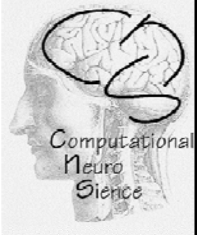
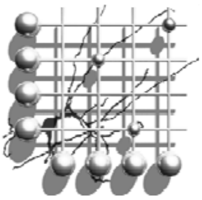
Computational Modelling In Neuroscience: Networks of Spiking Neurons





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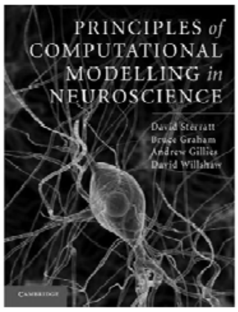
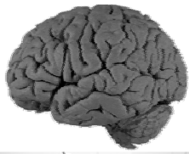
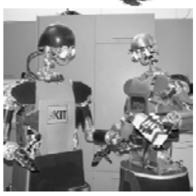
Here is a Nice Book…



Authors: David Sterratt, Bruce Graham, Andrew Gillies, David Willshaw
[Cambridge University Press, 2011]
Companion website at:
compneuroprinciples.org

Computational Neuroscience



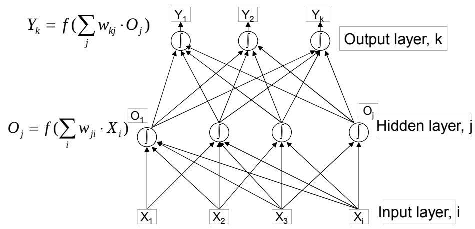


- Discover how the brain works
  - Models that can reproduce and explain experimental results
- Emulate the brain in computational devices
  - Models that retain only the important computational details

(KIT Armar-1 Robot)

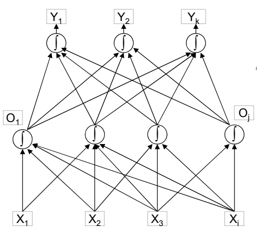
Artificial Neural Networks

- Networks of simple computing units ("*neurons*")
- Binary or analog signals and connection weights



Real Neural Networks

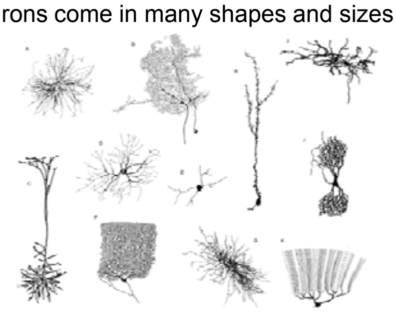
Complex neurons



Action potentials (spikes)

Complicated Neurons

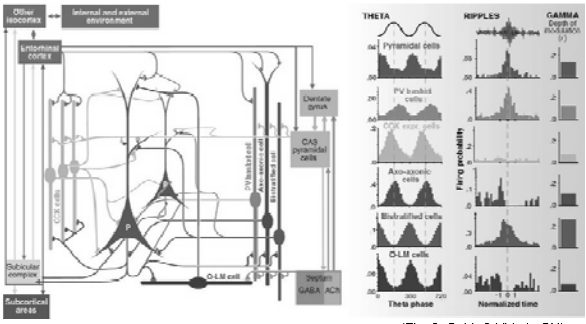
- Neurons come in many shapes and sizes



(Dendrites, Hausser et al (eds))

Complicated Neural Circuits

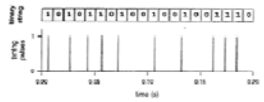
- CA1 region of hippocampus



(Fig. 2, Cobb & Vida in CU)

Information Coding

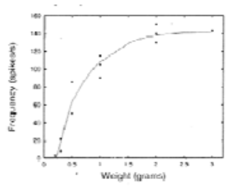
- Binary coding
  - Presence or absence of spikes in a time window
- Rate (analogue) coding
  - Average firing frequency over a given time period
- Temporal coding
  - Interspike intervals during temporal sequence of spikes

