Neural Networks

Computational Neuroscience 4G3

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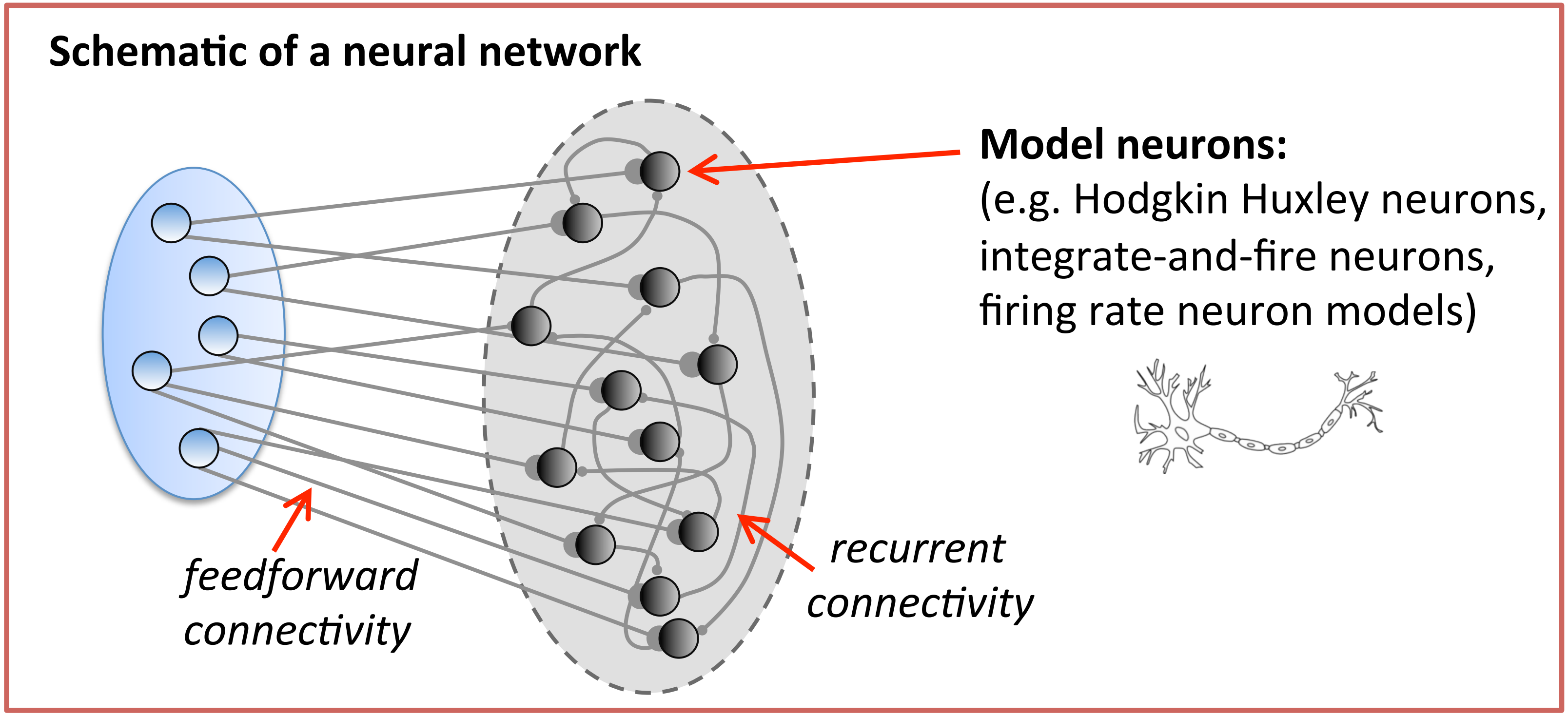
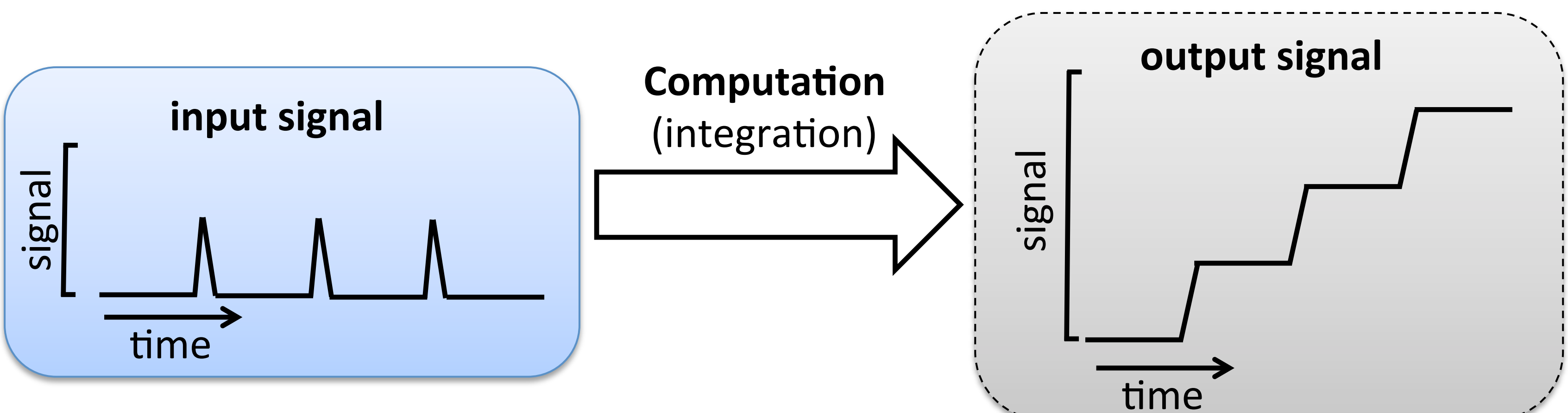
Introduction

