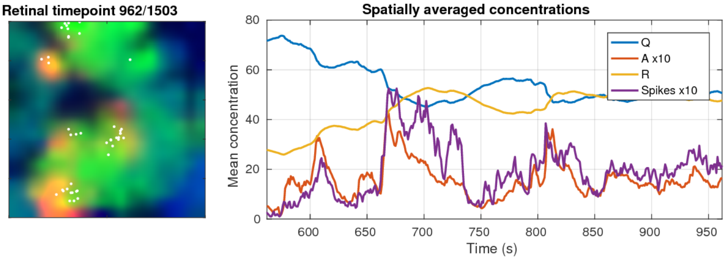

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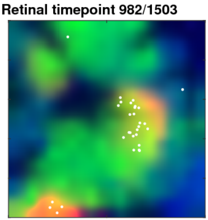

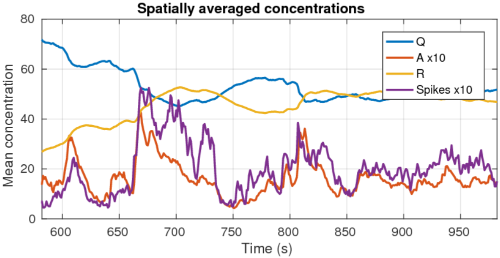

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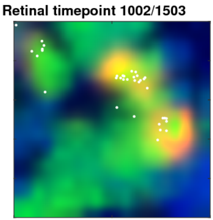

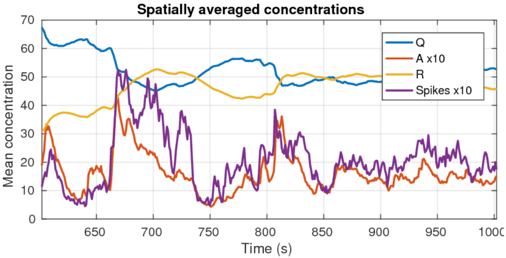

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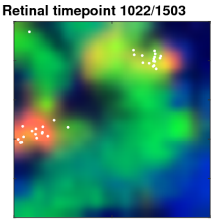

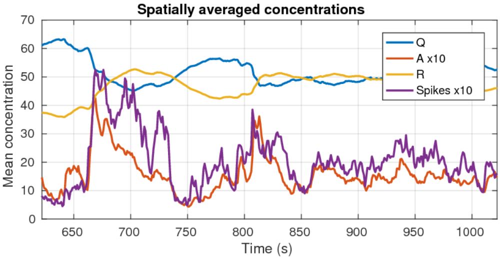

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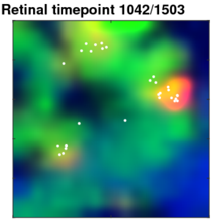

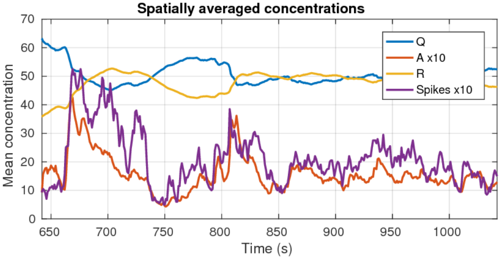

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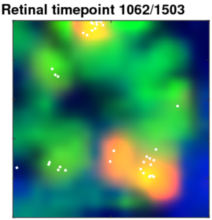

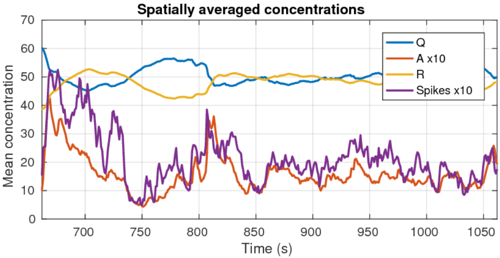

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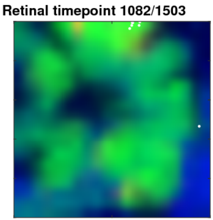

