Neuron Model Reduction → Integrate-and-fire

Hodgkin-Huxley model

↓

Two-dimensional models

↓

Integrate-and-fire models

→ Two-dimensional Integrate-and-fire

→ Spike Response Model

00_title.psd

Improvements of the Integrate-and-fire

Integrate-and-fire models

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e$$

If $V > V_{th}$, then $V = V_{reset}$

→ "Nonlinear" Integrate-and-fire

$$\begin{aligned} C\dot{v} &= k(v - v_r)(v - v_t) - u + I \\ u &= a\{b(v - v_r) - u\} \end{aligned} \qquad \begin{aligned} &\text{if } v \geq v_{peak}, \text{ then} \\ &v \to c,\ u \to u + d \end{aligned}$$

→ Spike Response Model ("Integrated" Integrate-and-fire)

$$V(t) = \eta(t - \hat{t}\,) + \int_0^\infty \kappa(t - \hat{t}, s)\, I(t - s)\, \mathrm{d}s$$

Convert a **differential** equation into an **integral** equation.

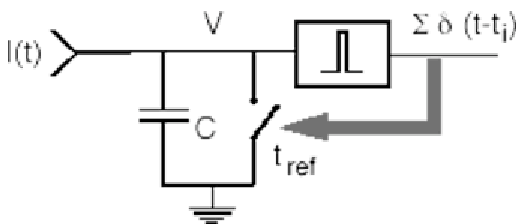
01_IF_improve.psd

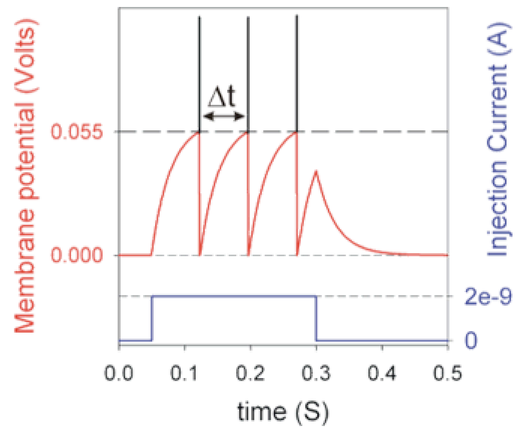
Integrate-and-Fire Model

One-variable, linear in V, with a threshold and reset to represent spikes.

$$c_m \frac{dV}{dt} = -\bar{g}_L (V - E_L) + \frac{I_e}{A}$$

If $V > V_{th}$, then $V = V_{reset}$





(Dayan & Abbott, 2001)

02_IF.psd

Integrate-and-Fire Model

If the injected current is time-independent, then the equation can be integrated to find analytic solutions for the firing rate.

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e \qquad \text{If } V > V_{th}, \text{ then } V = V_{reset}$$

Integrate from time=0, to time=t:

$$V(t) = E_L + R_m I_e + (V(0) - E_L - R_m I_e)\exp(-t/\tau_m)$$

If the neuron fired an action potential at t = 0, then $V(0) = V_{reset}$
The next action potential will occur when the membrane potential reaches the threshold.

$$V(t_{isi}) = V_{th} = E_L + R_m I_e + (V_{reset} - E_L - R_m I_e)\exp(-t_{isi}/\tau_m)$$

Linear, for large current injections.

(Dayan & Abbott, 2001)

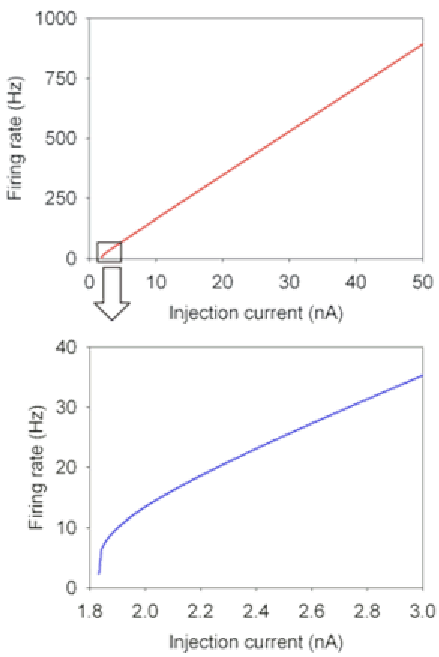
03_IF2 solu.psd

Integrate-and-Fire Model: Problems

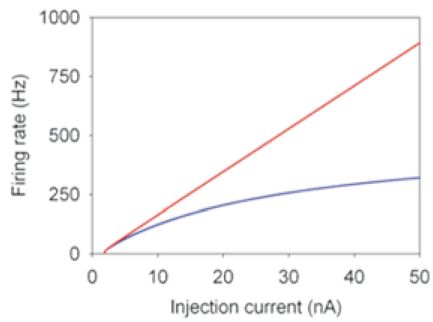
Simplifications results in inaccuracies when predicting spike rates.

Real neurons:

(1) Respond Nonlinearily to weak input



(2) Have an absolute ractory period



04_IF2 problems.psd

Integrate the Integrate-and-Fire Model

Start with an integrate-and-fire neuron driven by external current:

$$\frac{\mathrm{d}u}{\mathrm{d}t} = -u_i(t) + \frac{1}{C} I(t)$$

where we shifted the membrane potential, $u(t) = V(t) - V_{rest}$

Integrate with a **time-dependent** current:

$$u(t) = u_r \, \exp\left(-\frac{t-\hat{t}}{\tau_m}\right) + \frac{1}{C}\int_0^{t-\hat{t}} \exp\left(-\frac{s}{\tau_m}\right) \, I(t-s) \, \mathrm{d}s$$

(Gerstner, 2002)

05_IF-integ.psd

Synaptic Currents

Couple to presynaptic neurons with postsynaptic currents:

$$\alpha(t - t_j^{(f)}) = -g(t - t_j^{(f)})\ [u_i(t) - E_{\text{syn}}]$$

The total synaptic current is the weighted sum of synaptic inputs:

$$I_i(t) = \sum_j w_{ij} \sum_f \alpha(t - t_j^{(f)})$$

We will represent the postsynaptic current with an exponential decay function:

$$\alpha(s) = \frac{q}{\tau_s} \exp\left(-\frac{s}{\tau_s}\right)\ \Theta(s)$$

(Gerstner, 2002)

06_IF-synCur.psd

Integrate the Integrate-and-Fire Model

The integrated result with postsynaptic currents:

$$u(t) = u_r \exp\left(-\frac{t - \hat{t}_i}{\tau_m}\right) + \sum_j w_{ij} \sum_f \frac{1}{C} \int_0^{t-\hat{t}_i} \exp\left(-\frac{s}{\tau_m}\right) \alpha(t - t_j^{(f)} - s)\, \mathrm{d}s$$
$$+ \frac{1}{C} \int_0^{t-\hat{t}_i} \exp\left(-\frac{s}{\tau_m}\right) I_i^{\text{ext}}(t - s)\, \mathrm{d}s$$

The result is the **Spike-Response Model** (SRM)

$$= \eta(t - \hat{t}_i) + \sum_j w_{ij} \sum_f \epsilon(t - \hat{t}_i, t - t_j^{(f)}) + \int_0^{\infty} \kappa(t - \hat{t}_i, s)\, I_i^{\text{ext}}(t - s)\, \mathrm{d}s$$

= (post-spike response) + (presynaptic spike response) +(current response)

(Gerstner, 2002)

07_srm.psd

Presynaptic Spike Response Kernel

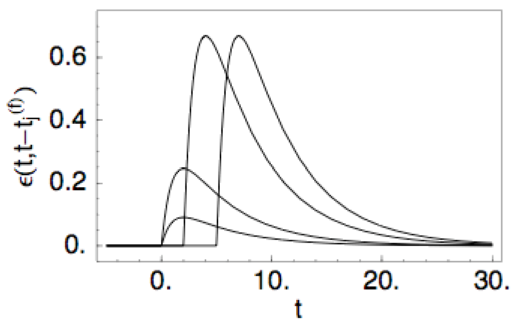
In order obtain an explicit expression for the presynaptic response kernel,

$$\epsilon(s,t) = \frac{1}{C}\int_0^s \exp\left(-\frac{t'}{\tau_m}\right)\,\alpha(t-t')\,\mathrm{d}t'$$

we specify the time course of the postsynaptic current: $\alpha(s) = \frac{q}{\tau_s}\exp\left(-s/\tau_s\right)\,\Theta(s)$

With $q = C = 1$, the integration yields:

$$\epsilon(s,t) = \frac{\exp\left(-\frac{\max(t-s,0)}{\tau_s}\right)}{1-\frac{\tau_s}{\tau_m}}\left[\exp\left(-\frac{\min(s,t)}{\tau_m}\right) - \exp\left(-\frac{\min(s,t)}{\tau_s}\right)\right]\Theta(s)\,\Theta(t)$$



$t_j^{(f)} = -2$, -1, 2, 5

$\tau_s = 1$ and $\tau_m = 5$

(Gerstner, 2002)

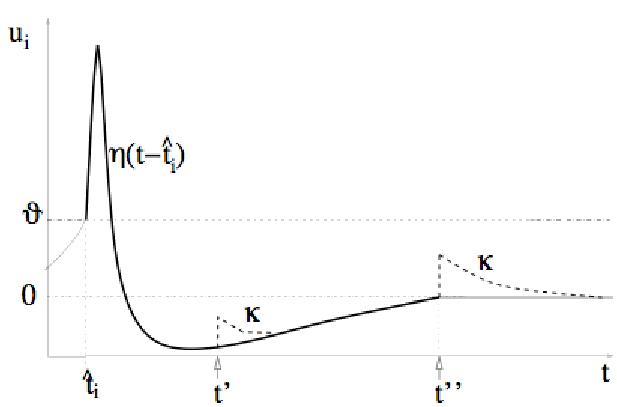
08_epsp.psd

Simplified Spike Response Model (SRM_0)

A simplified version of the spike response model can be constructed by neglecting the dependence of the response kernels upon the first argument:

$$\epsilon_0(s) \;=\; \epsilon_{ij}(\infty, s) \qquad \kappa_0(s) \;=\; \kappa_{ij}(\infty, s)$$

$$u_i(t) = \eta(t-\hat{t}_i) + \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_0(t - t_j^{(f)}) + \int_0^\infty \kappa_0(s)\, I^{\mathrm{ext}}(t-s)\,\mathrm{d}s$$



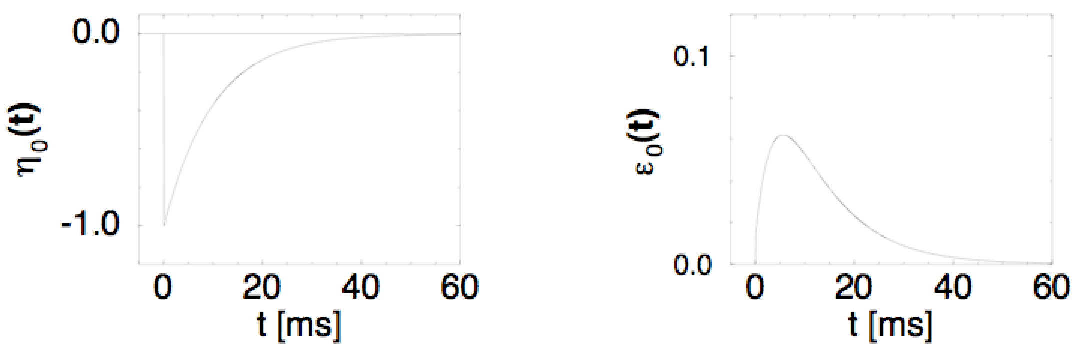
(Gerstner, 2002)