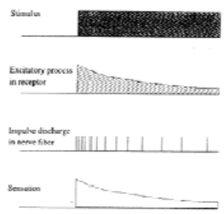


(C&S 92, Fig. 3.4)

Rate Coding in Sensorimotor System

- Muscle stretch receptors fire in proportion to stretch (weight)
  - Experimental data from Adrian, 1928
- Sensation of a stimulus proportional to firing rate
  - Hypothesis by Adrian

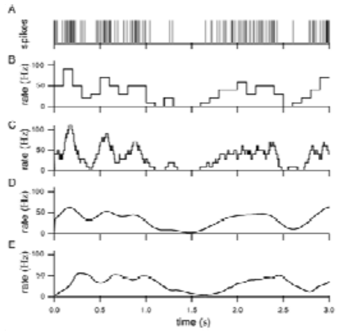




(from C&S 92)

Rate Coding Over Time

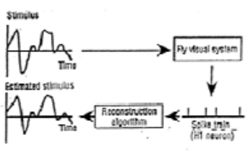
- Measure rate in a short time interval eg 100msec
- Filtered measure



(Dayan & Abbott, 2001)

Temporal Coding in Visual System

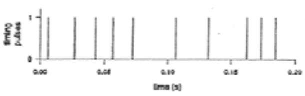
- H1 neuron in the fly visual system
- Responds to movement of objects in the world
  - Angular velocity
- Movements can be reconstructed from measurements of the interspike intervals



(from Spikes, MIT Press, 1997)

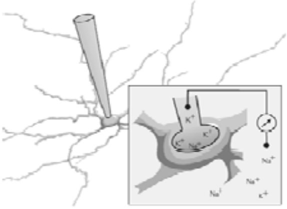
Dynamic Range of Codes

- Neuron can fire up to 100 spikes per sec
- Neurons that receive inputs from this neuron have 200 msecs to "*decode*" the signal from the neuron
  - Can "measure" spike times with 10 msec precision
- Given this scenario, what "*code*" is best?
  - Rate versus temporal coding
  - How many "states" could each code represent?

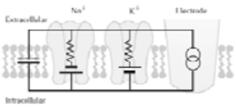


Electrical Potential of a Neuron

- Differences in ionic concentrations
- Transport of ions
  - Sodium (Na)
  - Potassium (K)



(Fig. 2.1 pg 14)

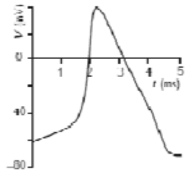


(Fig. 2.13 pg 31)

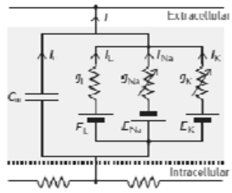
Action Potential Model

- Empirical model by Hodgkin and Huxley, 1952
  - Voltage-dependent Na and K channels

$$C_m \frac{dV}{dt} = -\bar{g}_L(V-E_L) - \bar{g}_{Na} m^3 h(V-E_{Na}) - \bar{g}_K n^4(V-E_K) + I_e$$



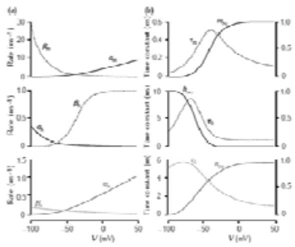
(Fig. 3.1 pg 47)



(Fig. 3.2 pg 50)

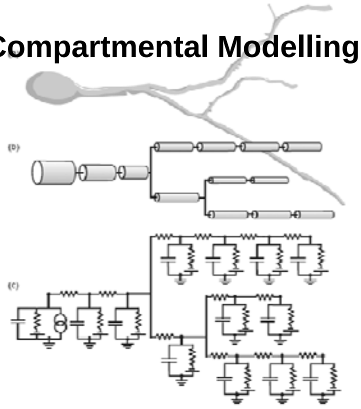
Complete Action Potential Model

Box 3.5 pg 61



(Fig. 3.10 pg 60)

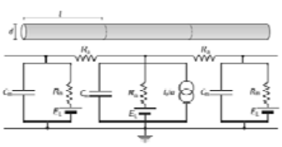
Compartmental Modelling



(Fig. 4.1 pg 73)

