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COLLEGE ON NEUROPHYSICS:
"DEVELOPMENT AND ORGANIZATION OF THE BRAIN"
7 November - 2 December 1988

"Noisy Neural Nets"

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Department of Mathematics
London, UK

Please note: These are preliminary notes intended for internal distribution only.

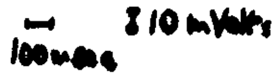
NOISY NEURAL NETS

Noise = 'Uncertainty'

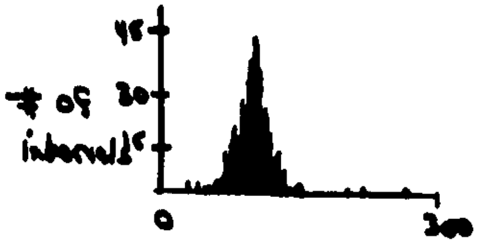
⇒ All neural activity noisy

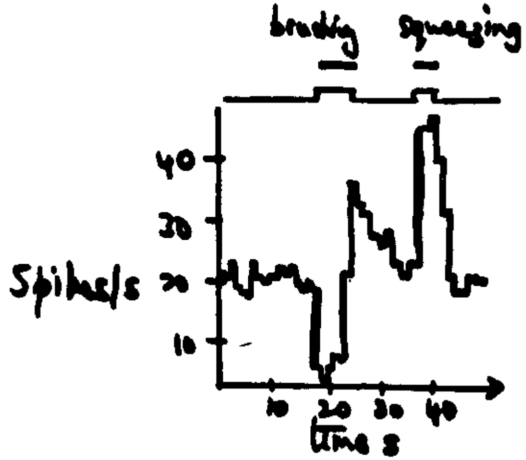
(to a greater or lesser extent)

e.g.



(neuron in cat spinal chord)
– decerebrate





(anaesthetized)

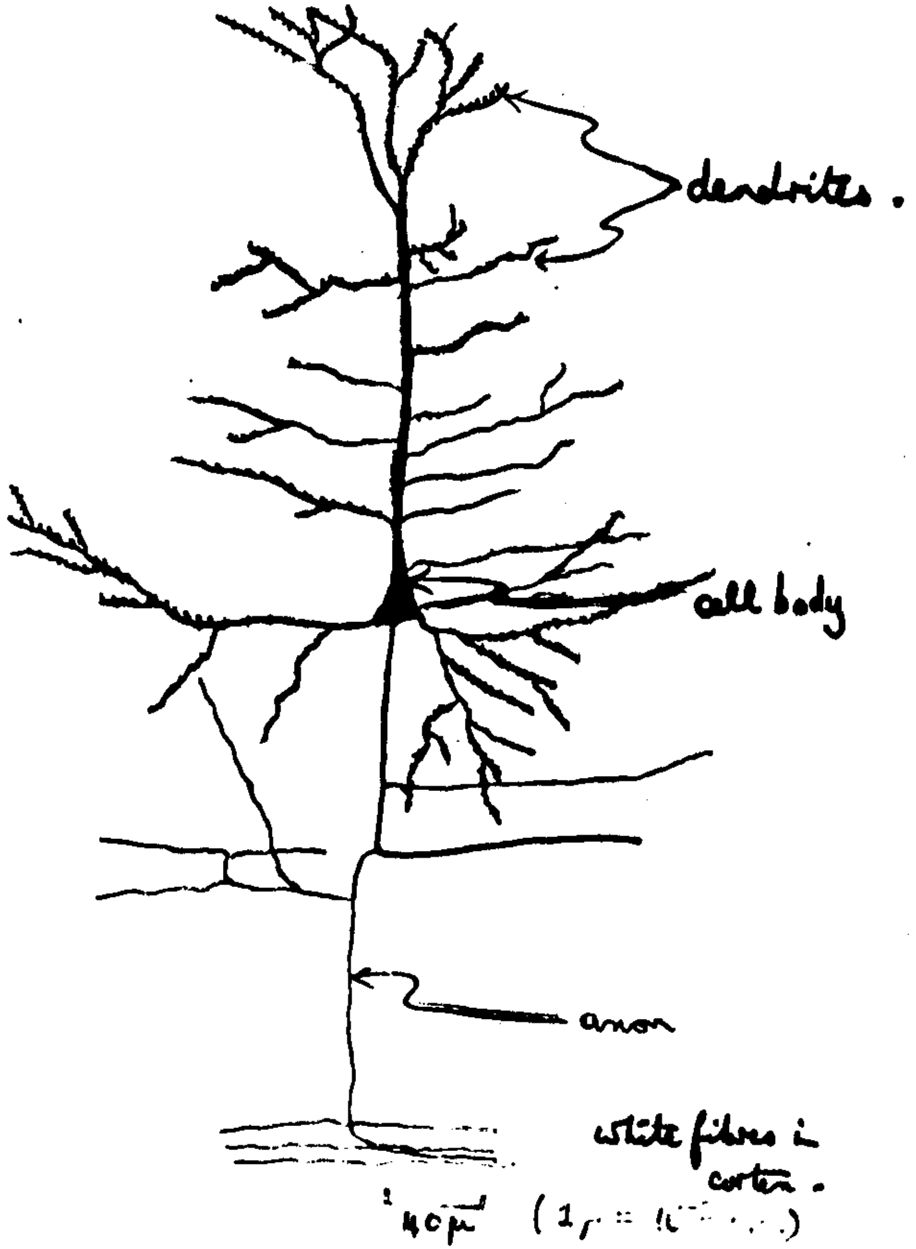
⇒ Information transfer in presence of noise.