09_srm_0.psd

Simplified Spike Response Model (SRM_0)

A simplified version of the spike response model can be constructed by neglecting the dependence of the response kernels upon the first argument:

$$u_i(t) = \eta(t - \hat{t}_i) + \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_0(t - t_j^{(f)}) + \int_0^\infty \kappa_0(s)\, I^{\text{ext}}(t - s)\, \mathrm{d}s$$



(Gerstner, 2002)

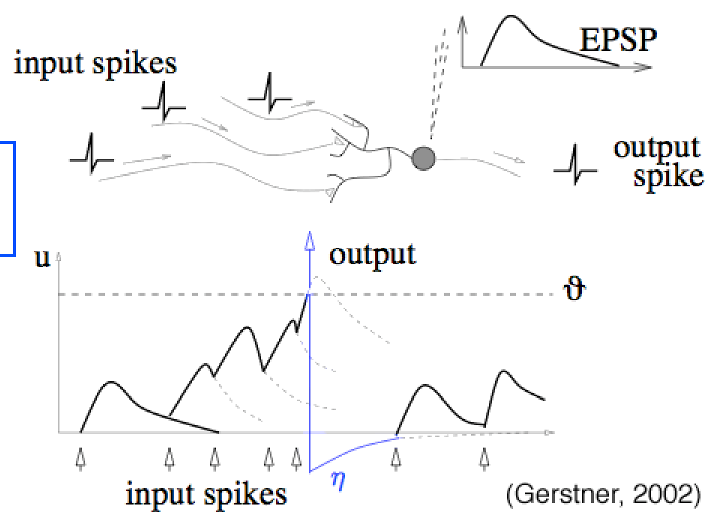
09b_srm_0.psd

Simplified Spike Response Model (SRM_0)

$$u_i(t) = \eta(t - \hat{t}_i) + \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_0(t - t_j^{(f)}) + \int_0^\infty \kappa_0(s)\, I^{\text{ext}}(t - s)\, \mathrm{d}s$$

Each output spike is approximated by a δ pulse, followed by a reset to a value below resting potential so as to account for a hyperpolarizing spike after-potential,

$$\eta(t - \hat{t}) = \delta(t - \hat{t}) - \eta_0 \exp\left(-\frac{t - \hat{t}}{\tau_{\text{recov}}}\right)$$



(Gerstner, 2002)

10_afterspk.psd

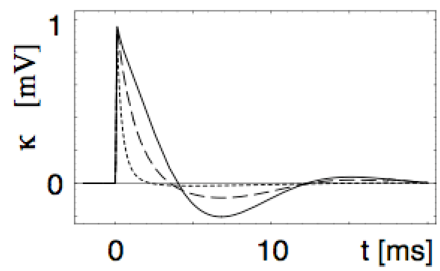
Simplified Spike Response Model (SRM_0)

$$u_i(t) = \eta(t-\hat{t}_i) + \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_0(t-t_j^{(f)}) + \int_0^\infty \quad (s)\, I^{\text{ext}}(t-s)\, ds$$

The kernel κ_0 characterizes the linear response of the neuron to a weak input current pulse.

The voltage response of the Hodgkin-Huxley model to a short sub-threshold current pulse defines the kernel.

$$\kappa(t-\hat{t}, t) = \frac{1}{c}\left[u(t) - \eta(t-\hat{t}) - u_{\text{rest}}\right]$$

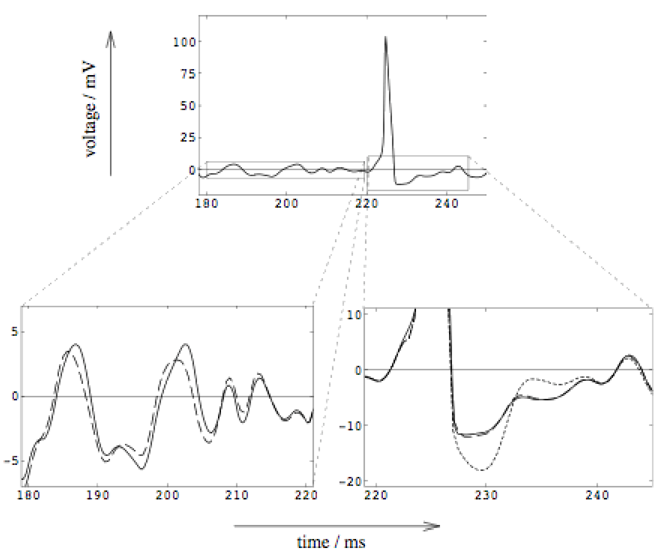


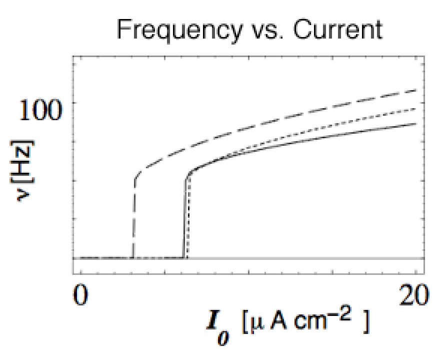
(Gerstner, 2002)

11_linearResponse.psd

Compare Spike Response Model with Hodgkin-Huxley

The voltage of theHodgkin-Huxley model (solid) together with the Spike Response Model (long-dashedline) and the approximation by the SRM_0 model which is significantly worse(dotted line).



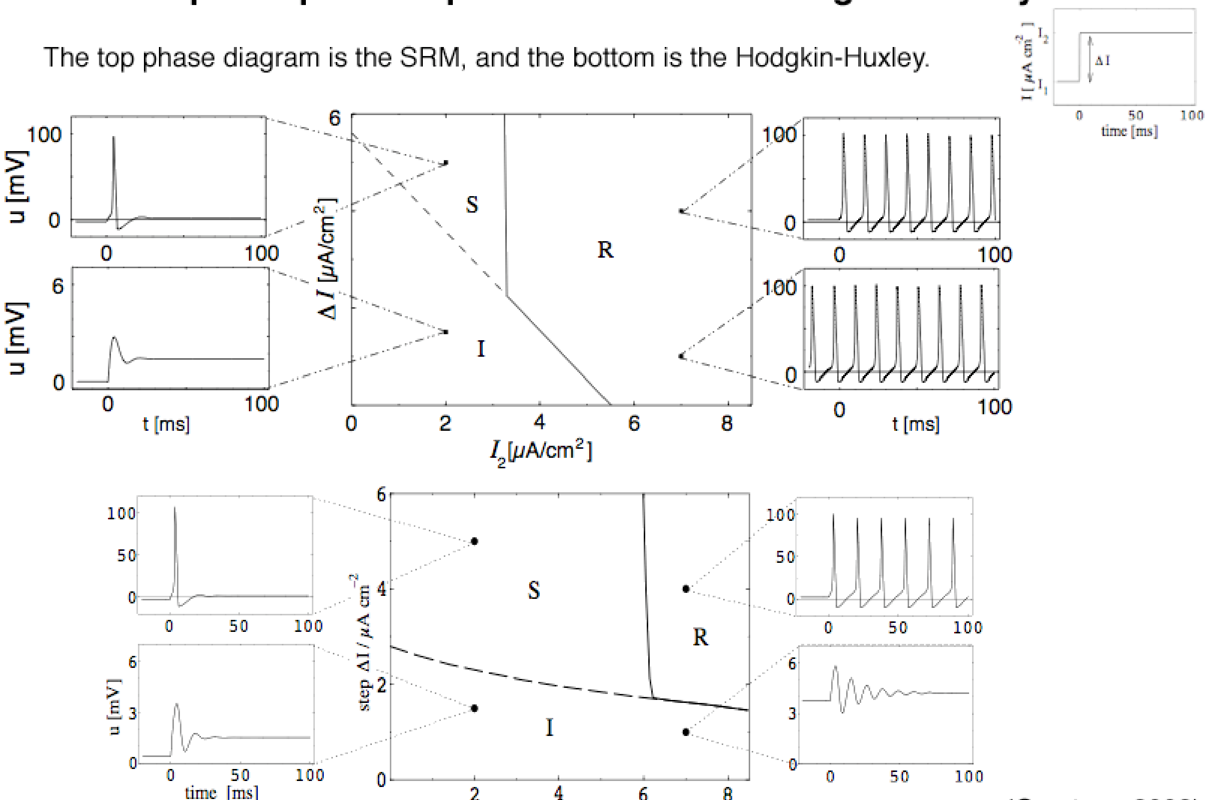


(Gerstner, 2002)

12_compare.psd

Compare Spike Response Model with Hodgkin-Huxley

The top phase diagram is the SRM, and the bottom is the Hodgkin-Huxley.

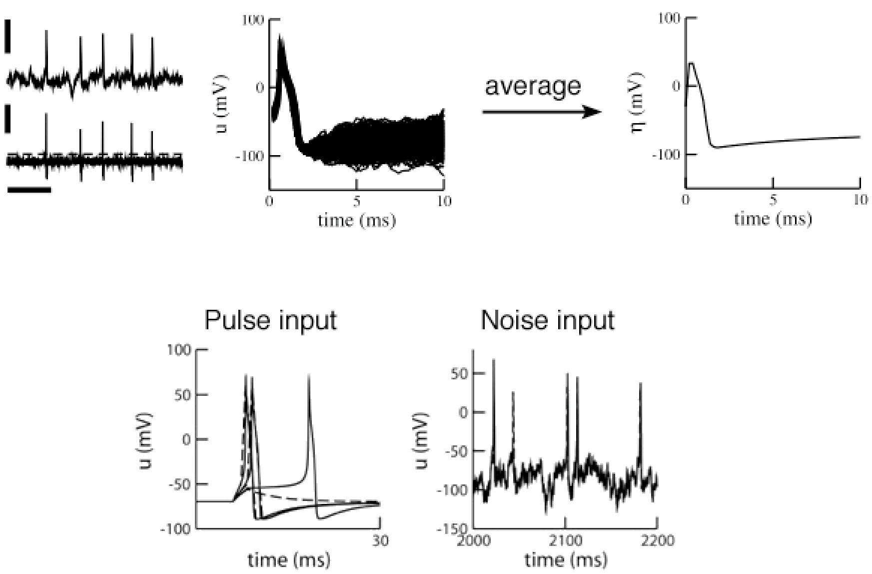


(Gerstner, 2002)

13_phaseDiagram.psd

Advantages of the Spike Response Model

Kernel functions can be directly fit to data: EPSPs, IPSPs, AHPs, linear responses, etc...