A Length of Membrane

- Membrane *compartments* connected by intracellular resistance



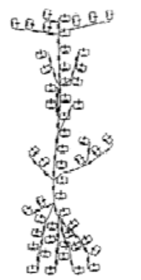
(Fig. 2.15 pg 36)

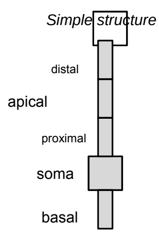
- Compartmental modelling equation

$$C_m \frac{dV_j}{dt} = \frac{E_m - V_j}{R_m} + \frac{d}{4R_a}\left(\frac{V_{j+1}-V_j}{l^2} + \frac{V_{j-1}-V_j}{l^2}\right) + \frac{I_{e,j}}{\pi d l}. \quad (2.23)$$

Varying Levels of Detail

- Capture essential features of morphology





Many, Many Ion Channels…

Current	Channel proteins	Other names	Activation $V_{1/2}$ (mV)	Activation σ (mV)	Activation τ (ms)	Inactivation $V_{1/2}$ (mV)	Inactivation σ (mV)	Inactivation τ (ms)	Note
I_{Na}	Na$_v$1.1–1.3,1.6		−30	6	0.2	−67	−7	5	a
I_{NaP}	Na$_v$1.1–1.3,1.6		−52	5	0.2	−49	−10	1500	b
I_{CaL}	Ca$_v$1.1–1.4	HVA$_l$	9	6	0.5	4	2	400	c
I_{CaN}	Ca$_v$2.2	HVA$_m$	−15	9	0.5	−13	−19	100	d
I_{CaR}	Ca$_v$2.3	HVA$_m$	3	8	0.5	−39	−9	20	e
I_{CaT}	Ca$_v$3.1–3.3	LVA	−32	7	0.5	−70	−7	10	f
I_{FO}	K$_v$3.1	Fast rectifier	−5	9	10	—	—	—	g
I_{DR}	K$_v$2.2, K$_v$3.2…	Delayed rectifier	−5	14	2	−68	−27	90	h
I_A	K$_v$1.4,3.4,4.1,4.2…		−1	15	0.2	−56	−8	5	i
I_M	K$_v$7.1–7.5	Muscarinic	−45	4	8	—	—	—	j
I_D	K$_v$1.1–1.2		−63	9	1	−87	−8	500	k
I_h	HCN1–4	Hyperpolarisation-activated	−75	−6	1000	—	—	—	l
I_C	K$_{Ca}$1.1	BK, maxi-K(Ca), fAHP	V & Ca^{2+}-dep			—	—	—	m
I_{AHP}	K$_{Ca}$2.1–2.3	SK1–3, mAHP	0.7 μM		40	—	—	—	n
I_{sAHP}	K$_{Ca}$?	Slow AHP	0.08 μM		200	—	—	—	o

Table 5.2 [illegible]

(Table 5.2 pg 102)

Potassium A-current: K_A

- Different characteristics from delayed rectifier: K_{DR}
- Low threshold activating / inactivating current

$$C_m \frac{dV}{dt} = -g_{Na}(V - E_{Na}) - g_K(V - E_K) - g_A(V - E_A) - g_L(V - E_L).$$

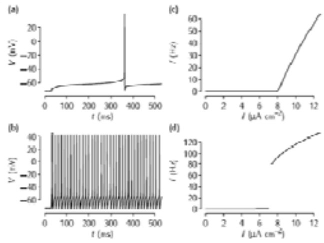
$$I_A = g_A(V - E_A), \qquad g_A = \overline{g}_A a^3 b,$$

$$a_\infty = \left(\frac{0.0761 \exp\left(\frac{V+99.22}{31.84}\right)}{1 + \exp\left(\frac{V+6.17}{28.93}\right)} \right)^{\frac{1}{3}}, \qquad \tau_a = 0.3632 + \frac{1.158}{1 + \exp\left(\frac{V+60.96}{20.12}\right)},$$

$$b_\infty = \frac{1}{\left(1 + \exp\left(\frac{V+58.3}{14.54}\right)\right)^4}, \qquad \tau_b = 1.24 + \frac{2.678}{1 + \exp\left(\frac{V+50}{16.027}\right)}.$$