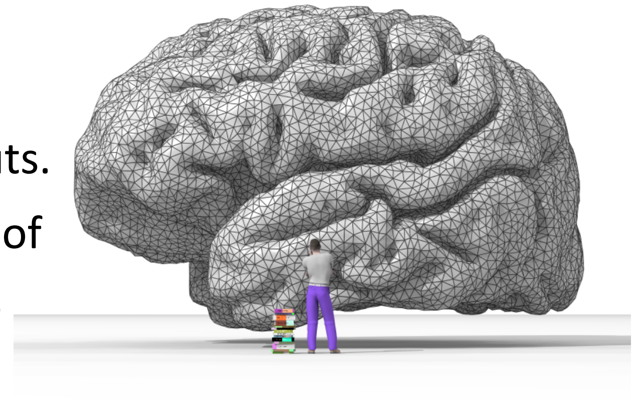


Neural networks can support a huge variety of computations

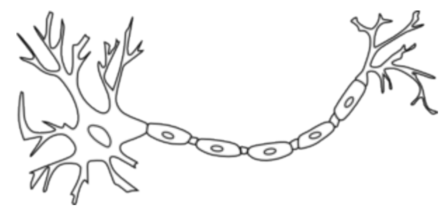


How should we model neural networks?

- In the mammalian neocortex, neural dynamics is predominantly determined by network activity.
- Many neuron receives thousands of synaptic inputs.
- This input is so strong that the detailed dynamics of individual neurons can be less important than the network-level interaction of neurons.