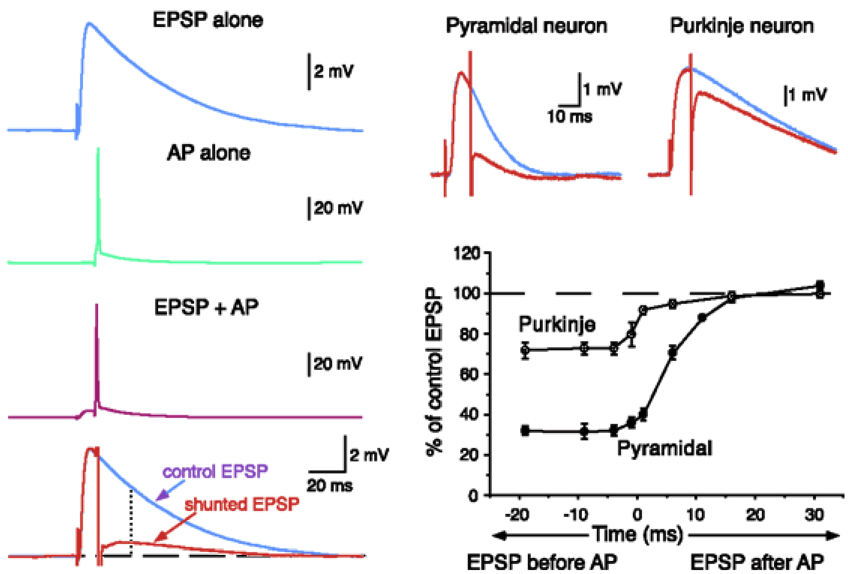


(Jolivet, Lewis, and Gerstner, 2004)

14_advantages.psd

Advantages of the Spike Response Model

Kernel functions can be ignored if neuron does not reset



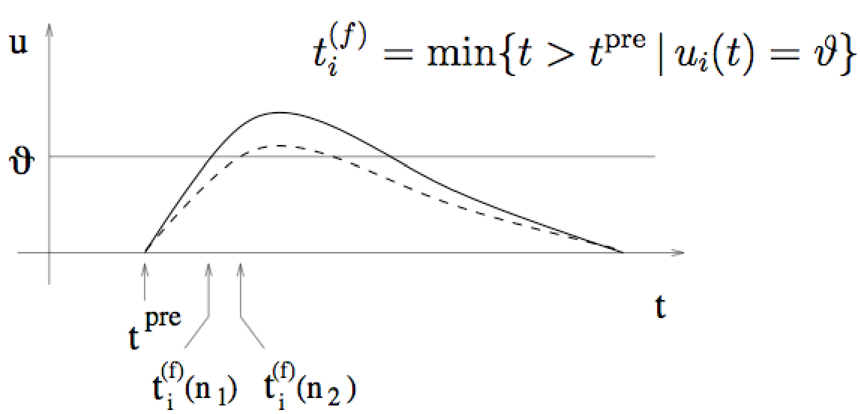
M. Hausser, G. Major, G. J. Stuart (2001) Science, 291: 138-141

15_Hausser011.psd

Coding by Spikes: Time to first spike

The firing latency encodes the number of presynpatic spikes which have been fired synchronously. If there are less presynaptic spikes, the potential rises more slowly (dashed) and the firing occurs later.

$$w_{ij} = w \longrightarrow u_i(t) = n\, w\, \epsilon(t - t^{\mathrm{pre}})$$

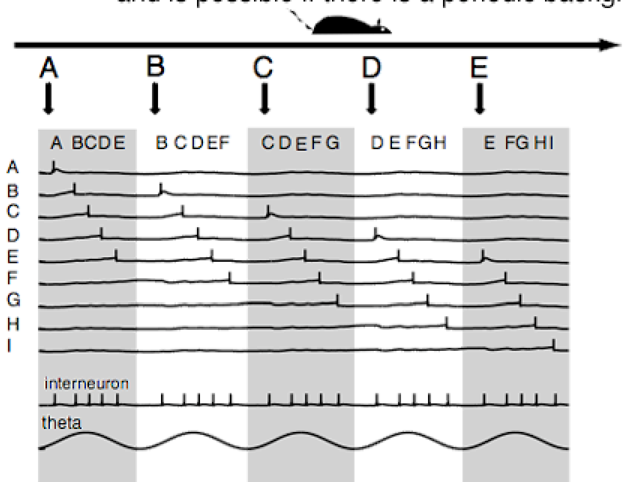


(Gerstner, 2002)

16_Code_latency.psd

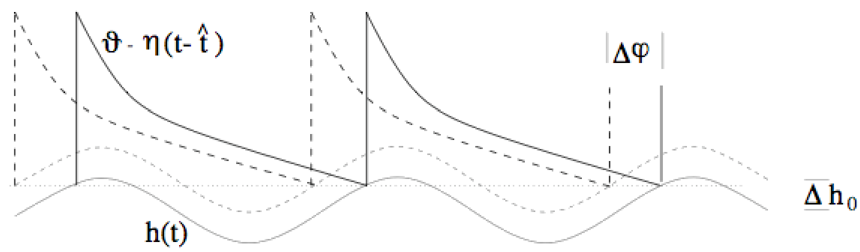
Coding by Spikes: Phase Coding

Phase coding is when the phase of a neuron's firing encodes information about the world, and is possible if there is a periodic background signal that can serve as a reference.



$$u(t) = \eta(t - \hat{t}) + h(t)$$

$$h(t) = h_0 + h_1 \cos\left(2\pi \frac{t}{T}\right)$$



(Gerstner, 2002)

17_Code_phase.psd

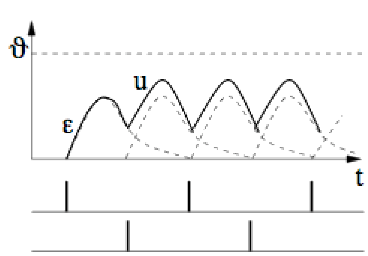
Decoding with Spikes: Synchronous versus asynchronous input

Synchronous input is more efficient than asynchronous input in driving a postsynaptic neuron.

$$u_i(t) \;=\; \eta(t - \hat{t}_i) + \sum_j \sum_{t_j^{(f)}} w\, \epsilon_0(t - t_j^{(f)}) \qquad \epsilon_0(s) = J\,\frac{s}{\tau}\exp\left(-\frac{s}{\tau}\right)\,\Theta(s)$$

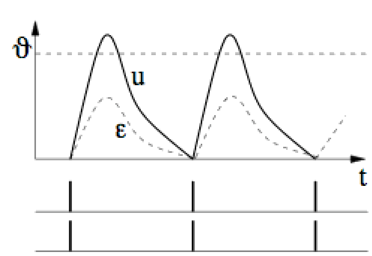
Asynchronous

$$u_i(t) \approx \;\; \eta(t - \hat{t}_i) + w \sum_{n=0}^{\infty} \epsilon_0(t - n\,\Delta t)$$



Synchronous

$$u_i(t) = \eta(t - \hat{t}_i) + N\, w\, \epsilon_0(t)$$



(Gerstner, 2002)

18_Decode_synch.psd

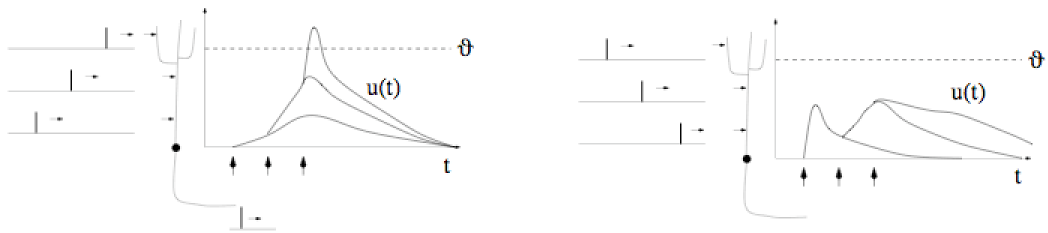
Decoding with Spikes: Spatio-temporal summation

In a spatially extended dendritic tree, the form of the postsynaptic potential depends on the location of the synapse.

$$u_i(t) = \sum_j w_{ij} \sum_f \epsilon_{ij}(t - t_j^{(f)})$$

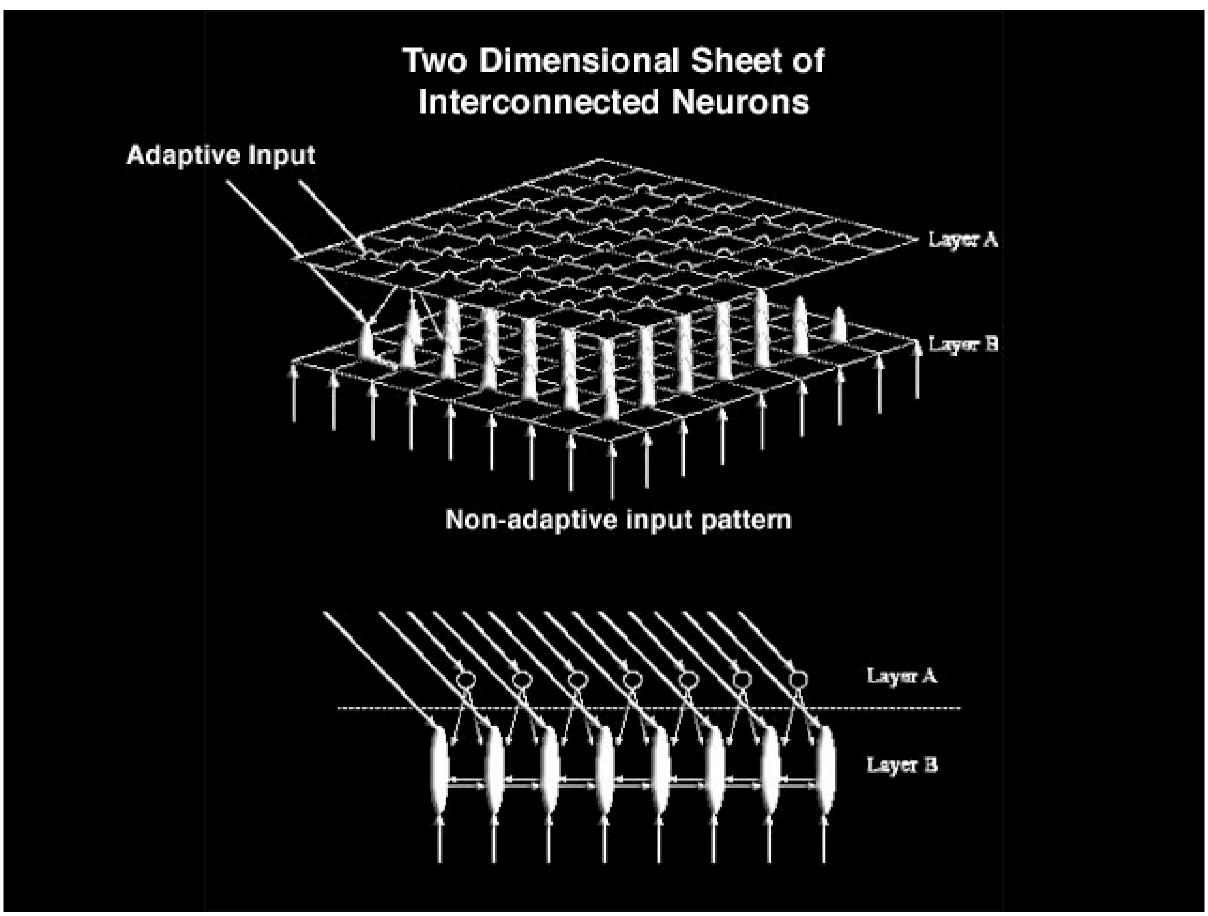
The subscripts of the kernel takes care of the fact that the postsynaptic potential depends on the location of the synapse on the dendrite.

Due to dendritic filtering, synaptic input at the tip of the dendrite causes postsynaptic potentials with a longer rise time and lower amplitude than input directly into the soma.