One Effect of A-current

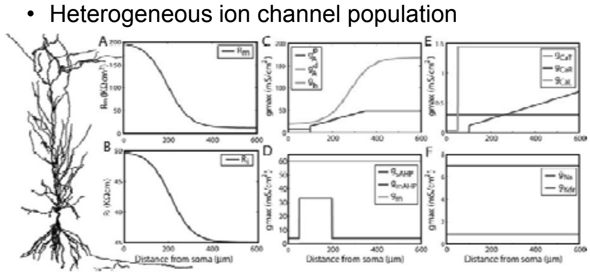
- Type I: with KA
  - Steady increase in firing frequency with driving current
- Type II: without KA
  - Suddent jump to non-zero firing rate



(Fig. 5.9 pg 106)

A Detailed Pyramidal Cell Model

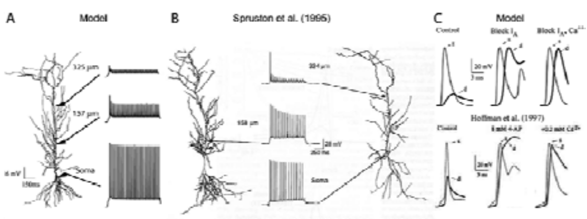
- 183 electrical compartments
- Heterogeneous ion channel population



(Poirazzi & Pissadaki, in CU)

Pyramidal Cell Model Responses

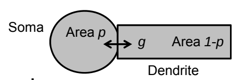
- Reproduces somatic and dendritic current injection experimental results
  - Sodium spiking with distance

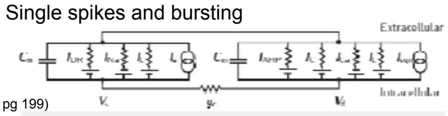


(Poirazzi & Pissadaki, in CU)

Reduced Pyramidal Cell Model

- 2-compartment model
  - Pinsky & Rinzel (1994)
- Captures essence of PC behaviour
  - Single spikes and bursting





(Fig. 8.1 pg 199)

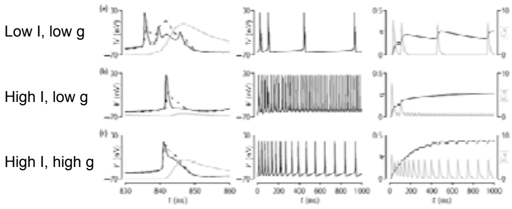
$$C_m \frac{dV_s}{dt} = -g_L(V_s - E_L) - g_{Na}(V_s - E_{Na}) - g_{DR}(V_s - E_K) + \frac{g_c}{p}(V_d - V_s) + \frac{I_s}{p}$$

$$C_m \frac{dV_d}{dt} = -g_L(V_d - E_L) - g_{Ca}(V_d - E_{Ca}) - g_{AHP}(V_d - E_K) - g_C(V_d - E_K) + \frac{g_c}{1-p}(V_s - V_d) + \frac{I_{syn}}{1-p}.$$

 (Box 8.1 pg 200)

Pinsky-Rinzel Model in Action

- Behaviour depends on
  - Compartment coupling strength (g)
  - Magnitude of driving current (I)



(Fig. 8.2 pg 201)

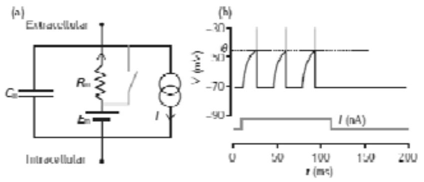
Simple Spiking Neuron Models

- Simple spiking models that DO NOT model the AP waveform
- Generally single compartment
  - Point neurons
- Family of “Integrate-and-fire” models

Integrate-and-Fire Model

- RC circuit with spiking and reset mechanisms
  - When V reaches a threshold
    - A spike (AP) event is “signalled”
    - Switch closes and V is reset to E_m
    - Switch remains closed for refractory period