Contents of talk:

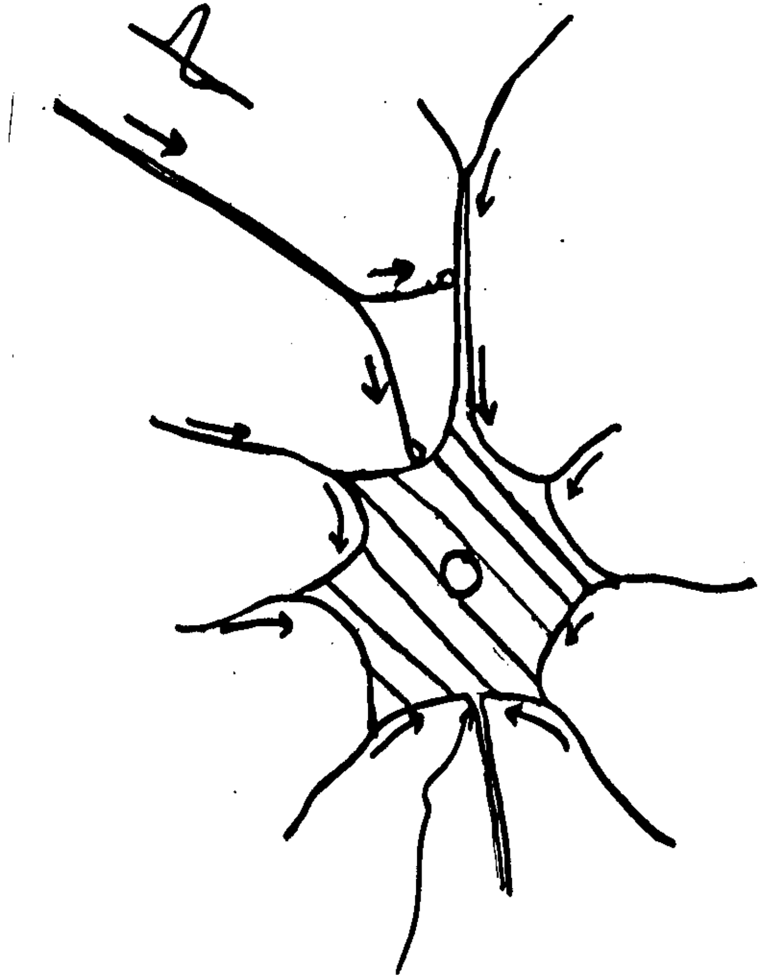
1) Sources of noise in N.N's.
2) Markov model (Little '74
3) Indep. Neuron model (J.G.T. '72
4) Properties of I.N. Model
5) Relation of Markov and IN Model
6) Learning
(7) applications: fibrillation in muscles; cardiac arrythmias; epilepsy; ageing; Parkinson's disease; ...; (and models of N.N. activity)