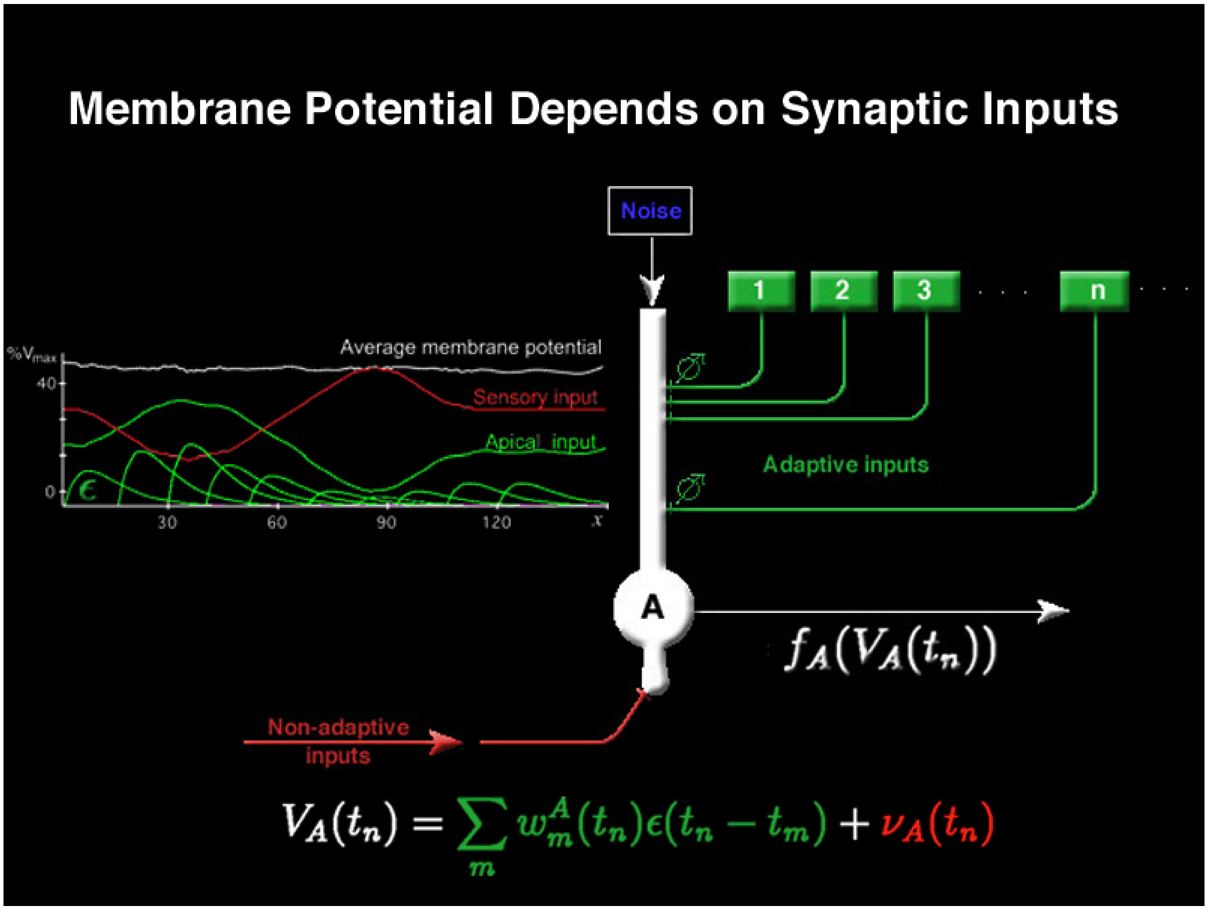


(Gerstner, 2002)