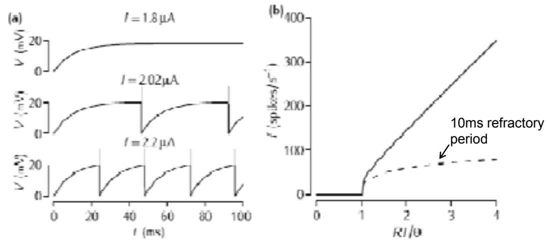
$$C_m \frac{dV}{dt} = -\frac{V - E_m}{R_m} + I$$



(Fig. 8.4 pg 204)

I&F Model Response

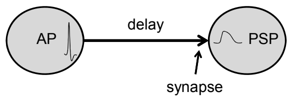
- Response to constant current injection
  - No refractory period



(Fig. 8.5 pg 205)

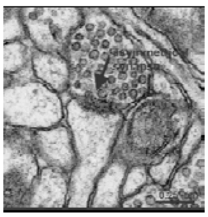
Networks of Neurons

- Neurons connected via synapses between axons and dendrites
- Need to account for:
  - action potential propagation along the axon
  - Neurotransmitter release at presynaptic terminal
  - Postsynaptic electrical response
  - Parameters: *delay* + *weight*

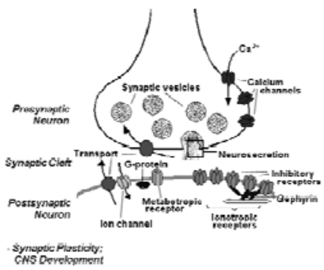


The Chemical Synapse

- A temporal signal filter
- Complex biochemical signalling pathways



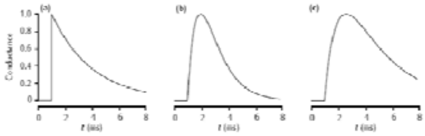
(The Synapse Web)



(biochem.uni-erlangen.de)

Synaptic Conductance

- 3 commonly used simple waveforms
  - a) Single exponential $g_{syn}(t)=\bar{g}_{syn}\exp\left(-\frac{t-t_s}{\tau}\right)$
  - b) Alpha function $g_{syn}(t)=\bar{g}_{syn}\frac{t-t_s}{\tau}\exp\left(-\frac{t-t_s}{\tau}\right)$
  - c) Dual exponential $g_{syn}(t)=\bar{g}_{syn}\frac{\tau_1\tau_2}{\tau_1-\tau_2}\left(\exp\left(-\frac{t-t_s}{\tau_1}\right)-\exp\left(-\frac{t-t_s}{\tau_2}\right)\right)$

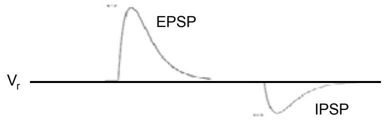


– Current: $I_{syn}(t) = g_{syn}(t)(V(t)-E_{syn})$

(Fig. 7.2 pg 174)

Excitation and Inhibition

- Equilibrium potential of postsynaptic current:
  - $I_{syn}(t) = g_{syn}(t)(V(t)-E_{syn})$
  - Excitatory postsynaptic potential (EPSP) if $E_{syn}>V_r$
  - Inhibitory postsynaptic potential (IPSP) if $E_{syn}<V_r$



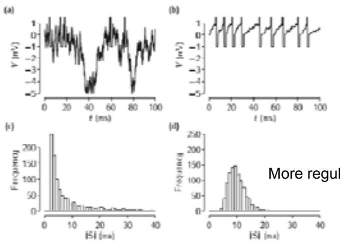
- *A presynaptic neuron is either excitatory or inhibitory to all of its targets*

Application of I&F Neurons

- Variability of neuronal firing
  - Balance of excitation and inhibition
  - I&F neuron driven by 100Hz Poisson spike trains