Direct approach: construct a network of interconnected realistic spiking neurons

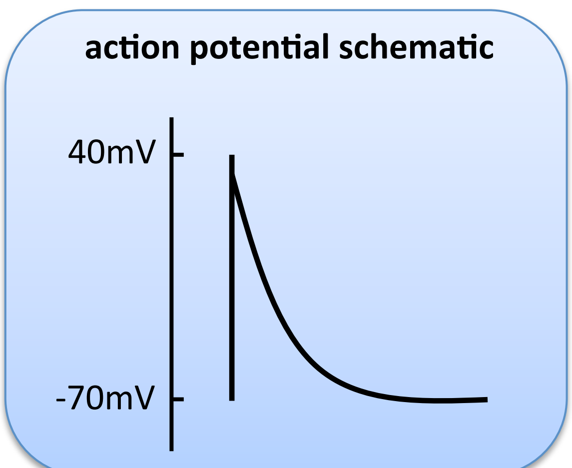


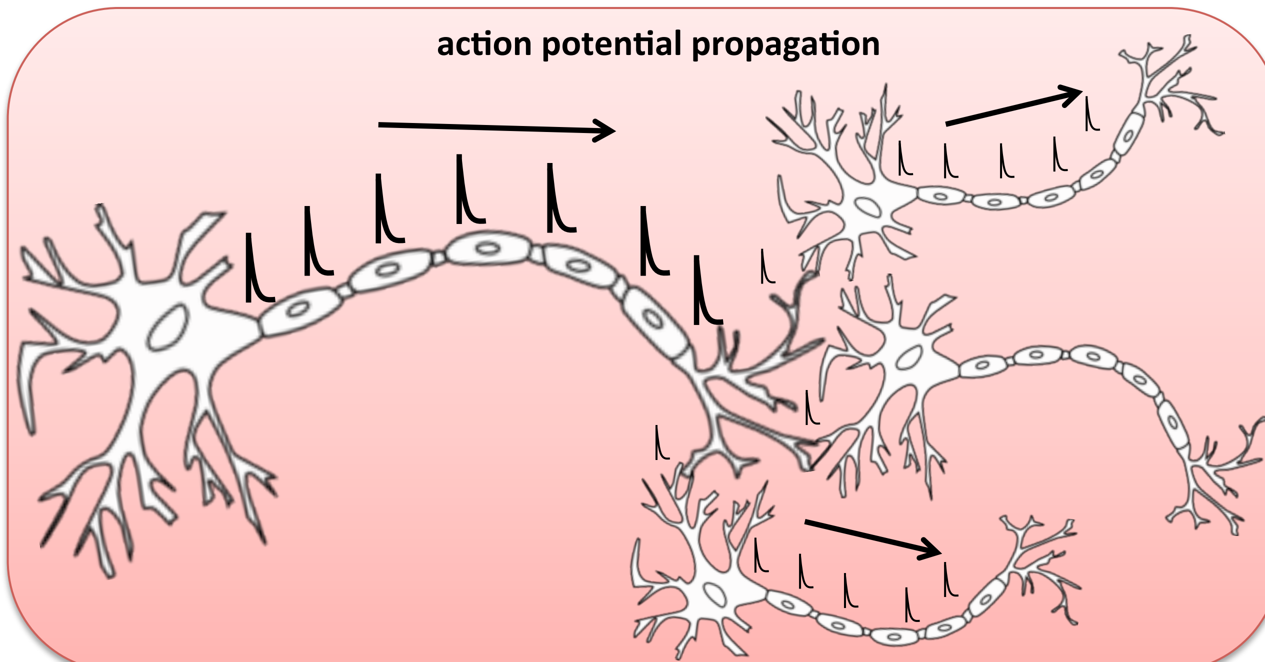
Disadvantages:

- Analysing these networks is difficult.
- Simulations of large-scale cortical networks can involve prohibitive computational expense.
- We do not know the precise value of all the parameters for these models, and the network behaviour may depend sensitively on these choices.

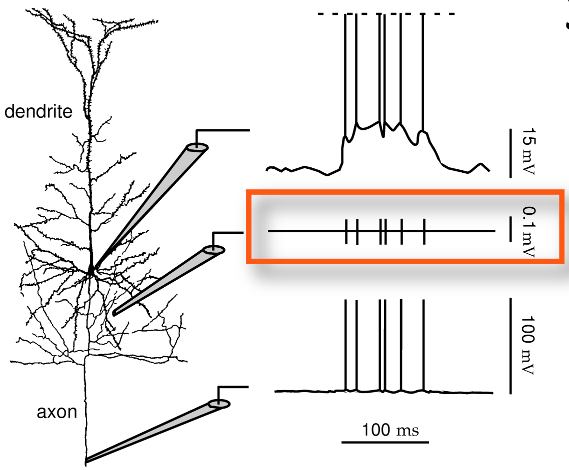
Single neuron spiking dynamics

- A neuron produces an signal called the action potential.
- This is an electrical signal that propagates from the soma of the neuron, down the axon to the synapses.
- At the synapses, the electrical action potential is converted into a chemical signal that is communicated to the dendrites of post-synaptic neurons.
- The signals from pre-synaptic neurons are combined at the soma to initiate an action potential