SOURCES OF NOISE

Typical Nerve Cell (Cortical Neuron)

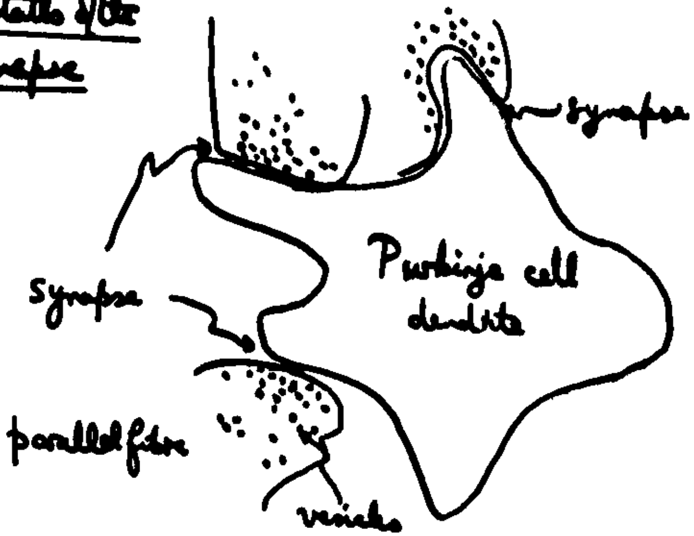


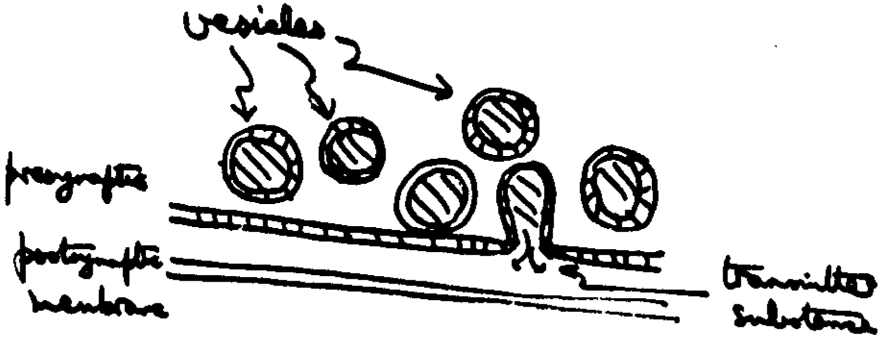
Summation of Excitation.