Excitation + inhibition

Excitation only



Irregular firing

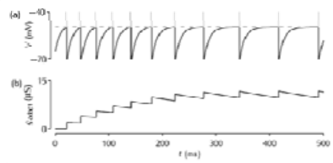
More regular

(Fig. 8.6 pg 209)

More Realistic I&F Neurons

- Basic I&F model does not accurately capture the diversity of neuronal firing patterns
- Adaptation of interspike intervals (ISIs) over time

$$\frac{dg_{adapt}}{dt} = -\frac{g_{adapt}}{\tau_{adapt}} \quad \text{and} \quad I_{adapt} = g_{adapt}(V-E_m).$$



(Fig. 8.8 pg 213)

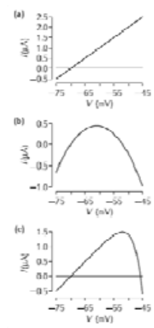
Modelling AP Initiation

- Basic I&F is a poor model of the ionic currents near AP threshold
  - Timing of AP initiation
- Quadratic I&F

$$C_m\frac{dV}{dt} = -\frac{(V-E_m)(V_{thresh}-V)}{R_m(V_{thresh}-E_m)}+I.$$

- Exponential I&F

$$C_m\frac{dV}{dt} = -\left(\frac{V-E_m}{R_m}-\frac{\Delta_T}{R_m}\exp\left(\frac{V-V_T}{\Delta_T}\right)\right)+I,$$



(Fig. 8.9 pg 214)

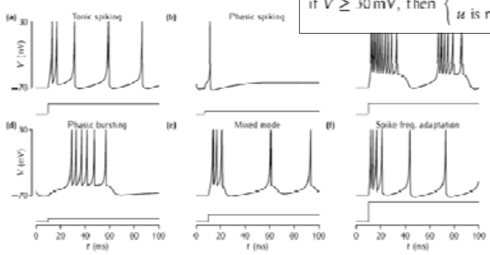
The Izhikevich Model

- Quadratic I&F plus dynamic recovery variable

$$\frac{dV}{dt} = k(V-E_m)(V-V_{thresh})-u+I$$

$$\frac{du}{dt} = a(b(V-E_m)-u)$$

if $V \geq 30$ mV, then $\begin{cases} V \text{ is reset to } c \\ u \text{ is reset to } u+d, \end{cases}$



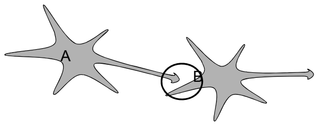
(Fig. 8.10 pg 215)

Learning in the Nervous System

- ANNs "learn" by adapting the connection weights
  - Different learning rules
- Real chemical synapses do change their strength in response to neural activity
  - Short-term changes
    - Milliseconds to seconds
    - Not classified as "learning"
  - Long term potentiation (LTP) and depression (LTD)
    - Changes that last for hours and possibly lifetime
- Evidence that LTP/LTD corresponds to "learning"

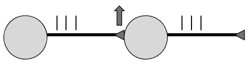
Hebbian Learning

- Hypothesis by Donald Hebb, "The Organization of Behaviour", 1949
  - "When an axon of cell A excites cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells so that A's efficiency, as one of the cells firing B, is increased."

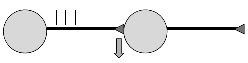


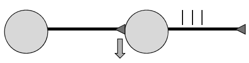
Associative Learning

- Increase synaptic strength if both pre- and postsynaptic neurons are active: LTP



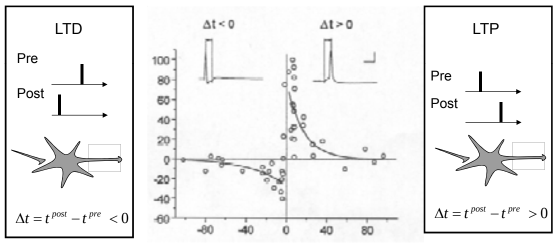
- Decrease synaptic strength when the pre- or postsynaptic neuron is active alone: LTD





Spike Time Dependent Plasticity

- STDP depends on relative timing of pre- and postsynaptic spiking activity
  - Single spikes or short bursts