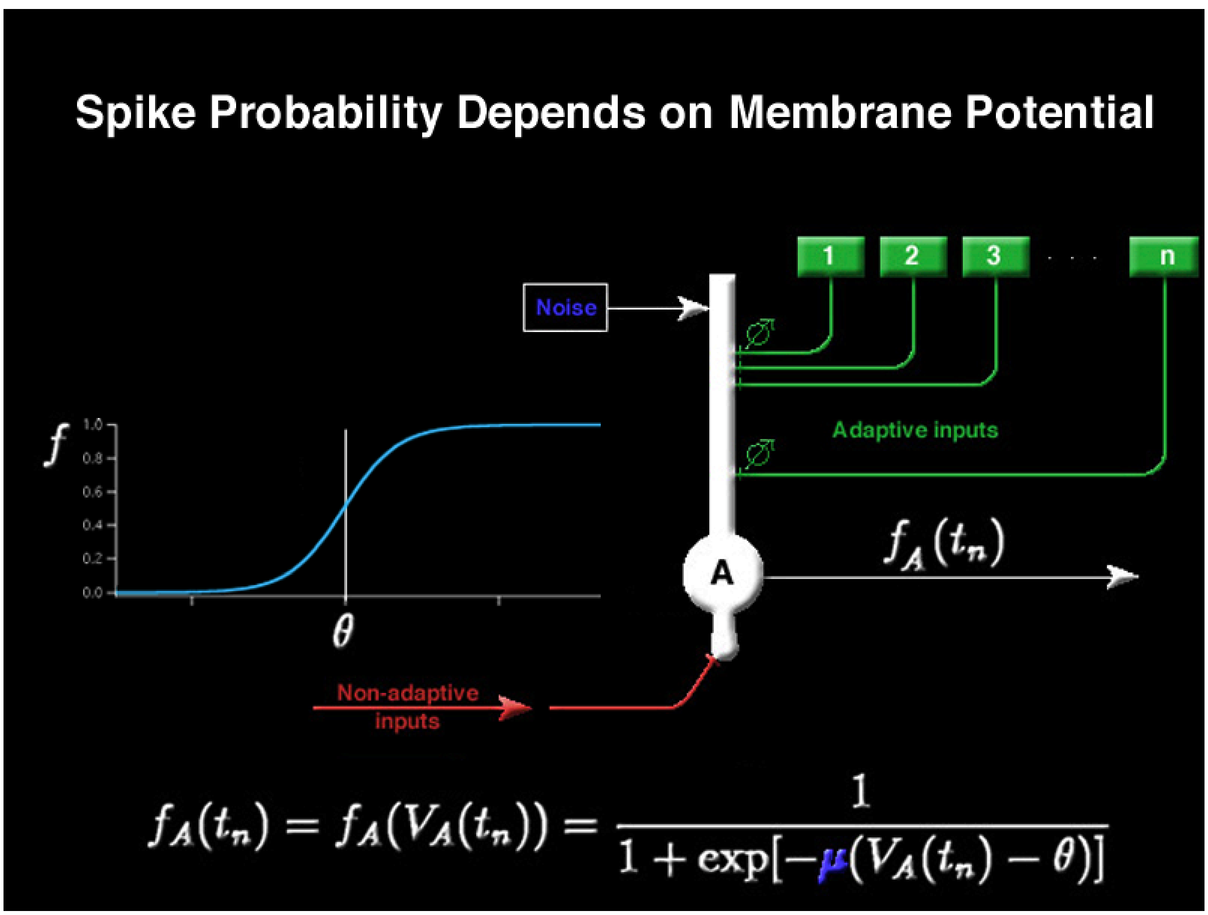
19_Decode_sum.psd



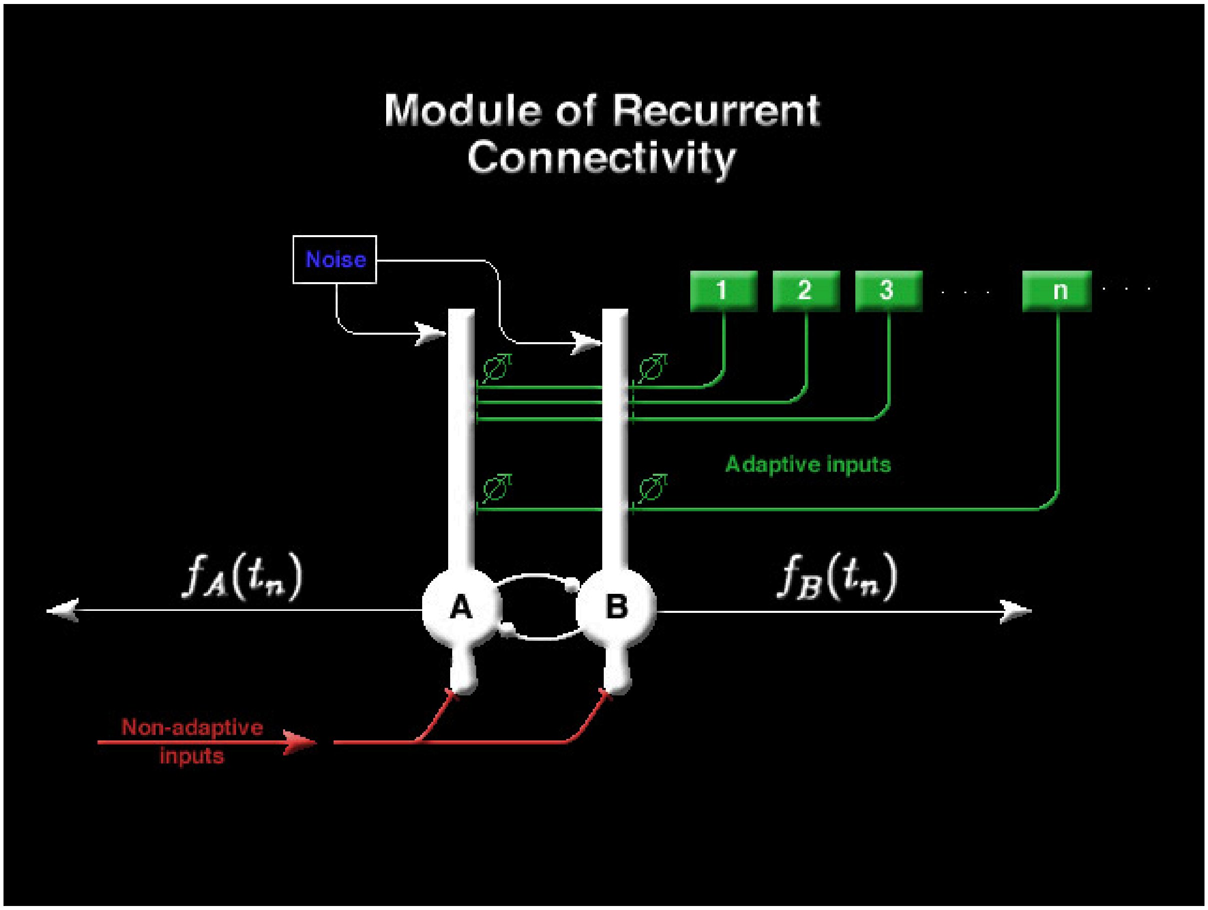
21neuralSheet.jpg



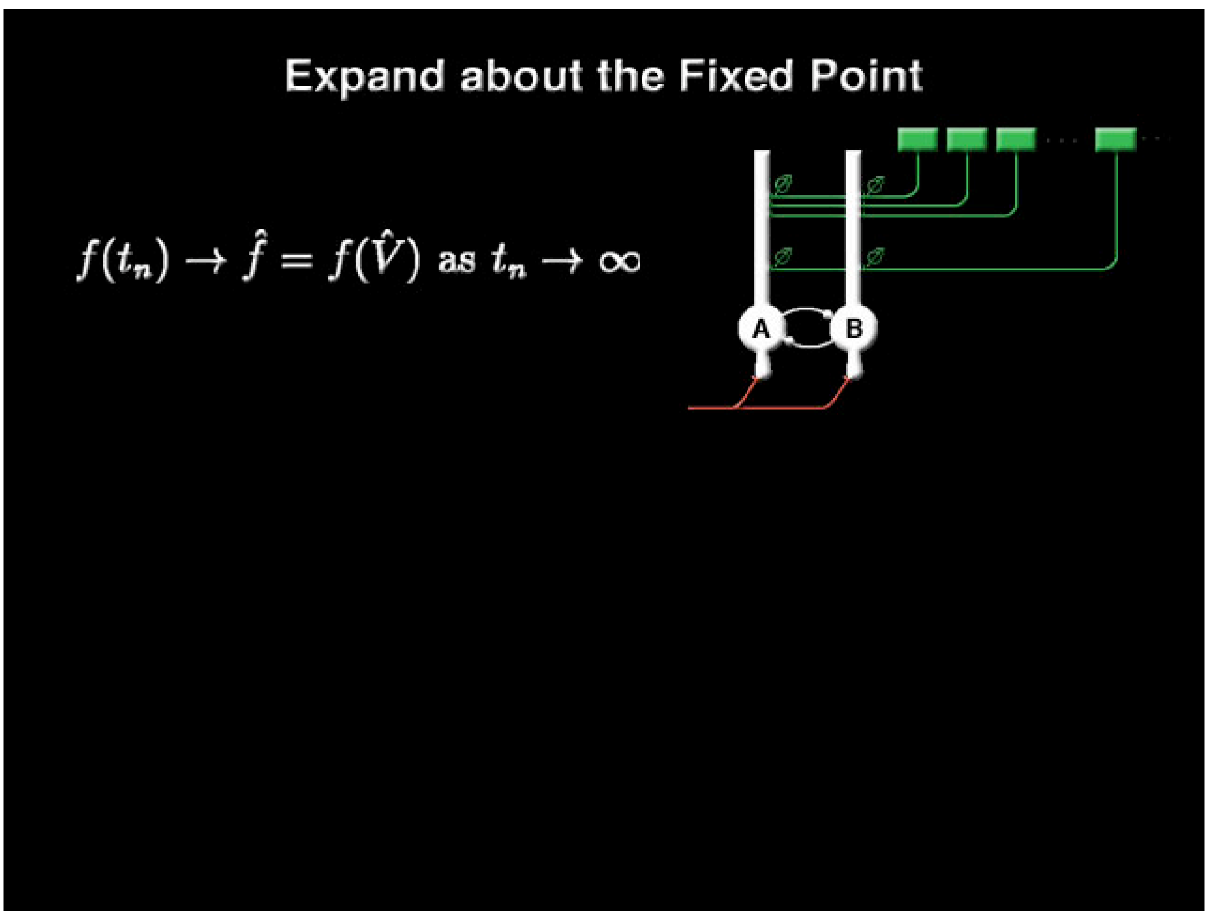
22_Module.psd



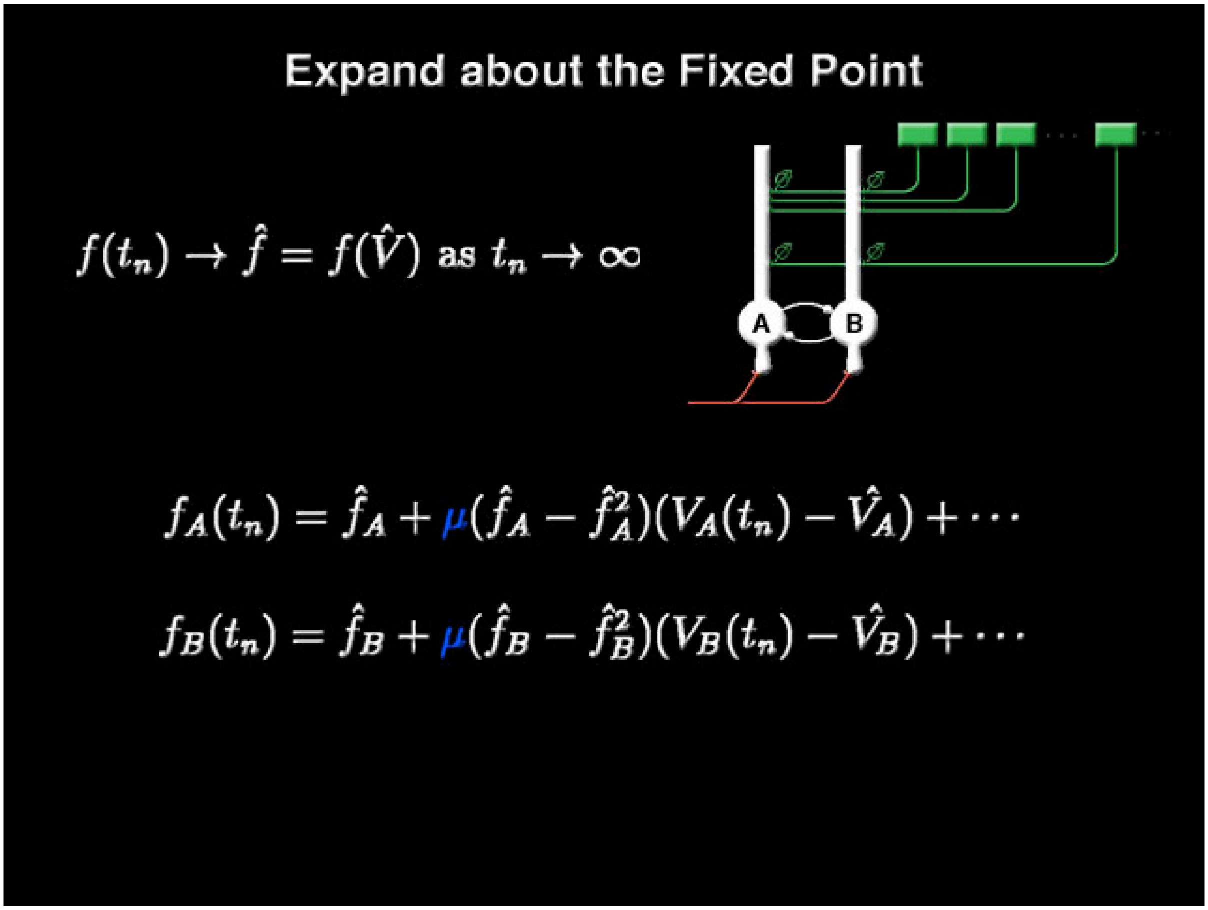
23_Module.psd



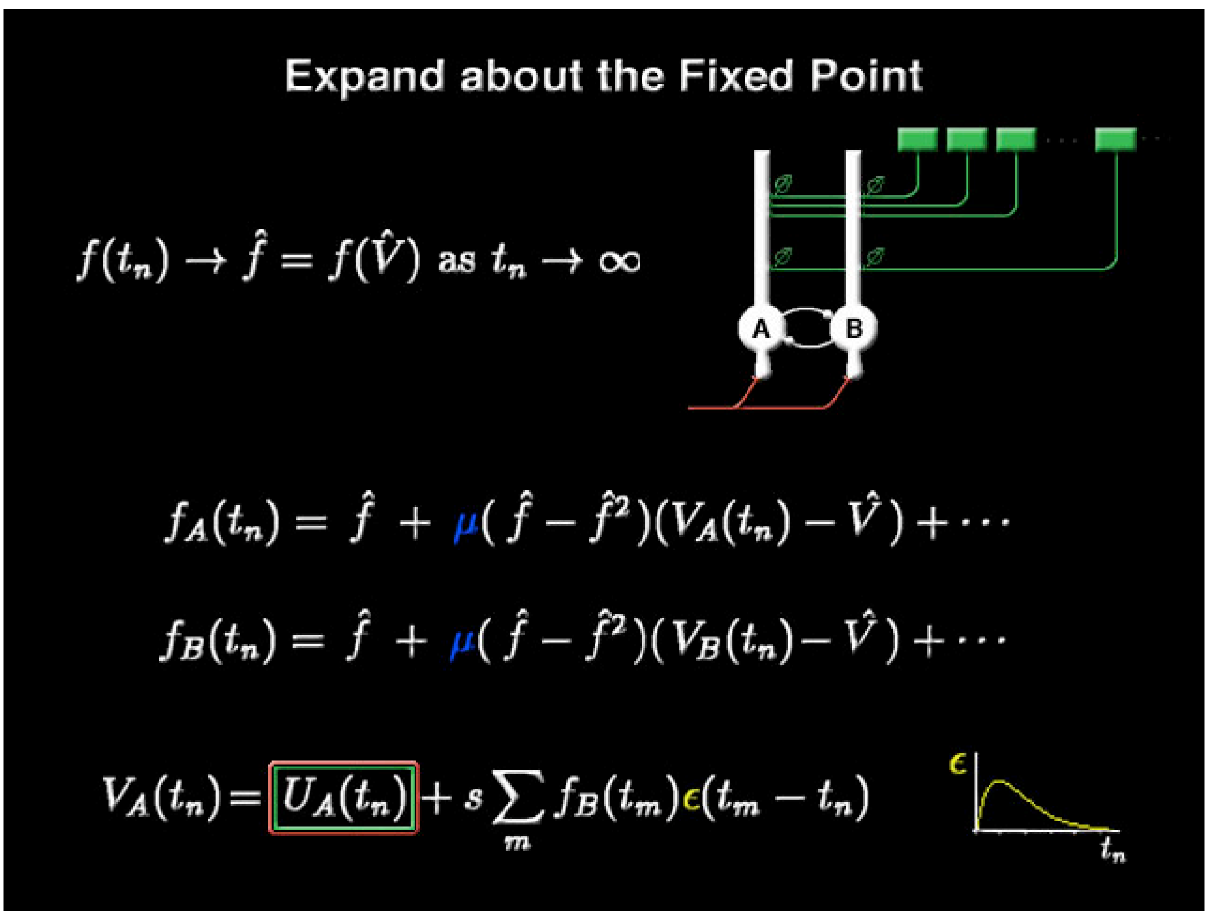
24bModule.jpg



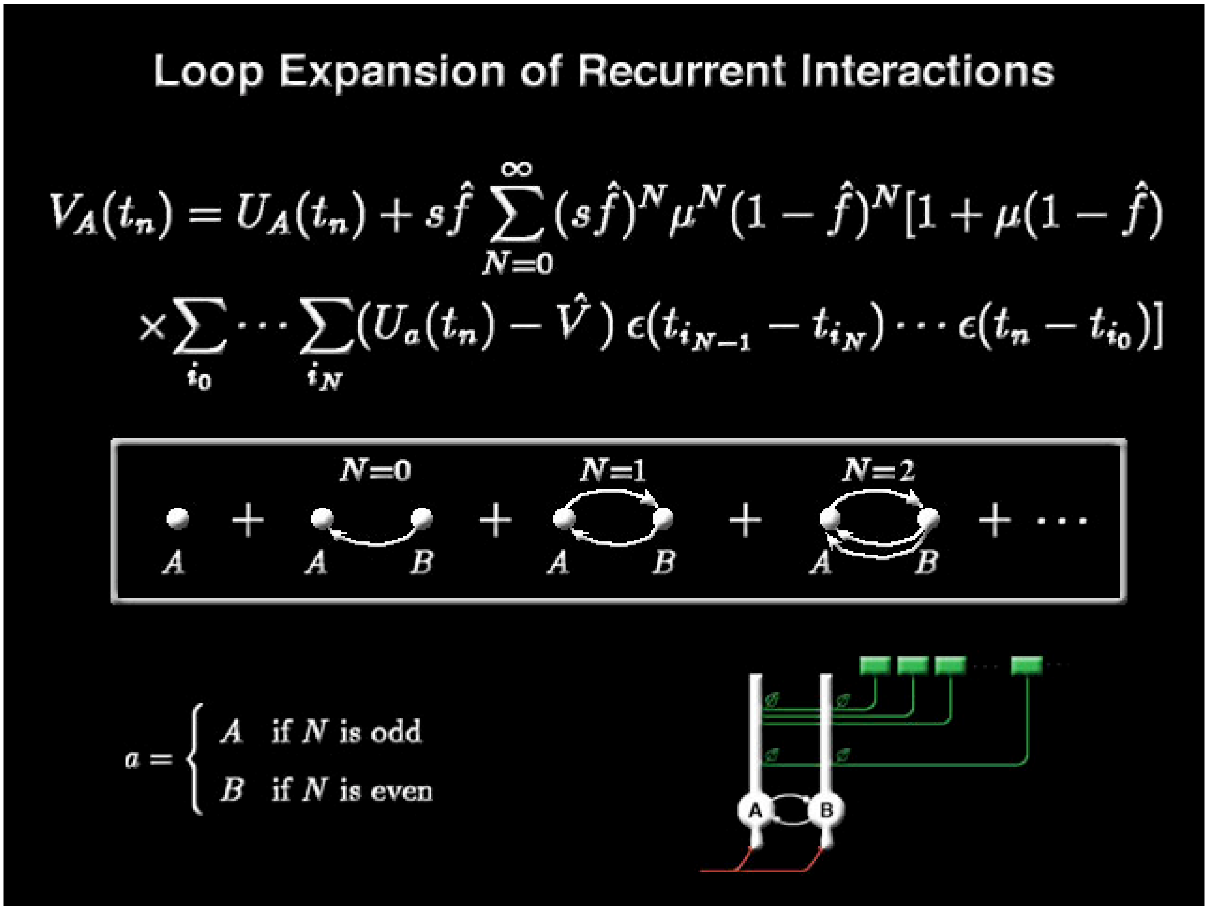