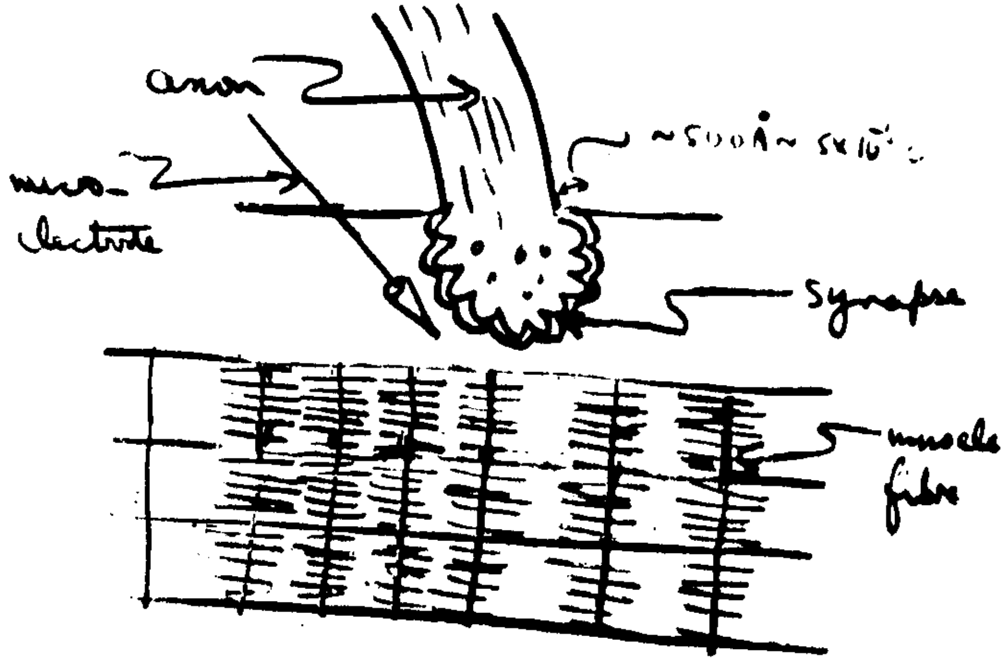
Summation of excitation at axon hillock.
Nerve impulse generated there if total excitation > critical depolarisation level (~15mV)

Details of the Synapse





Neuromuscular Junction

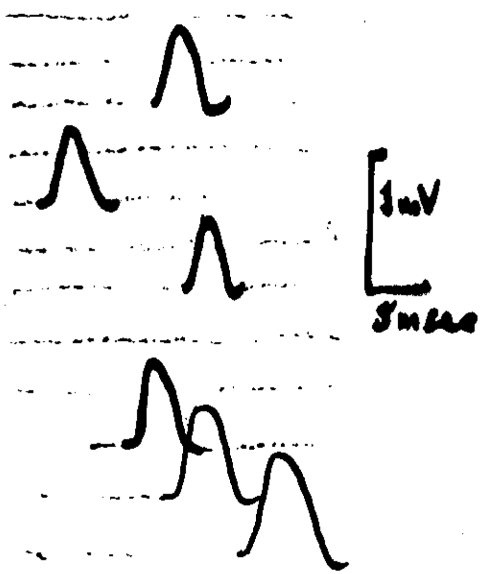


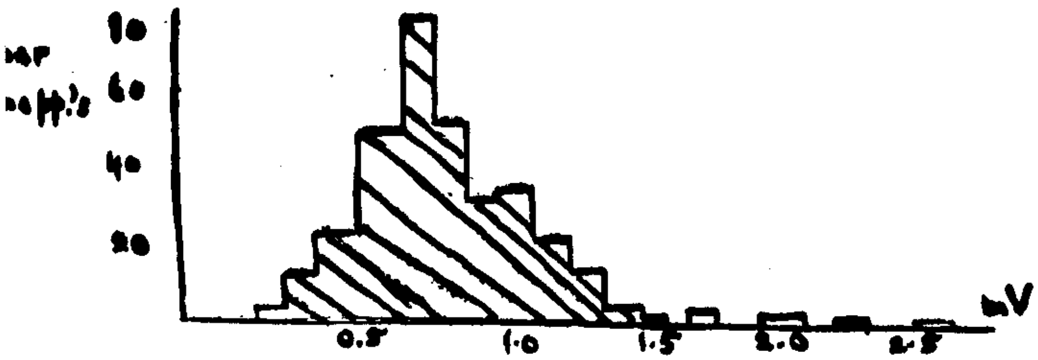
End-Plate potential (e.p.p) caused by nerve pulse

Generation of e.p.p reduced by +Mg, −Ca

Fatt & Katz (Nature 166, 597, 1950
J. Physiol. 117, 109, 1952)

m.e.p.p (neuromuscular synapse in rat diaphragm)

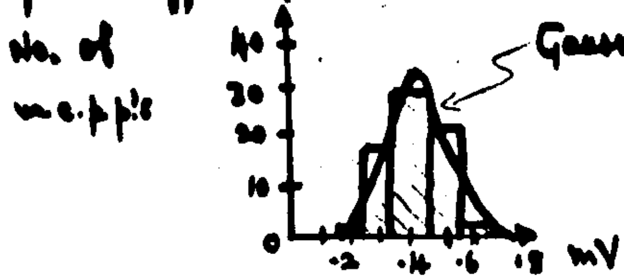




⇒ size of m.e.p.p roughly constant.