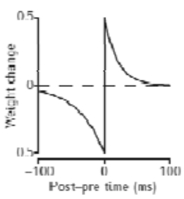
(Bi & Poo, 1998, 2001)

STDP Learning Rule

- Synaptic weight change as a function of pre- and postsynaptic spike times for a single spike pair

$$\Delta w_{ij} = A^{LTP}\exp(-\Delta t/\tau^{LTP}) \quad \text{if } \Delta t \geq 0$$
$$\Delta w_{ij} = -A^{LTD}\exp(\Delta t/\tau^{LTD}) \quad \text{if } \Delta t < 0.$$

(Song et al 2000; van Rossum et al 2000)



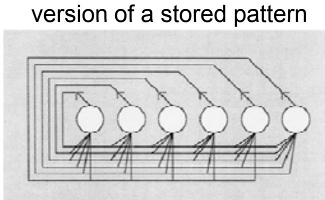
(Fig. 7.13 pg 190)

Typical parameter values:

$A^{LTP} > A^{LTD}$
τ^{LTP} = 20 msecs
τ^{LTD} = 40 msecs

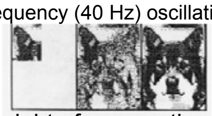
Associative Memory

- Recurrent network of binary state "neurons"
  - Hopfield
- Binary "patterns" stored by Hebbian learning
  - Each bit corresponds to state of a neuron
- Recall via initial state that is a noisy or partial version of a stored pattern



Spiking Associative Memory

- What constitutes a “pattern” over a set of neurons whose activity changes with time?
  - (near) synchronous firing of neurons
- What is an update cycle during recall?
  - A gamma frequency (40 Hz) oscillation cycle



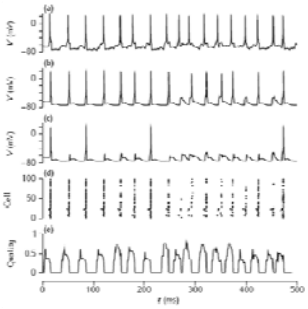
- What is the weight of a synaptic connection?
  - Amplitude of excitatory synaptic conductance
- How is firing threshold for recall set?
  - Inhibition in proportion to excitatory activity

Example Spiking Network

- 100 PC recurrent network
  - Sommers and Wennekers (2000, 2001)
  - Pinsky-Rinzel 2-compartment neuron model
- Excitatory connections determined by predefined binary Hebbian weight matrix that sets synaptic conductance
  - Conductance either 0 or g_{max}
- Threshold setting via all-to-all fixed weight inhibitory connections
  - Should really be provided by a separate population of inhibitory neurons driven by the excitatory neurons

Cued Recall in Spiking Network

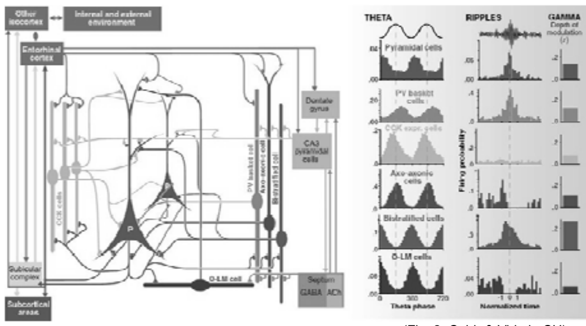
- Cue: 4 of 10 PCs in a stored pattern receive constant excitation
- Network fires with gamma frequency
- Pattern is active cells on each gamma cycle
- Timing and strength of inhibition



(Fig. 9.10 pg 253)

Rhythmic Neural Circuits

- CA1 region of hippocampus



(Fig. 2, Cobb & Vida in CU)

NEURON Exercises

1. Frequency-Input Current (F-I) Firing Curve
2. Simple Excitation-Inhibition (E-I) Oscillator
3. Excitation-Inhibition Balance in an I&F Neuron
4. Excitation-Inhibition Balance in a Network
5. STDP in Action
   a. Phase precession of spike timing
   b. Sequence learning
6. Associative Memory in a Network