27aExpand.jpg



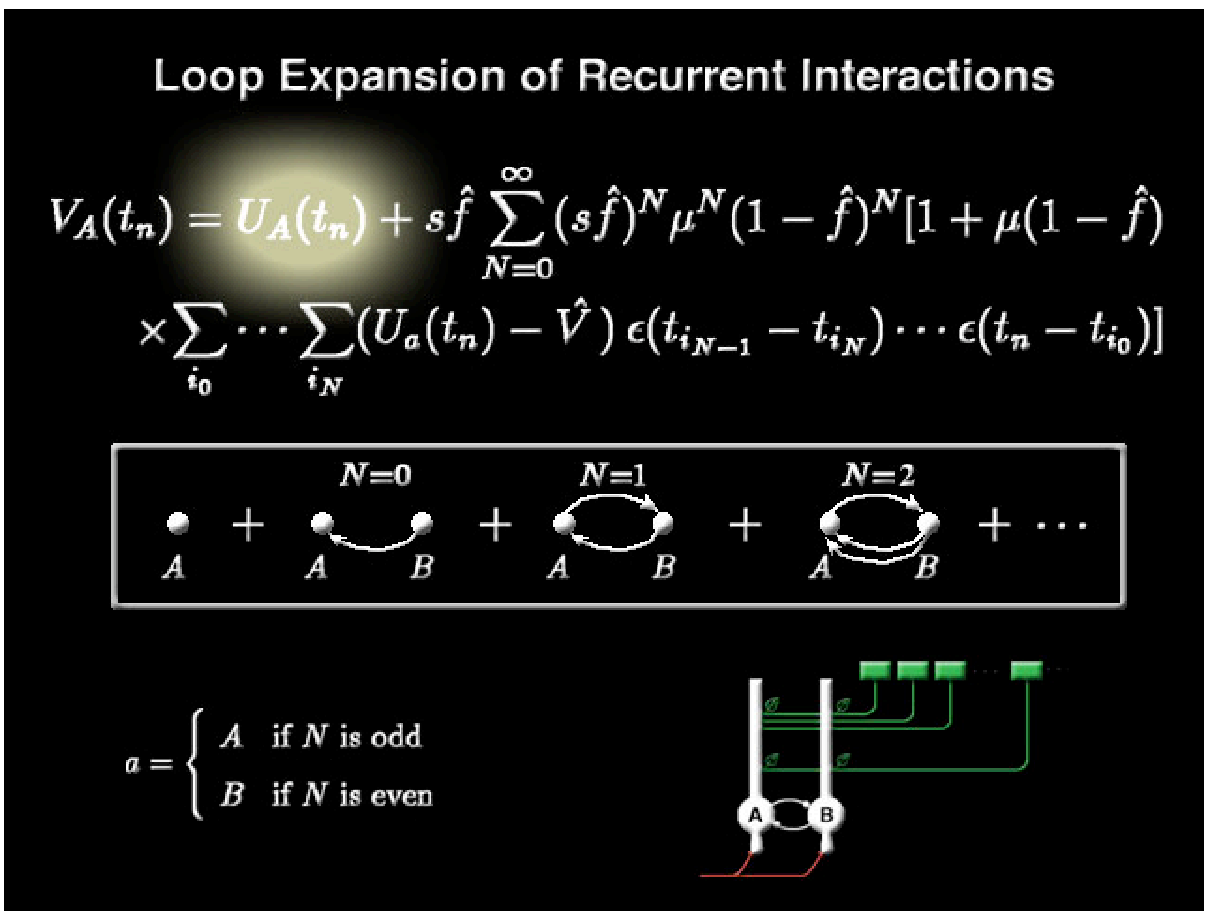
27bExpand.jpg



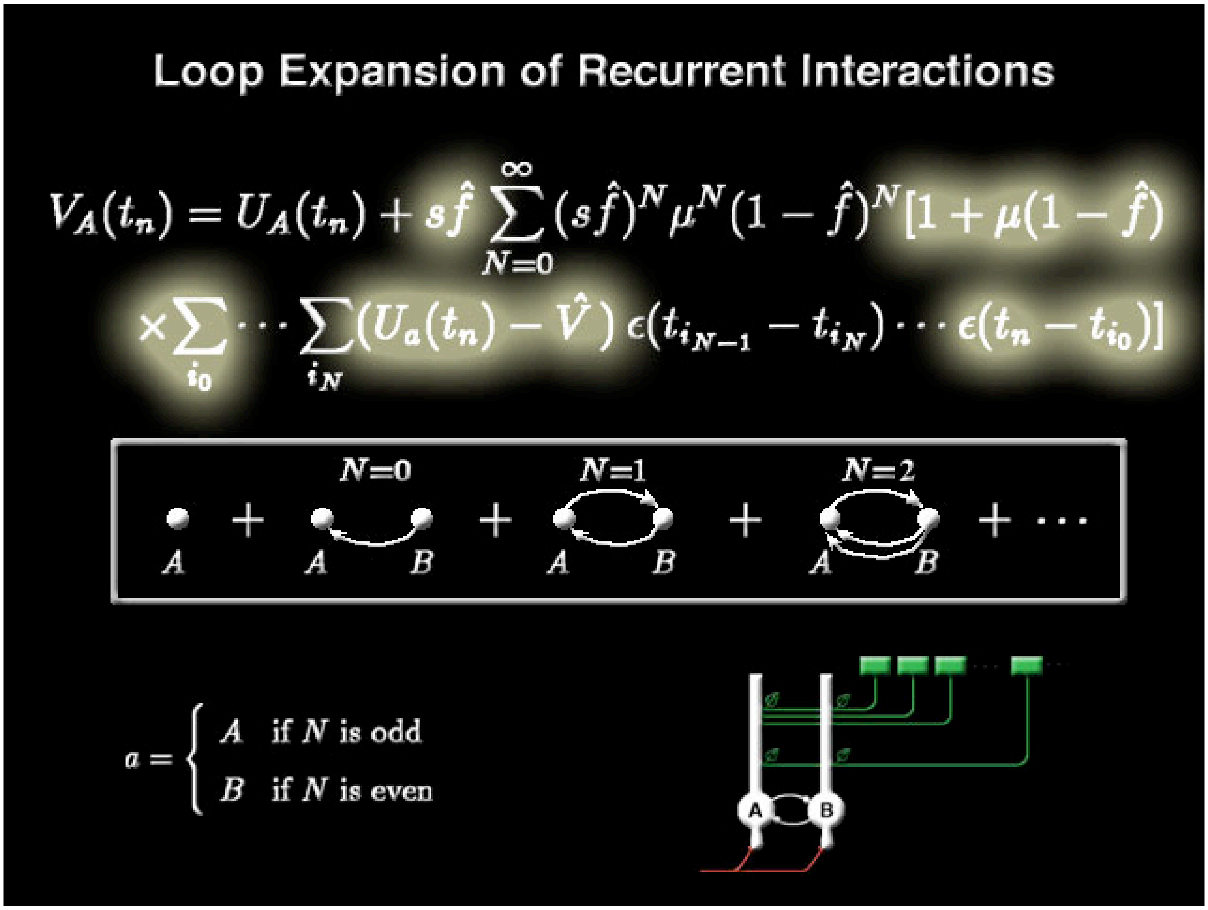
27cExpand.jpg



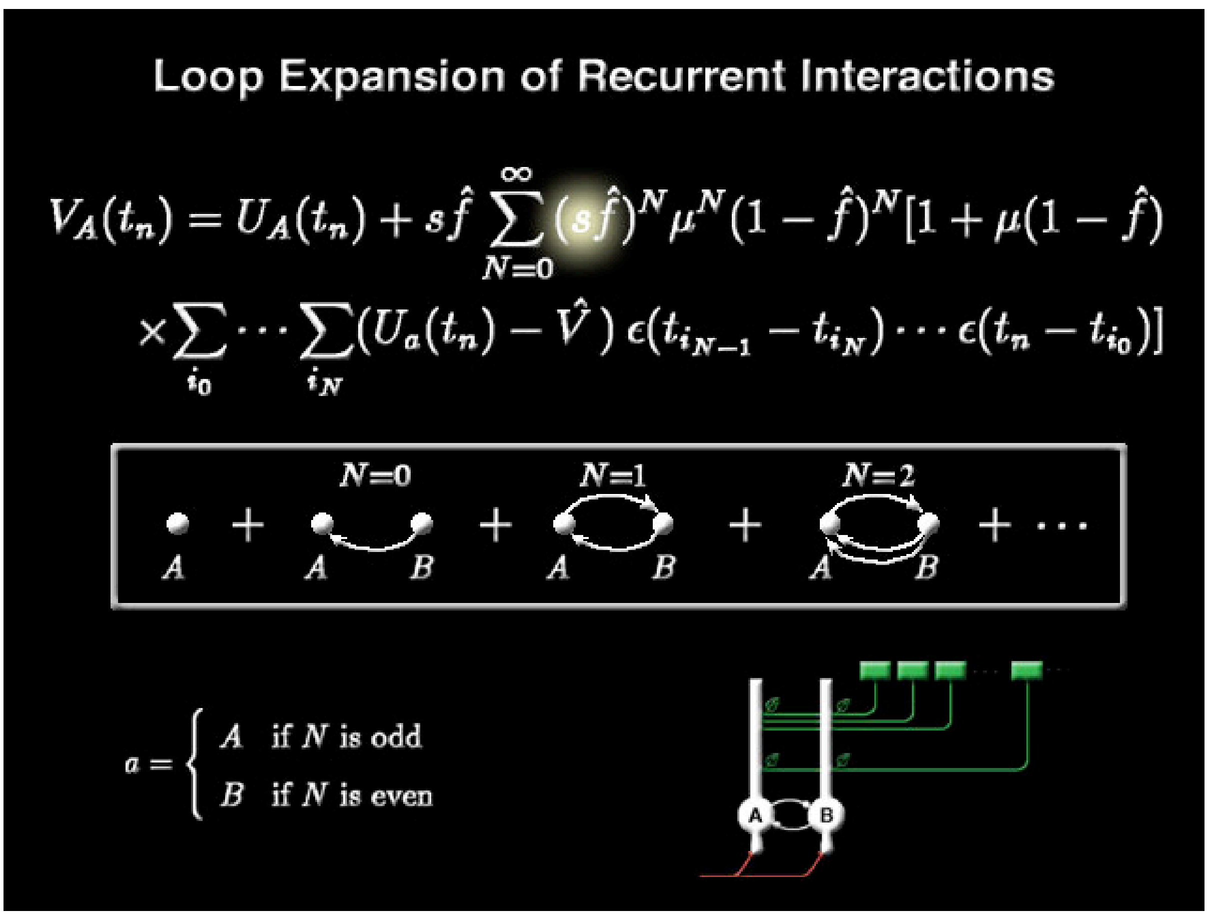
28aLoop.jpg



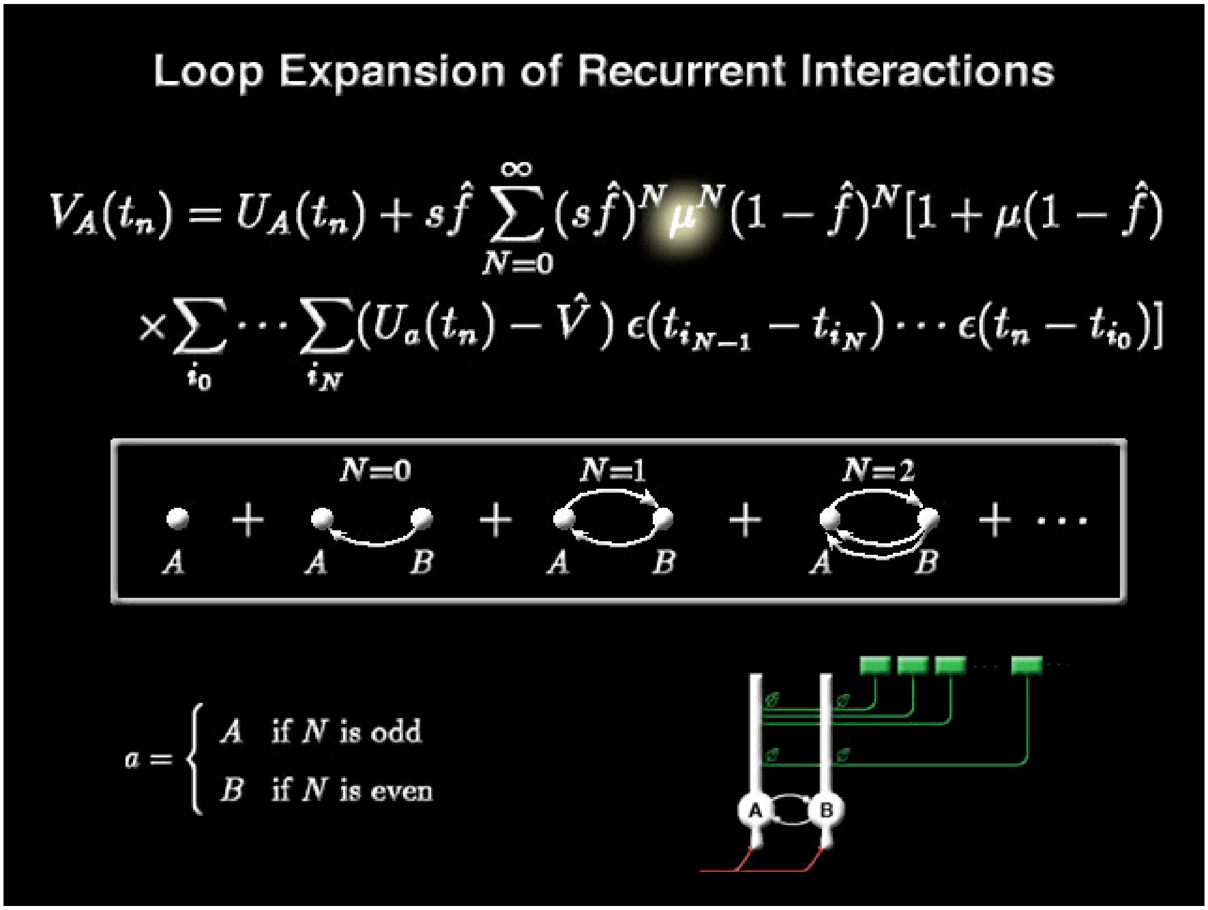
28bLoop.jpg



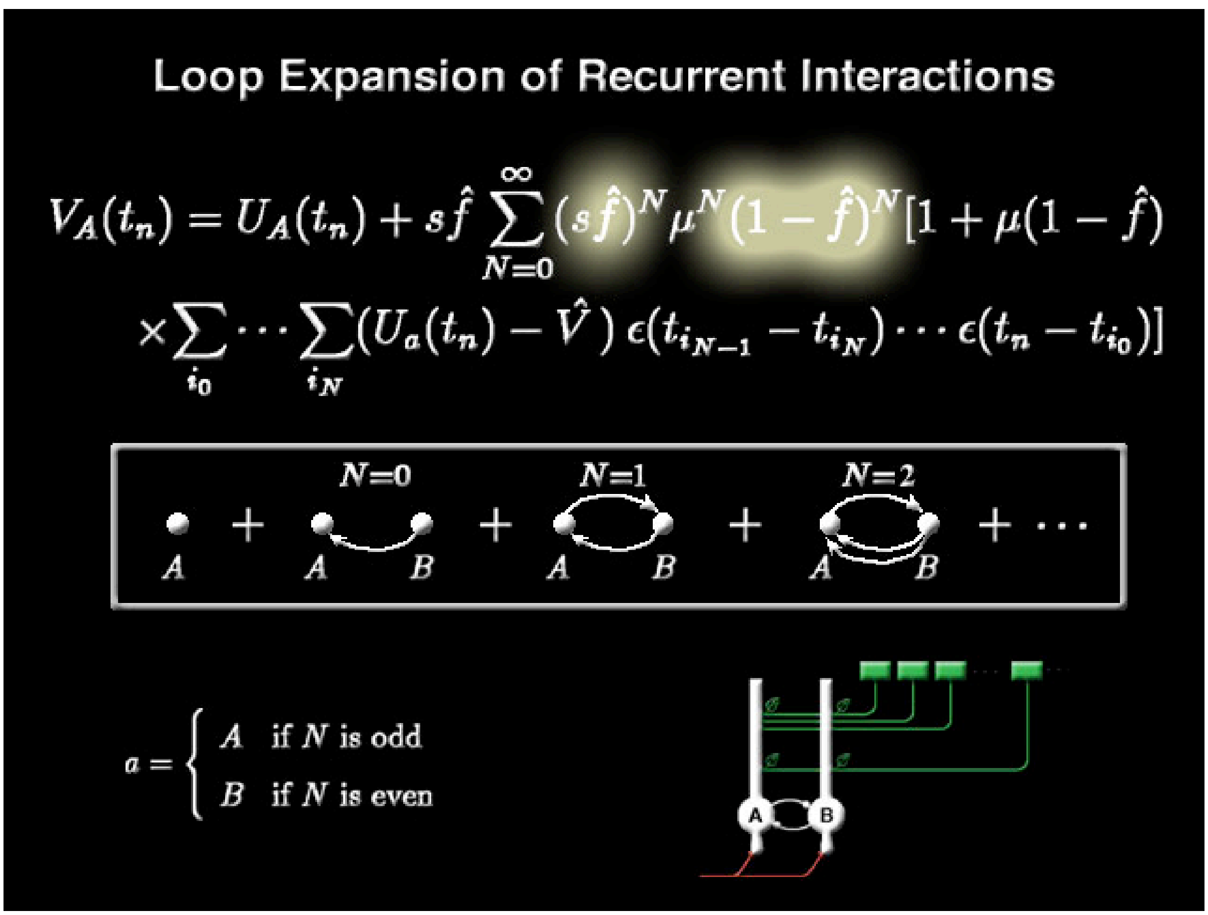
28cLoop.jpg



28dLoop.jpg



28eLoop.jpg