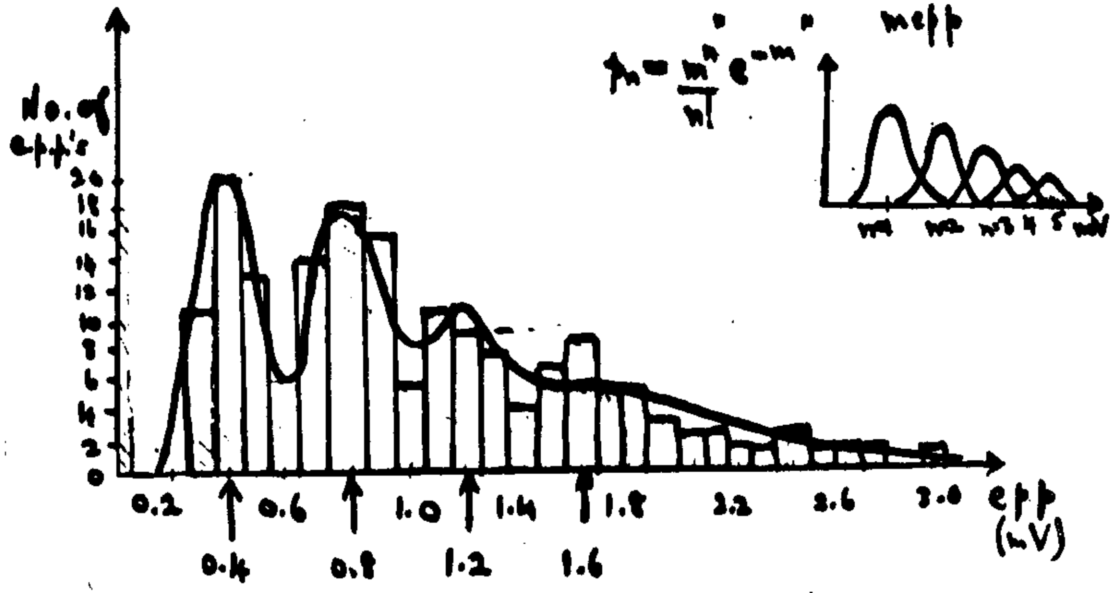
Quantum hypothesis: e.p.p. built up of integer number of m.e.p.p.'s.

Exptal support (cat neuromuscular junction, Mg rich)



$m = \frac{\text{mean amplitude of e.p.p}}{\text{" " m.e.p.p}} = 2.33$

$p_n = \frac{m^n}{n!} e^{-m}$



(Boyd & Martin, J. Physiol. 132, 74, 1956).

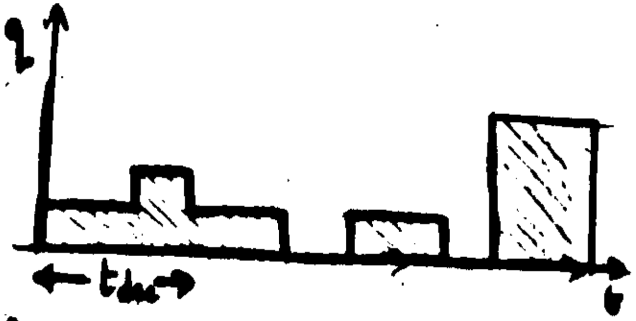
Noisy Neural Nets

Noise at each synapse:

Frequency of quanta (or vesicles) $= 1/t_1 = \nu$

Decay of " $= t_{dec}$

amount of transmitter



Mean no. of quanta $\} = t_{dec}/t_1$

Spontaneity if $t_{dec}/t_1 > n_{thresh}$ = no. of vesicles required to fire next cell.