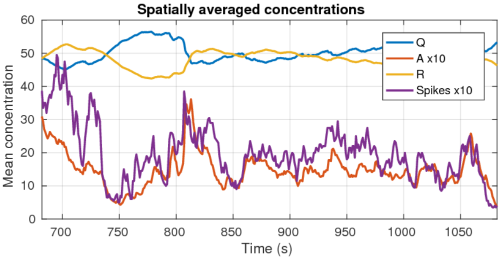

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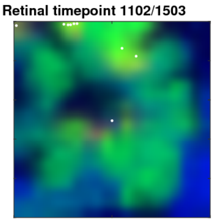

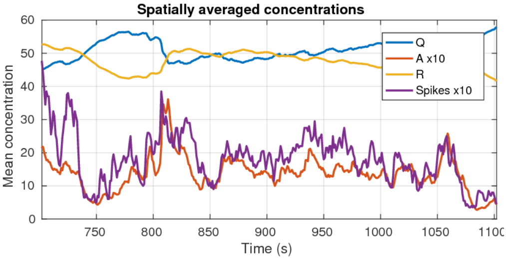

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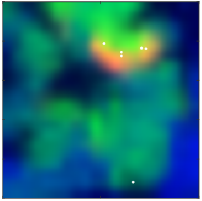

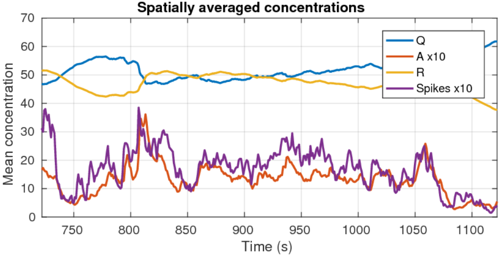

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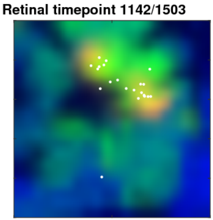

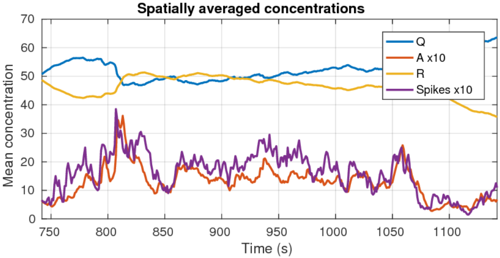

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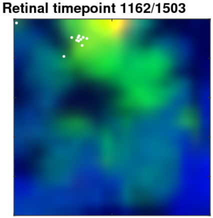

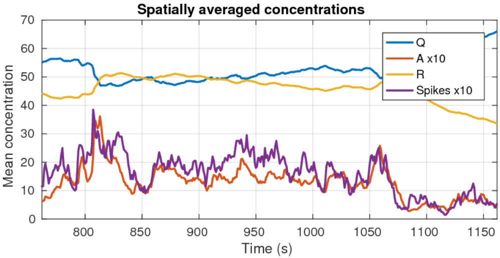

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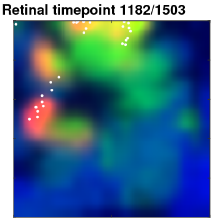

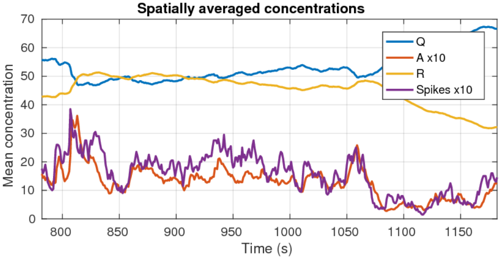

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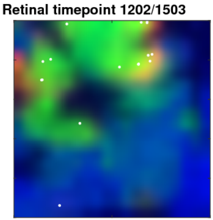