Single neuron spike trains



mathematical representations

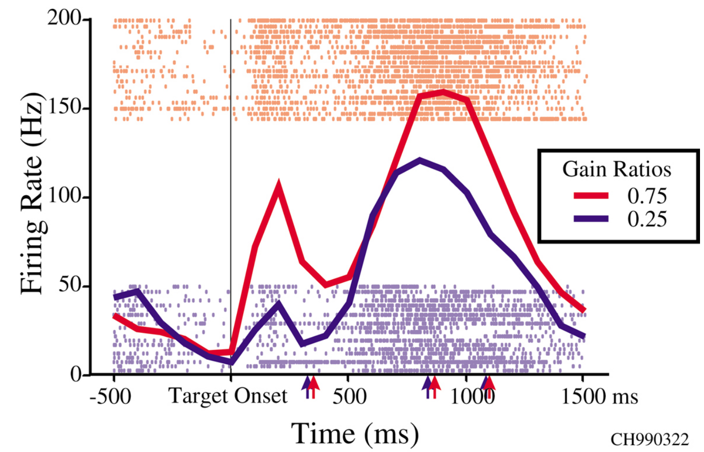
set of spike times: $\mathcal{S} = \{t_1, t_2, \ldots, t_n\}$

neural response function: $\rho(t) = \sum_{i=1}^{n} \delta(t - t_i)$

firing rates

spike-count rate: $r = \frac{n}{T} = \frac{1}{T}\int_0^T \rho(\tau)\, d\tau$

firing rate (trial average): $r(t) = \frac{1}{\Delta t}\int_t^{t+\Delta t} \langle \rho(\tau) \rangle\, d\tau$

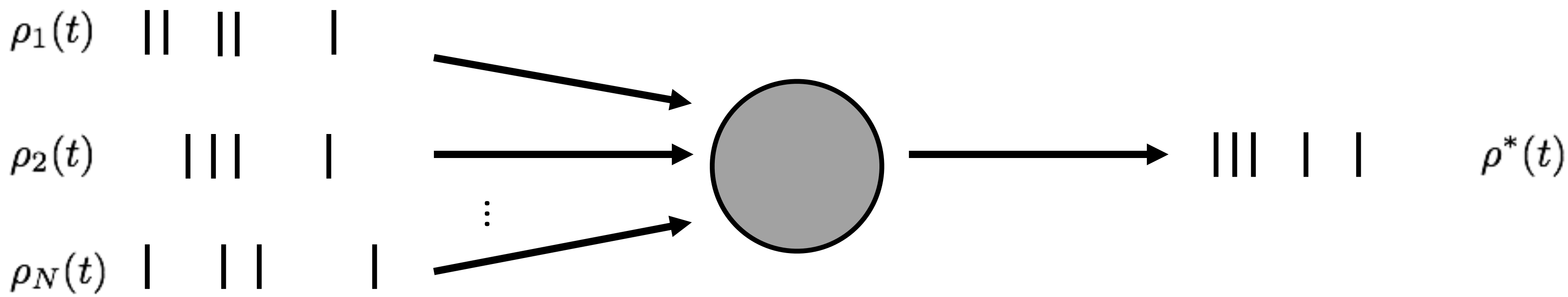


aka post-stimulus time histogram (PSTH)

average firing rate: $\langle r \rangle = \frac{\langle n \rangle}{T} = \frac{1}{T}\int_0^T \langle \rho(\tau) \rangle\, d\tau = \frac{1}{T}\int_0^T r(\tau)\, d\tau$

Firing rate models: Construction

We can approximate spiking dynamics with firing rate dynamics in many neural networks.