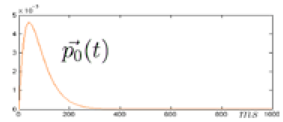


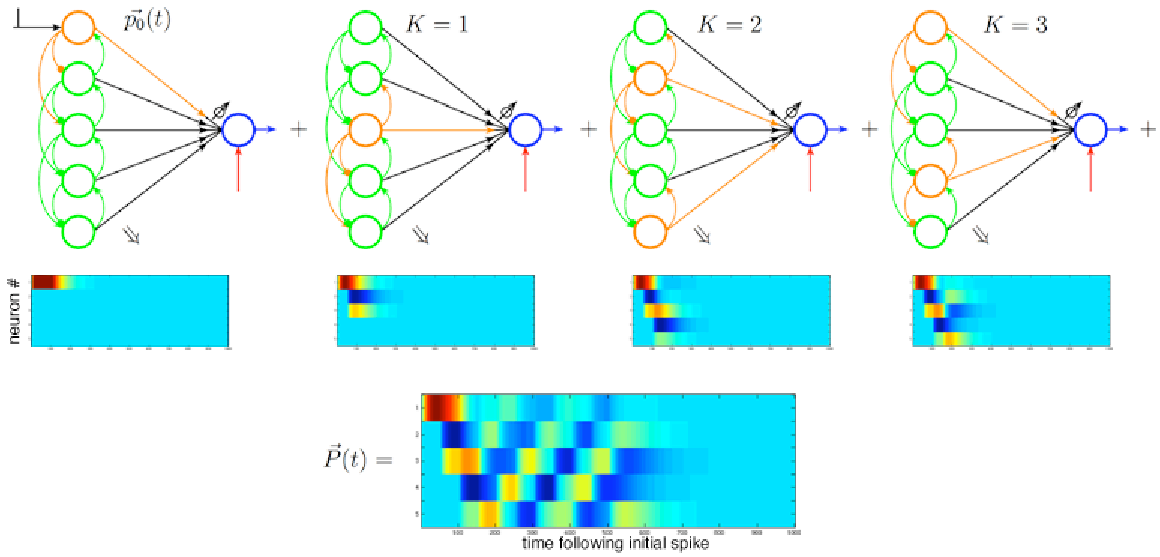
28fLoop.jpg

Input to a Single Neuron Reverberates Throughout the Network

The loop expansion can be applied to the echo network to calculate the activity of each cell in the network. In this example, the connections are represented as a simple synaptic delay.