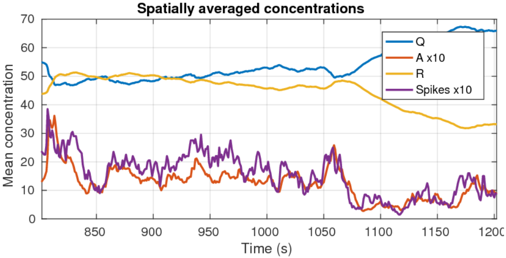

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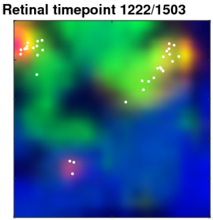

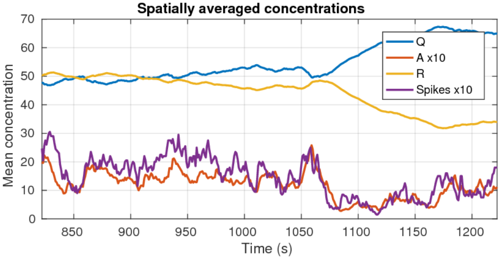

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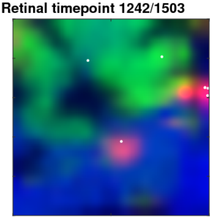

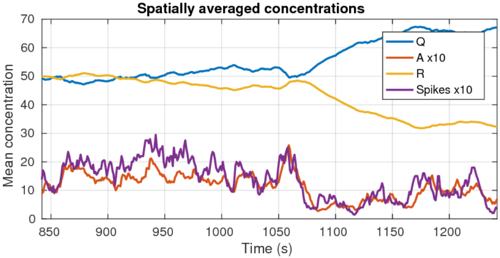

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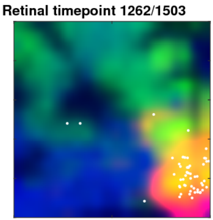

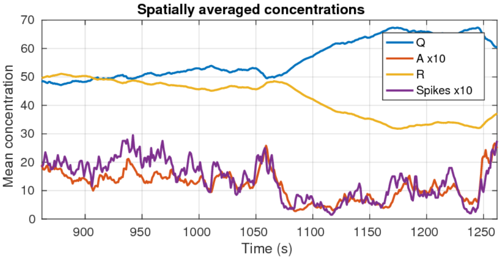

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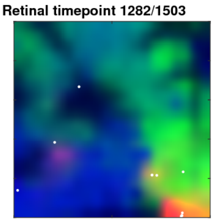

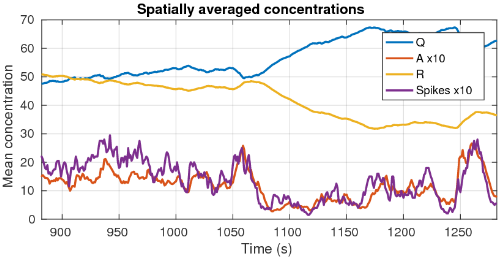

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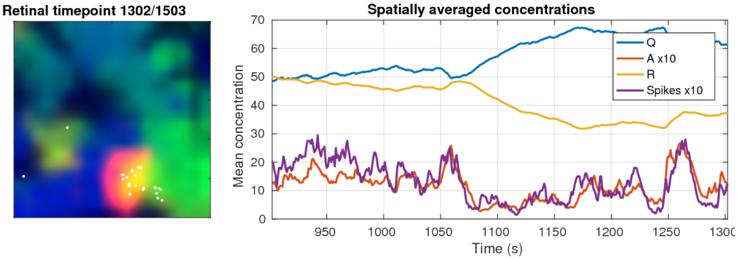

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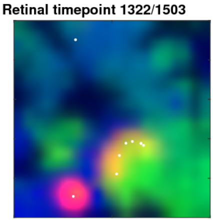