If m synapses to a given neuron

spontaneity if $m t_{dec}/t_1 > n_{thresh}$

or

Spontaneity number $S = \dfrac{m t_{dec}}{n_{thresh} t_1} > 1$

Sizes: $t_{dec} \sim 1\text{–}10$ msec

$(n_{thresh} t_1)^{-1} \sim 0.25\ \text{sec}^{-1}$ (CNS + peripheral)

(n_{thresh} ↓ overall, t_1 ↑ overall; Kuno et al, 1971)

$\Rightarrow \quad S \sim \left(\frac{1}{4000} \text{ to } \frac{1}{400}\right) m$

$$\left.\begin{array}{ll} m \sim 10^3 & \text{(cortex)} \\ \sim 10^5 & \text{(cerebellum)} \\ \sim 1 & \text{(peripheral N.S.)} \end{array}\right\} \Rightarrow \begin{array}{l} S \ll 1 \text{ (peripheral)} \\ \gtrsim 1 \text{ (CNS)} \end{array}$$

Detailed eqns for noisy nets constructed (and $\longrightarrow$ Caianiello's eqns as $t_{dec} \to 0$)

$$u_i(t+\tau) = \Theta\left[\sum a_{ij} u_j(t) - t_i\right]$$

u_i: ith neuron activity fn: $\begin{cases} 0 : \text{inactive} \\ 1 : \text{active} \end{cases}$

t_i: threshold

Can regard $\underbrace{S}_{\text{intrinsic 'noise' level}} \sim$ temperature (for a single neuron or a net)

Other sources of noise:

J. Clark
Phys. Rep. 158 (1988)
93–157

a) external (input variability)

b) fluctuations in # of transmitter molecules at receptor sites

c) fluct. of post-synaptic efficiency

d) " " dendritic/soma membrane constants (capacity, resistance, etc)

e) " " threshold for cell firing

f) effects of nearby cells (electric or magnetic)

Models constructed of all of these: lead to v. difficult math. analyses

Concentrate on internal noise (initially synaptic)

II. MARKOV MODEL OF NOISY NETS.

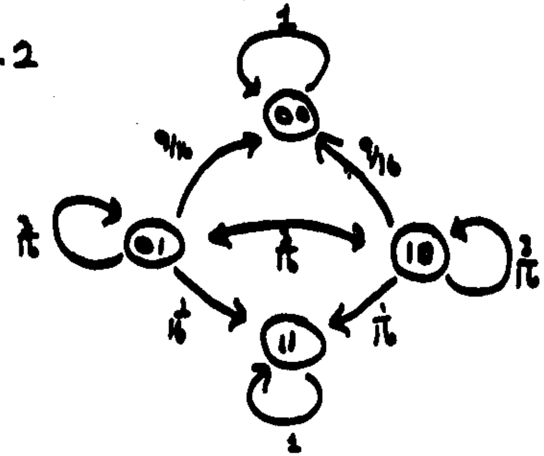
State space of N neurons $= \{0,1\}^N$: 2^N dim.

states i $(1 \leq i \leq 2^N)$

probabilities $p_i(t)$ at time t

transfer matrix M_{ij} : prob. of state $i \longrightarrow$ state j

e.g. $N=2$



$$M = \begin{array}{c} \begin{pmatrix} 1 & 9/16 & 9/16 & 0 \\ 0 & 3/16 & 3/16 & 0 \\ 0 & 3/16 & 3/16 & 0 \\ 0 & 1/16 & 1/16 & 1 \end{pmatrix} \end{array} \begin{array}{c} (00) \\ (01) \\ (10) \\ (11) \end{array}$$