1. total synaptic inputs → somatic current injection

$$
\begin{aligned}
I_{\mathrm{s}}(t) &= \sum_{j}^{N} w_j \int_{-\infty}^{t} d\tau \, K_{\mathrm{s}}(t-\tau)\, \rho_j(\tau) \\
&\rightarrow \sum_{j}^{N} w_j \int_{-\infty}^{t} d\tau \, K_{\mathrm{s}}(t-\tau)\, r_j(\tau)
\end{aligned}
$$

exponential synaptic kernel: $K_{\mathrm{s}}(t) = \frac{1}{\tau_{\mathrm{s}}} e^{-\frac{t}{\tau_{\mathrm{s}}}}$

$$\tau_{\mathrm{s}} \frac{dI_{\mathrm{s}}}{dt} = -I_{\mathrm{s}}(t) + \sum_{j}^{N} w_j r_j(t) = -I_{\mathrm{s}}(t) + \mathbf{w}^{\top}\mathbf{r}(t)$$

2. somatic current → firing rate

$$\tau_{\mathrm{r}} \frac{dr^*}{dt} = -r^*(t) + F(I_{\mathrm{s}}(t))$$

special cases

$\tau_{\mathrm{r}} \ll \tau_{\mathrm{s}}$ $\qquad r^*(t) = F(I_{\mathrm{s}}(t))$

$\tau_{\mathrm{r}} \gg \tau_{\mathrm{s}}$ $\qquad \tau_{\mathrm{r}} \frac{dr^*}{dt} = -r^*(t) + F\left(\mathbf{w}^{\top}\mathbf{r}(t)\right)$

Recurrent network models

Firing rate dynamics:
(single neuron notation)

$$\tau_r \frac{dr_i}{dt} = -r_i(t) + F(\underbrace{h_i}_{\text{external input}} + \underbrace{\sum_j W_{ij} r_j(t)}_{\text{recurrent input}})$$

Firing rate dynamics:
(vector notation)

$$\tau_r \frac{d\mathbf{r}}{dt} = -\mathbf{r}(t) + F(\mathbf{h} + \mathbf{W}\mathbf{r}(t))$$

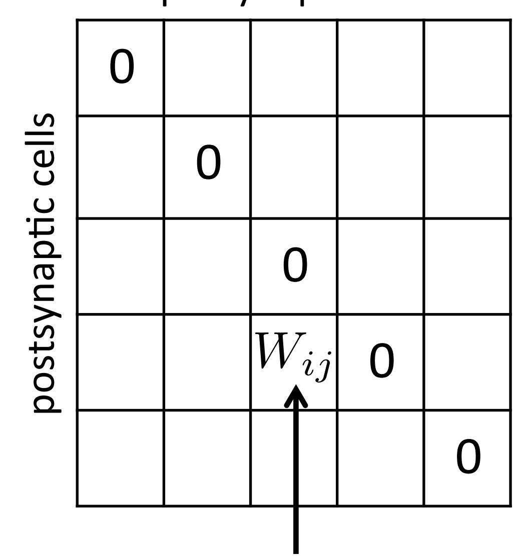
$$\mathbf{r}(t) = [r_1(t), \ldots, r_i(t), \ldots, r_N(t)]^T$$

Non-linear network properties

- Recurrent network models can produce realistic cortical dynamics
- They can perform difficult computations with their inputs.
- However, they can be difficult to analyse.

synaptic weight matrix W

presynaptic cells



synaptic weight between presynaptic cell j and postsynaptic cell i

Linear Recurrent network models

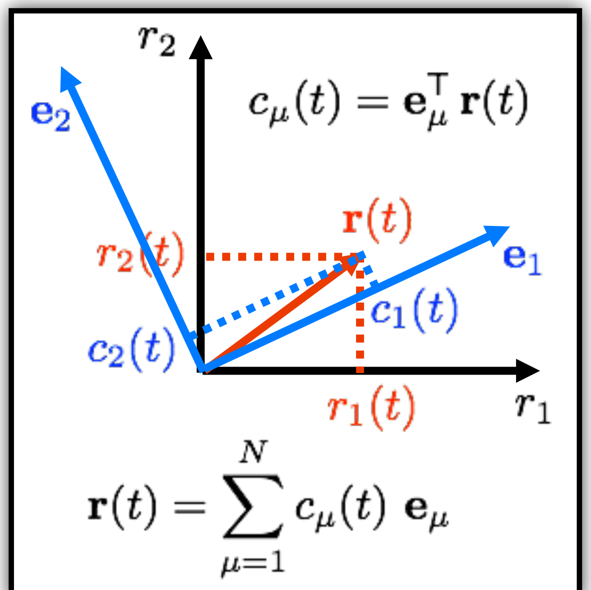
Firing rate dynamics: $\tau_r \frac{d\mathbf{r}}{dt} = -\mathbf{r}(t) + \mathbf{h} + \mathbf{W}\mathbf{r}(t)$

- Linear recurrent networks are easier to analyse than non-linear recurrent networks.
- However, they are not as realistic e.g. they can produce negative firing rate values.
- They are useful for understanding simulations of non-linear networks.