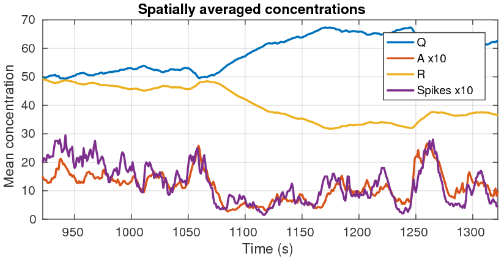

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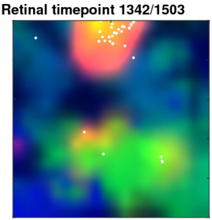

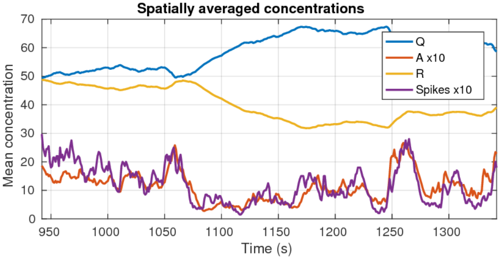

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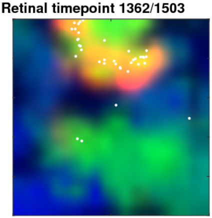

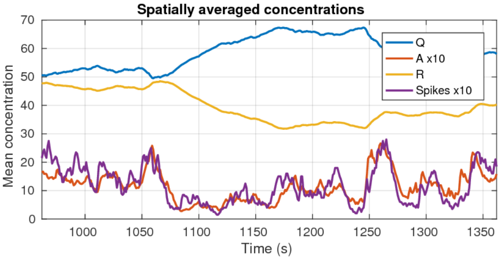

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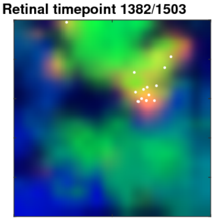

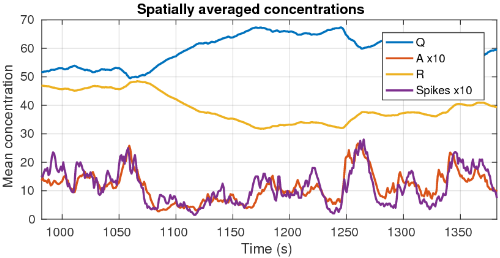

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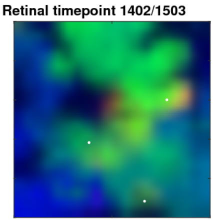

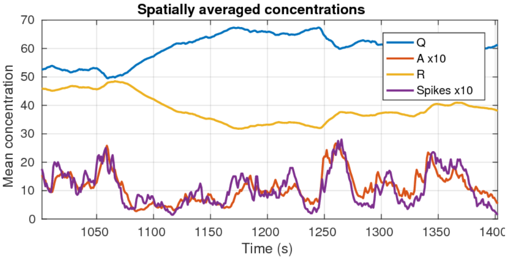

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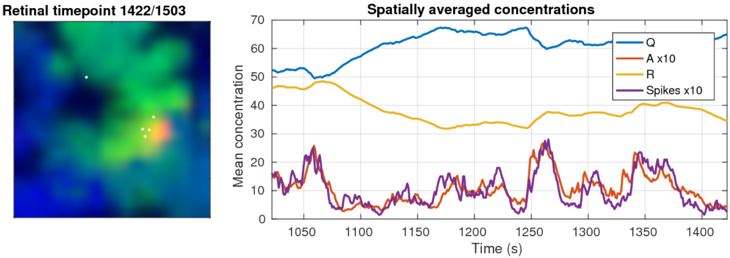

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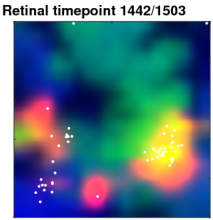

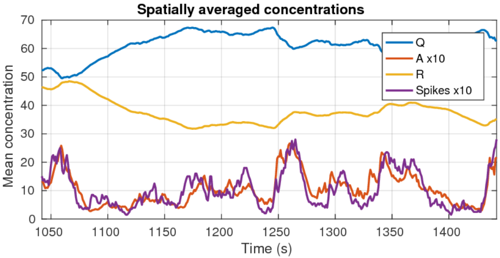

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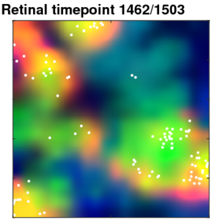