Little model:

$$M_{ij} = \prod_{\nu=1}^{N} \left\{ 1 + e^{-\beta_\nu \sigma_\nu^{(i)} \left[\sum_\mu a_{\nu\mu} \frac{1}{2}(1+\sigma_\mu^{(j)}) - \theta_\nu \right]} \right\}^{-1}$$

$\sigma_\nu^{(i)} = \begin{cases} +1 & \text{neuron } \nu \text{ active} \\ -1 & \text{" inactive} \end{cases} \text{ in } i$

$\beta_\nu \sim 1/T^\circ$; weights ; threshold

(Little '74)

- Justifiable in model of synaptic noise (Shaw & Vasudevan '74)

(altho' $\beta_\nu^{-\frac{1}{2}} \propto \sum_\mu a_{\nu\mu} \frac{1}{2}(1+\sigma_\mu)(1-\varepsilon) + \text{spont. term}$

depends on activity of presynaptic neurons

— lost in Little model)

- Can attempt to use ideas of stat. mech

— macroscopic forces & fluxes ← Schnakenberg

(but have $O(2^{2N})$ such quantities) (given by indep. set of cycles.

- final state of net always same:

only one asymptotic state ($T^\circ > 0$) (Perron-Frobenius Thm

$\left(\lim_{n\to\infty} M^n = \underline{x}\,(1,\dots,1),\ \lim_{n\to\infty} M^n \underline{p} = \underline{x} \right)$

- can try to work "on boundary of parameters"

i.e. $T \sim 0$, $\beta_\nu \sim \infty$ ($\longrightarrow$ 'decision' model of Caianiello)

and have behaviours

i) cyclic $\rightsquigarrow$ disruption $\rightsquigarrow$ cyclic again .... ($\lambda' s \neq 1$)

ii) static for extended period ($|\lambda| \approx 1$)

$\xrightarrow{\text{exit}}$ static " "

$\longrightarrow$ ...

$\sim$ manifestations of order (for a finite # of time steps)

but no phase transitions ($N < \infty$) (Thompson, Gibson '81)

N.B. Hopfield $\sim$ Little for asymptotic structure (Amit et al $N = \infty$)

update only one neuron at each time step

chosen at random

or by fixed order

so expect Hopfield model ($N < \infty$) only one final state

e.g. if update 1, 2, ..., after N steps have

$$M_{ij}^{(N)} = \left[\prod_{\nu=1}^{N} M^{(\nu)} \right]_{ij}$$

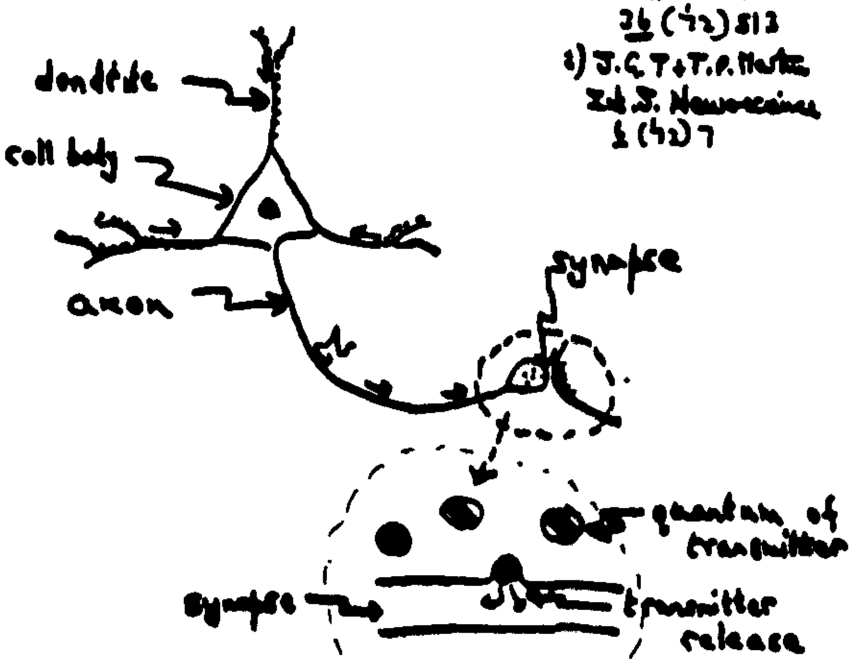
$$M_{ij}^{(\nu)} = \left\{ 1 + e^{-\beta_\nu \sigma_\nu^{(i)} \left[\sum a_{\nu\mu} \frac{1}{2}(1+\sigma_\mu^{(j)}) - \theta_\nu \right]} \right\}^{-1}$$