Solving for r*(t)*:

- We can solve a system of coupled linear equations using an eigenvector decomposition.
- To simplify this analysis, we will consider symmetric neural networks: $W_{ij} = W_{ji}$

Eigenvector decomposition



Eigenvectors and eigenvalues of W

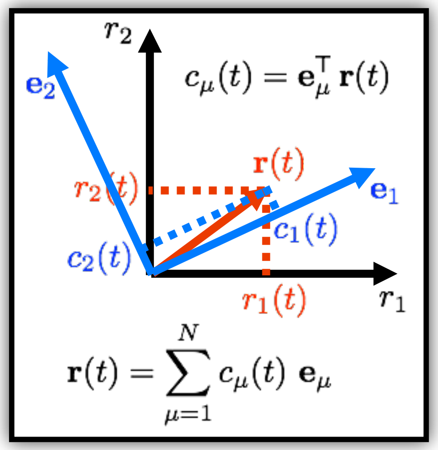
$$\mathbf{W}\mathbf{e}_\mu = \lambda_\mu \mathbf{e}_\mu$$

$$\mathbf{e}_\mu^\top \mathbf{e}_\nu = \delta_{\mu\nu} = \begin{cases} 1 & \text{if } \mu = \nu \\ 0 & \text{otherwise} \end{cases}$$

Solving linear recurrent network models

Firing rate dynamics: $$\tau_r \frac{d\mathbf{r}}{dt} = -\mathbf{r}(t) + \mathbf{h} + \mathbf{W}\mathbf{r}(t)$$

Solving for **r(*t*)**: $$\tau_r \frac{d}{dt}\left(\sum_{\mu=1}^{N} c_\mu(t)\mathbf{e}_\mu\right) = -\left(\sum_{\mu=1}^{N} c_\mu(t)\mathbf{e}_\mu\right) + \mathbf{h} + \mathbf{W}\left(\sum_{\mu=1}^{N} c_\mu(t)\mathbf{e}_\mu\right)$$



$$\tau_r \sum_{\mu=1}^{N} \mathbf{e}_\mu \frac{dc_\mu(t)}{dt} = -\sum_{\mu=1}^{N} c_\mu(t)\mathbf{e}_\mu + \mathbf{h} + \sum_{\mu=1}^{N} c_\mu(t)\underbrace{\mathbf{W}\mathbf{e}_\mu}_{\lambda_\mu \mathbf{e}_\mu}$$

$$\tau_r \sum_{\mu=1}^{N} \mathbf{e}_\mu \frac{dc_\mu(t)}{dt} = -\sum_{\mu=1}^{N} (1-\lambda_\mu)c_\mu(t)\mathbf{e}_\mu + \mathbf{h}$$

$$\tau_r \sum_{\mu=1}^{N} \underbrace{(\mathbf{e}_\nu^T\mathbf{e}_\mu)}_{\delta_{\nu\mu}} \frac{dc_\mu(t)}{dt} = -\sum_{\mu=1}^{N} (1-\lambda_\mu)c_\mu(t)\underbrace{(\mathbf{e}_\nu^T\mathbf{e}_\mu)}_{\delta_{\nu\mu}} + \underbrace{\mathbf{e}_\nu^T\mathbf{h}}_{g_\nu}$$

$$\tau_r \frac{dc_\nu(t)}{dt} = -(1-\lambda_\nu)c_\nu(t) + g_\nu$$

Solution:

$$c_\nu(t) = \frac{g_\nu}{1-\lambda_\nu} + \left[c_\nu(0) - \frac{g_\nu}{1-\lambda_\nu}\right] e^{-t/(\tau_r/(1-\lambda_\nu))}$$

$$\mathbf{r}(t) = \sum_{\nu=1}^{N} c_\nu(t)\mathbf{e}_\nu$$

Input amplification $\lambda_\nu < 1$

- The value of the eigenvalues determine the dynamics of the network.