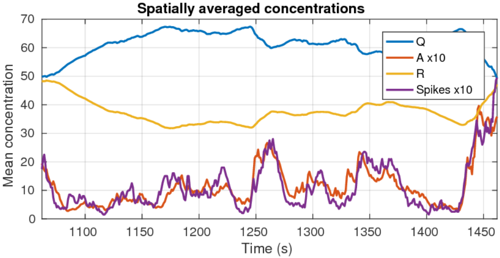

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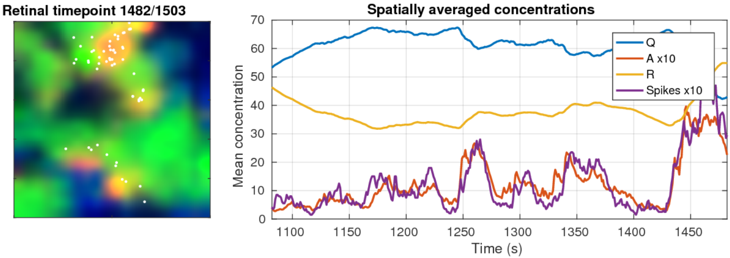

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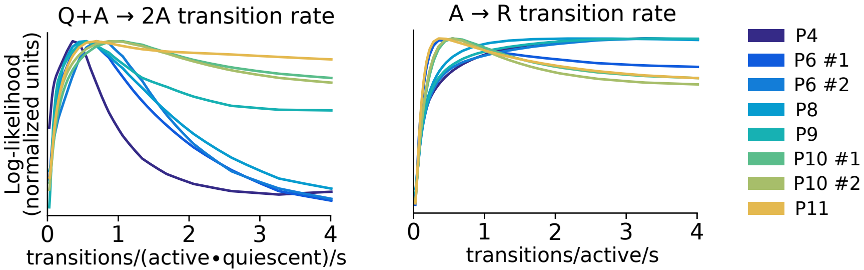
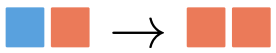
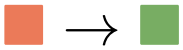
Inferring parameters...



ρ_e Excite quiescent cells



ρ_a Cells become refractory



Neural field → SSMs: **New directions**

Neural field moment closure applied to retinal waves:

- 3-state model (??)
- **Infer retinal wave states**
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Statistical mechanics → Bayesian inference

- *Posterior for population states*
  - Partially **observed via spiking data**
- *Posterior for neural field parameters* given data
  - New algorithms to optimize, sample, variational approx.

In Summary...

Moment Closure Point-Process Generalized Linear Model

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- Moment-closure on Langevin approximation to history process

Moments in time and space

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Single-neuron→collective dynamics **in 5 easy steps**

1. Microscopic description

Stochastic Descriptions of Microscopic Dynamics

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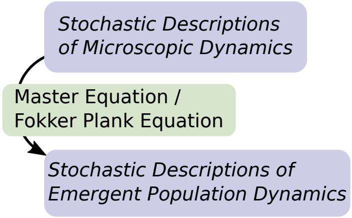

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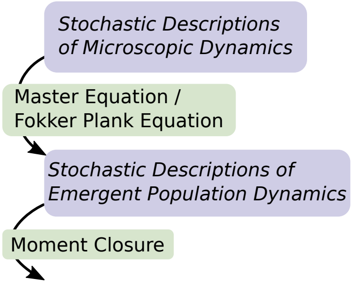

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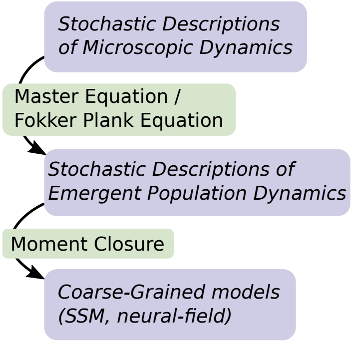