$$\vec{P}(t) = \vec{p_0}(t) + \sum_{K=1}^{\infty} \left(\frac{\mu}{4}\right)^K \mathbf{W}^K \cdot \vec{p_0}(t - K\delta)$$

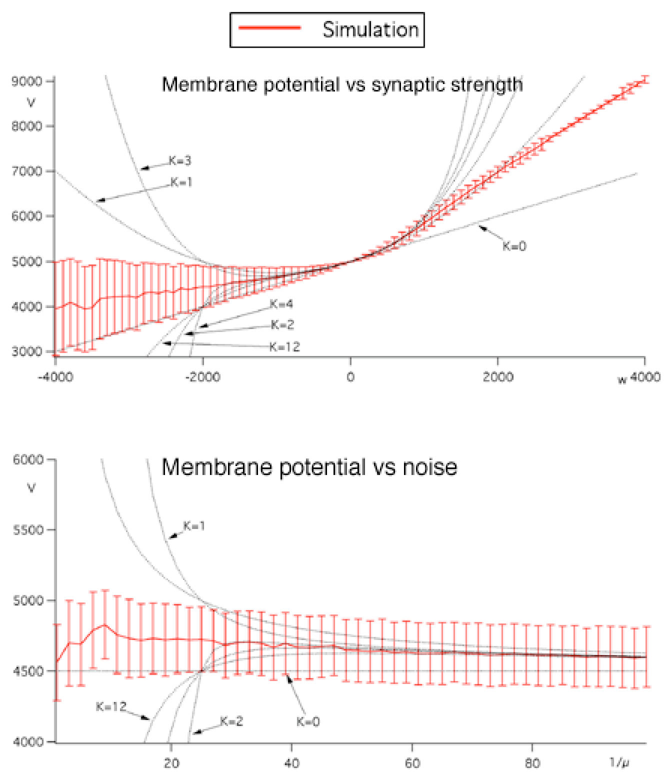




28gpulseInput.psd

Comparison of Expansion with Simulation

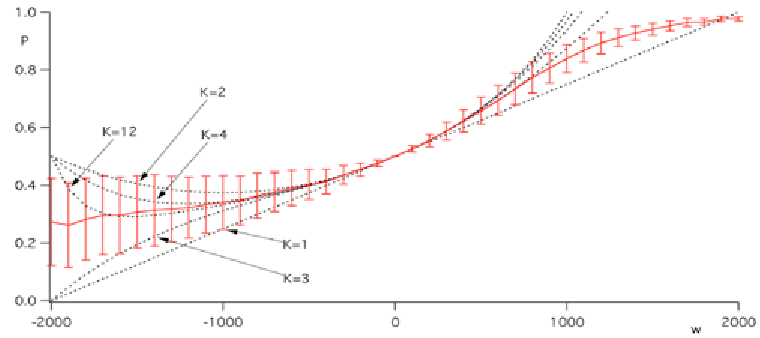
Analysis agrees with numerical simulation in the weak and noisy limit.



34potComp.psd

Spike Probability Expansion

$$P_i(t_n) = \sum_{K=0}^{\infty} (w\mu\hat{p}(1-\hat{p}))^K \epsilon^{(K)} * \bar{P}_a(t_n)$$



Diagrammatic rules:

For a chain of K synaptic links, $1 \to 2 \to \cdots i \to j \to \cdots K \to K+1$

The influence of neuron 1 on neuron $(K+1)$ is given by a term containing the following factors:

1. $w_{ji}\mu_j\hat{p}_j(1-\hat{p}_j)$ for each *synaptic link*, $i \to j$.
2. $\epsilon^{(K)} * \bar{P}_1(t_n)$

35probComp.psd

Correlation Functions

Diagrammatic rules can be used to calculate corollation functions:

Auto-correlation function:

$C_{ii}(t_n) =$

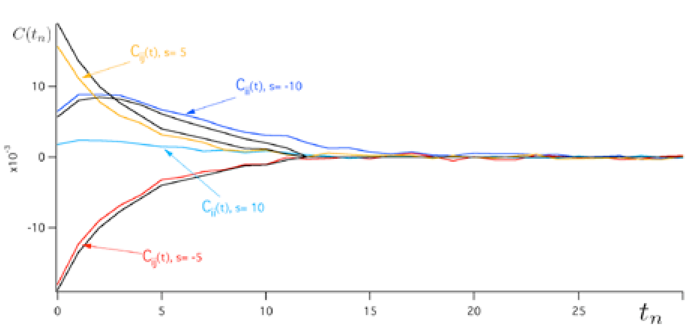
$$= \hat{p}^2 \sum_{K=1}^{\infty} (w\mu\hat{p}(1-\hat{p}))^{2K} \epsilon^{(2K)}(t_n)$$

Cross-correlation function:

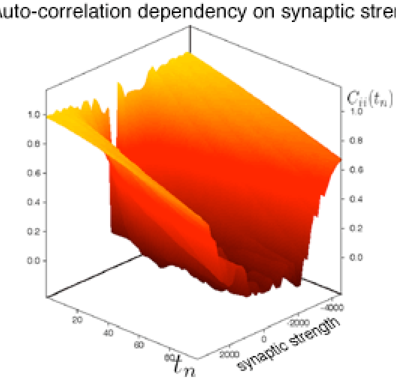
$C_{ij}(t_n) =$

$$= \hat{p}^2 \sum_{K=1}^{\infty} (w\mu\hat{p}(1-\hat{p}))^{2K-1} \epsilon^{(2K-1)}(t_n)$$

Comparison of analysis with numerical results.



Auto-correlation dependency on synaptic strength.

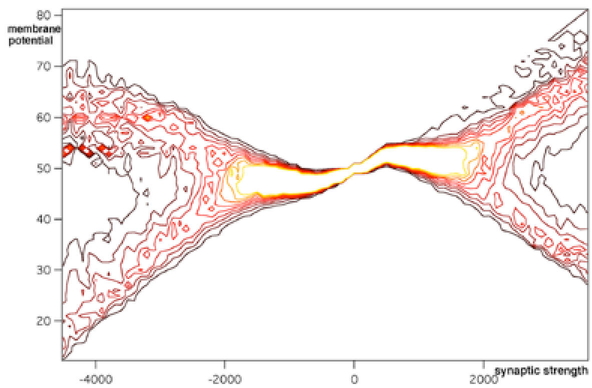


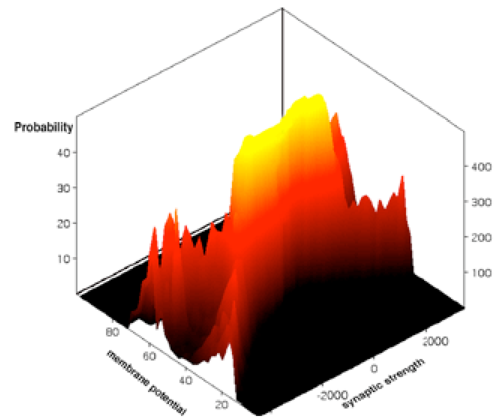
36corComp.psd

Beyond the Weak & Noisy Limit

Simulations suggest that the membrane potential becomes bistable for systems with strong synaptic connections or with little noise.

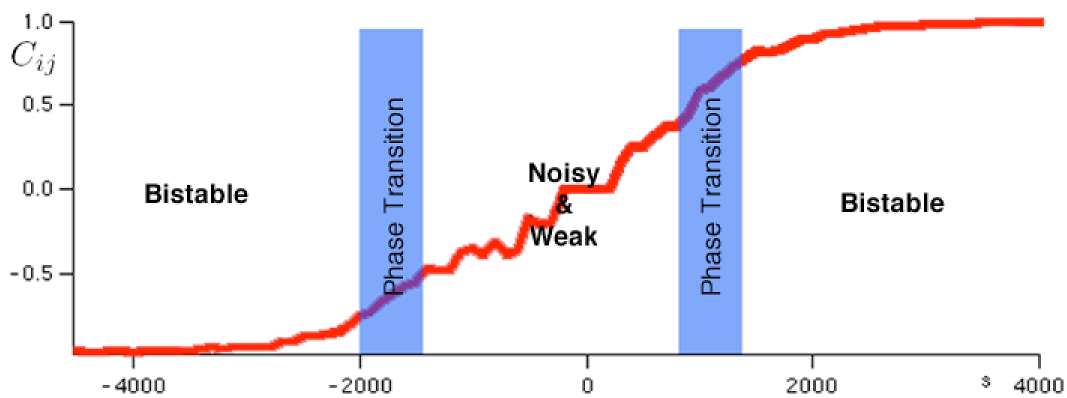
Higher order moments of the probability distribution contribute to the expansion and cause it to diverge.



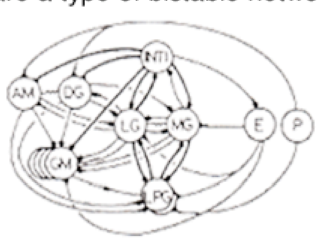


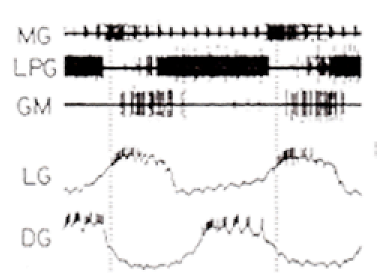
37beyondWeak.psd

Classification of Network Dynamics



Central pattern generators are a type of bistable network.



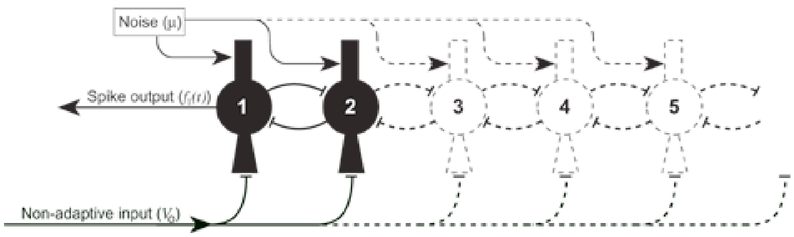


Heinzel and Selverston. (1988) *J. Neurophysiol.* **59**: 566-585.

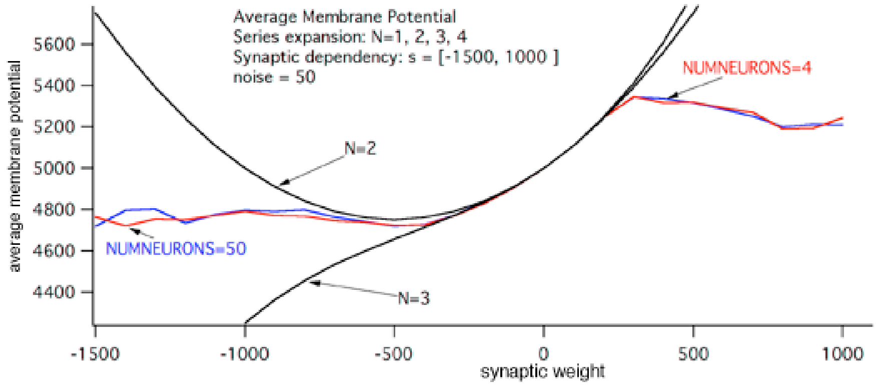
38phases.psd

Information Traverses Few Synapses

The formalism generalizes to larger networks. In the case of a chain of synapses, we find that the network effects on a single neuron are only dependent on the nearest neighbors in the weak and noisy limit.



A 50-neuron network is equivalent to a 4-neuron network.



39networkSize.psd