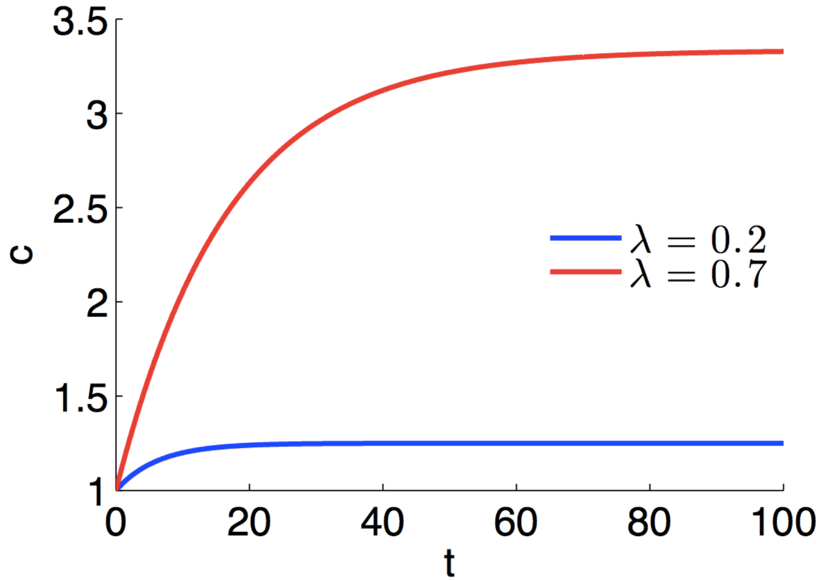
$$c_\nu(t) = \frac{g_\nu}{1-\lambda_\nu} + \left[c_\nu(0) - \frac{g_\nu}{1-\lambda_\nu}\right] e^{-t/(\tau_r/(1-\lambda_\nu))}$$

$$\to \frac{g_\nu}{1-\lambda_\nu} \quad \text{as} \quad t \to \infty \quad \text{for} \quad \lambda_\nu < 1$$

$$\mathbf{r}(t) = \left(\sum_{\nu=1}^{N} c_\nu(t)\mathbf{e}_\nu\right) \to \left(\sum_{\nu=1}^{N} \frac{g_\nu}{1-\lambda_\nu}\mathbf{e}_\nu\right) = \left(\sum_{\nu=1}^{N} \frac{\mathbf{e}_\nu \cdot \mathbf{e}_\nu^T}{1-\lambda_\nu}\mathbf{h}\right)$$

- In this case, the network converges towards a steady state.
- The size of the input amplification is determined by the connectivity eigenvalues.

Example: Amplification of a constant input h



Input integration $\lambda_\nu = 1$

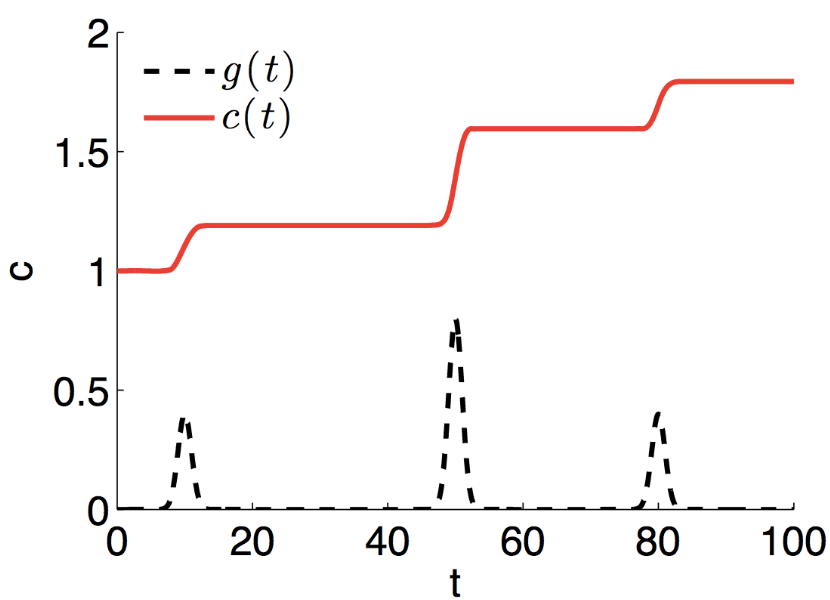
- In this case, the solution of our firing rate equations takes a different form:

$$\tau_r \frac{dc_\nu(t)}{dt} = -(1-\lambda_\nu)c_\nu(t) + g_\nu = g_\nu$$

$$c_\nu(t) = \frac{1}{\tau_r}\int_0^t g_\nu(t)\,dt + c_\nu(0) = \frac{\mathbf{e}_\nu^T}{\tau_r}\left[\int_0^t \mathbf{h}(t)\,dt\right] + c_\nu(0)$$

- The network performs a perfect integration of its input.

Example: Integration of a time dependent input



Divergent dynamics $\lambda_\nu > 1$

- In this case, the firing rates get exponentially larger, as time increases.

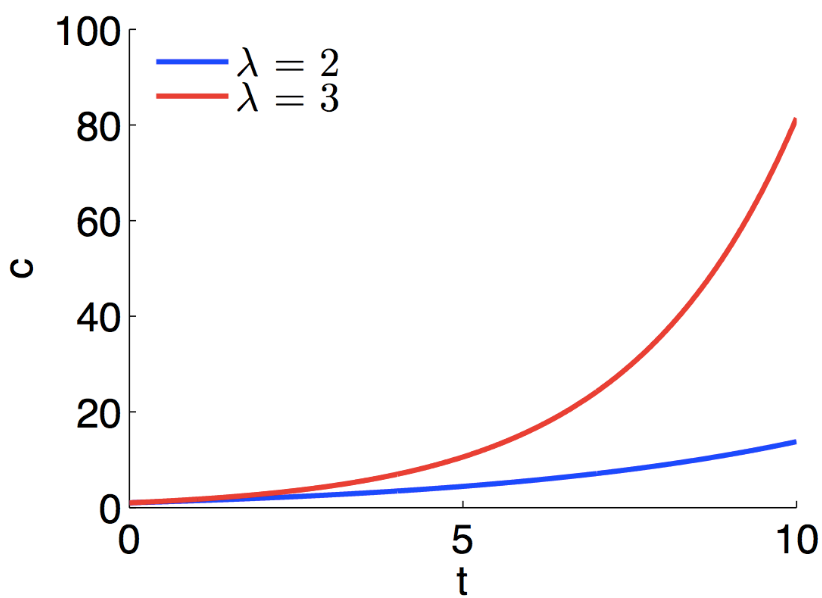
$$c_\nu(t) = \frac{g_\nu}{1-\lambda_\nu} + \left[c_\nu(0) - \frac{g_\nu}{1-\lambda_\nu}\right] e^{-t/(\tau_r/(1-\lambda_\nu))}$$

$$\rightarrow \left[c_\nu(0) - \frac{g_\nu}{1-\lambda_\nu}\right] e^{t/(\tau_r/|1-\lambda_\nu|)} \quad \text{for } t \gg 0 \quad \text{for } \lambda_\nu > 1$$

$$|\mathbf{r}| \rightarrow \infty \quad \text{as} \quad t \rightarrow \infty$$

- The speed of divergence is determined by the size of the eigenvalues

Example: Divergent dynamics with a constant input



Transient dynamics

- The dynamics of the network are determined by the eigenvectors with the largest eigenvalues.
- Consider a network with $\lambda_1 \gg \lambda_\nu > 1$ for $\nu > 1$

$$c_1 \to \left[c_1(0) - \frac{g_1}{1-\lambda_1}\right] e^{t/(\tau_r/|1-\lambda_1|)} \gg c_\nu \quad \text{for } t \gg 0 \text{ and } \nu > 1$$

$$\mathbf{r}(t) = \left(\sum_{\nu=1}^{N} c_\nu(t)\mathbf{e}_\nu\right) \to \; c_1(t)\mathbf{e}_1$$