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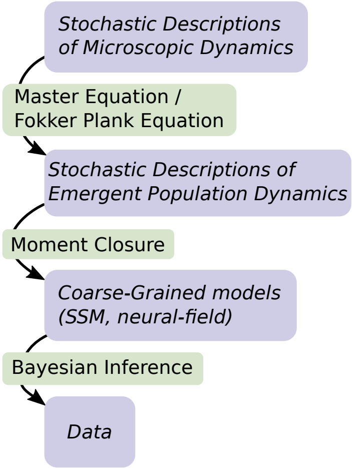

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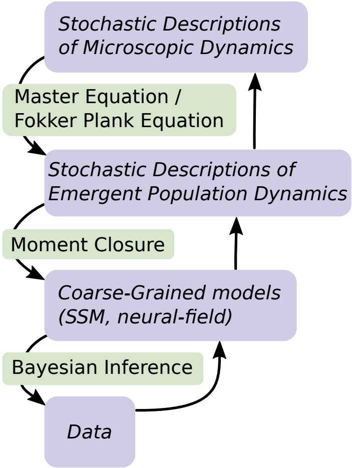
   - Optimize likelihood via filtering



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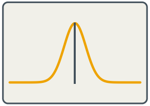
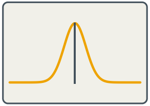
- Requires new algorithms



Neural mass/field:

- **Bayesian framework** from **statistical mechanics**?
- Far from μ-field: Statistical *fields of point-processes*?
- Fields as both *spatial* ***and*** *temporal* coarse-graining?

Single-neuron→collective dynamics: **Directions**



Neural mass/field:

- **Bayesian framework** from **statistical mechanics**?
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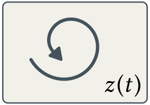

State Space Models:

- Incorporate nonlinearities and Poisson $\mathcal{O}(\sqrt{N})$ noise?
- *States not latent:* partially-observed point-process?

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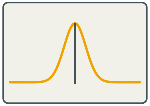

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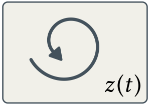

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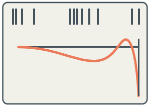

Autoregressive Point Process Models:

- *Bayesian estimation:* add **dynamical fidelity** into loss?
- *Statistical field description* of point process?
- *Coarse-graining* of pairwise models?

Acknowledgements

Project supervisors:

- Guido Sanguinetti
- Matthias Hennig

Experimental collaborators:

- Evelyne Sernagor
- Gerrit Hilgen

Computational and theoretical collaborators:

- David Schnoerr
- Martino Sorbaro
- Botond Cseke

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- Anastasis Georgoulas
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- David Schnoerr
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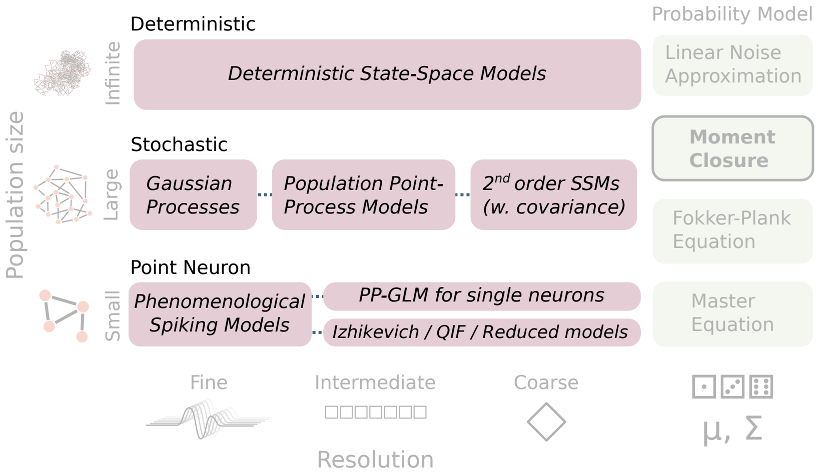
- Edward Wallace
- Gabriele Schweikert
- Giulio Caravagna
- Michalis Michaelides
- Tom Mayo
- Yuanhua Huang

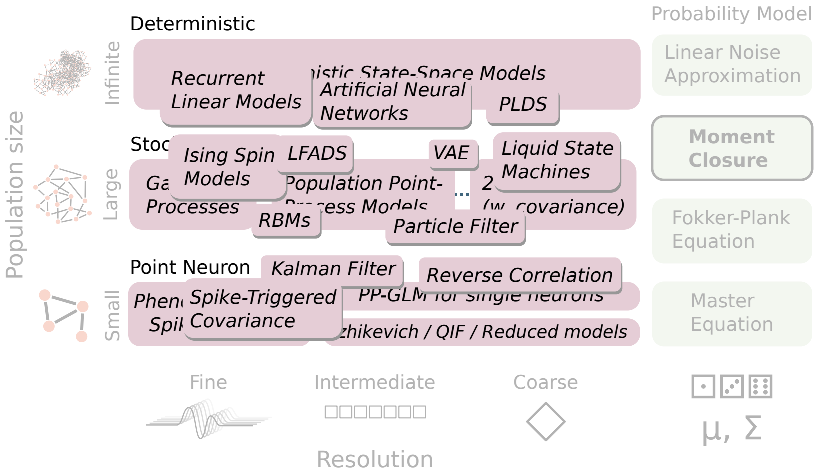
Stop Here

Appendix

Statistical Models



Statistical Models



Moment closure: how to?

Write down equations for moments of density

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Closed system

Moment closure, short cut:

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Hope that expectations w.r.t. assumed density have closed form

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e.g. for Gaussian $\langle x^2 \rangle$ $\langle e^x \rangle$ $\langle e^{x^2} \rangle$ etc. convenient

Three approaches to spiking population models

Generalized Linear **Point-Process Models** (PP-GLM)

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- **Pairwise** spike$\leftrightarrow$spike

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Autoregressive PP-GLM with history dependence

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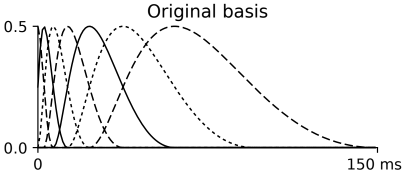


Time evolution of the covariance

Compute the deterministic contribution to the derivative of the covariance:

$$\Sigma = \left\langle hh^\top \right\rangle - \langle h \rangle \langle h \rangle^\top$$

Time evolution of the covariance

Differentiating the covariance:

$$\begin{aligned}
\partial_t \Sigma &= \partial_t \left(\left\langle h h^\top \right\rangle - \langle h \rangle \langle h \rangle^\top \right) \\
&= \partial_t \left\langle h h^\top \right\rangle - \partial_t \left(\langle h \rangle \langle h \rangle^\top \right) \\
&= \left\langle (\partial_t h) h^\top \right\rangle + \left\langle h (\partial_t h^\top) \right\rangle - \left(\partial_t \langle h \rangle \right) \langle h \rangle^\top - \langle h \rangle \left(\partial_t \langle h \rangle^\top \right)
\end{aligned}$$

Time evolution of the covariance

Symmetric terms from the product rule. Examine one set of terms, substitute delay-line evolution:

$$\begin{aligned}\left\langle (\partial_t h) h^\top \right\rangle - \left(\partial_t \langle h \rangle\right) \langle h \rangle^\top &= \left\langle [\delta_{\tau=0}\lambda - \partial_\tau h] h^\top \right\rangle - [\delta_{\tau=0} \langle \lambda \rangle - \partial_\tau \langle h \rangle] \langle h \rangle^\top \\ &= \delta_{\tau=0} \left[\left\langle \lambda h^\top \right\rangle - \langle \lambda \rangle \langle h \rangle^\top \right] - \partial_\tau \left[\left\langle h h^\top \right\rangle - \langle h \rangle \langle h \rangle^\top \right]\end{aligned}$$

Linear, except $\left\langle \lambda h^\top \right\rangle$

Time evolution of the covariance

Evaluate $\left\langle \lambda h^\top \right\rangle$ by completing the square $m = \langle h \rangle + \Sigma H$

$$
\begin{aligned}
\left\langle \lambda h^\top \right\rangle &= \left\langle h^\top e^{H^\top h + I} \right\rangle \\
&= e^{I(t)} \int_{dh} h e^{H^\top h} \frac{1}{\sqrt{|2\pi\Sigma|}} e^{-\frac{1}{2}(h - \langle h \rangle)^\top \Sigma^{-1} (h - \langle h \rangle)} \\
&= e^{I(t)} e^{\frac{1}{2}(m^\top \Sigma^{-1} m - \langle h \rangle^\top \Sigma^{-1} \langle h \rangle)} \cdot m^\top \\
&= e^{H^\top \langle h \rangle + I(t) + \frac{1}{2} H^\top \Sigma H} \cdot m^\top \\
&= \langle \lambda \rangle \left(\langle h \rangle + \Sigma H \right)^\top .
\end{aligned}
$$

Time evolution of the covariance

Overall, the deterministic contribution to the covariance is:

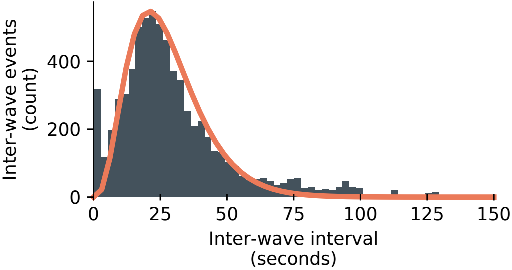
$$\left\langle (\partial_t h) h^\top \right\rangle - \left(\partial_t \langle h \rangle\right) \langle h \rangle^\top = \delta_{\tau=0} \left(\langle \lambda \rangle \left(\langle h \rangle + \Sigma H \right)^\top - \langle \lambda \rangle \langle h \rangle^\top \right) - \partial_\tau \Sigma$$

$$= \underbrace{\left(\delta_{\tau=0} \langle \lambda \rangle H^\top - \partial_\tau \right)}_{J} \Sigma$$

Finite Basis Projected Gaussian Moment Closure for PP-GLMs

$$
\begin{aligned}
\partial_t \mu_z &= -A\mu_z + C\langle\lambda\rangle \\
\langle\lambda\rangle &= \exp\left(\beta^\top \mu_z + I(t) + \tfrac{1}{2}\beta^\top \Sigma_z \beta\right) \\
\partial_t \Sigma_z &= J\Sigma_z + \Sigma_z J^\top + Q(t) \\
J &= C\langle\lambda\rangle \beta^\top - A \\
Q &= C\langle\lambda\rangle C^\top
\end{aligned}
$$

Inter-wave intervals suggest multiple refractory states



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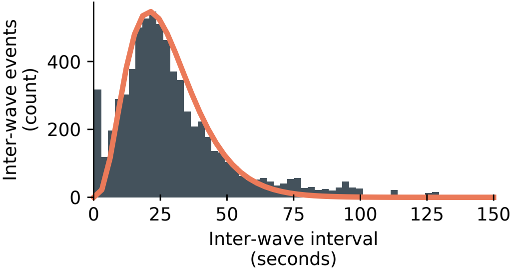

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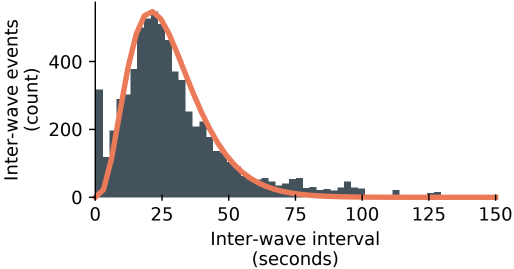

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$$A \to R_1 \to R_2 \to R_3 \to S$$

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Part 2:

- Bayesian State-Space Inference for Stochastic Neural fields
- Applied to waves in the developing retina