$\Rightarrow M^{(N)}$ is a strictly +ve stochastic matrix

$\Rightarrow$ only one final state!

I INDEP. NEURON MODEL

1) JGT J. Th. Biol. 36 ('72) 513
2) J.G.T + T.P. Harte Int. J. Neuroscience 5 ('72) 7



i) n_0 quanta released/nerve impulse

ii) constant leakage into synapse ~ Poisson process

prob. of n quanta released $= \frac{\lambda^n}{n!} e^{-\lambda}$

($\lambda = t_{dur}/t_1$) in the time t_{dur}; t_1 = release freq.

⇒ prob. distn. fn. for transmitter q

$$\rho_s(q) = \sum_n \frac{\lambda^n}{n!} e^{-\lambda}\, \delta(nq^{(0)} - q) \quad \text{(SPONT.)}$$

amount/quantum

$$\rho_d(q) = \delta(n_0 q^{(0)} - q) \quad \text{(DET.)}$$

Discrete time, no decrement of q to axon hillock

Prob. of cell i firing at time t $= p_i(t)$

$$p_2(t+1) = \int_{q_c}^{\infty} dq \left[p_1(t)\,\delta(q - n_0 q^{(0)}) + (1 - p_1(t))\,\rho_s(q) \right]$$

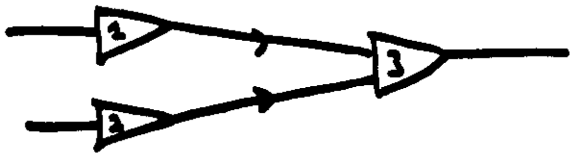
threshold condition

from cell 1 firing at t

from cell 1 not firing at t.

$$= \alpha_1 p_1(t) + \alpha_0 \bar{p}_1(t) \quad \text{: LINEAR}$$

$0 \le \alpha_0, \alpha_1 \le 1$. $\quad (\bar{x} = 1 - x)$



$$\phi_3(t+1) = \int_{q_c}^{\infty} dq\, \delta(q - q_1 - q_2) \times$$
$$\times \left[\phi_1(t)\,\delta(q_1 - n_0 q^{(0)}) + \bar{\phi}_1(t)\,\rho_0(q_1)\right]$$
$$\times \left[\phi_2(t)\,\delta(q_2 - n_0 q^{(0)}) + \bar{\phi}_2(t)\,\rho_0(q_2)\right]$$

threshold condition

summing excitation

1st cell contribution

2nd cell contribution

$$= \left(\alpha_{11}\phi_1\phi_2 + \alpha_{01}\bar{\phi}_1\phi_2 + \alpha_{10}\phi_1\bar{\phi}_2 + \alpha_{11}\bar{\phi}_1\bar{\phi}_2\right)(t)$$

$$0 \le \alpha_{ij} \le 1.$$

In general:

$$\phi_i(t+1) = \int_{q_c}^{\infty} dq \prod_j \int dq_{ij}\, \delta(q - \sum_j q_{ij}) \times$$
$$\prod_j \left[\phi_j(t)\,\delta(q_{ij} - n_{ij} q_{ij}^{(0)}) + \bar{\phi}_j(t)\,\rho_{ij}(q_{ij})\right]$$

summation of excitation

threshold condition

prob. of j^{th} cell firing at t

prob. of j^{th} cell not firing at t.

$\bar{\phi} = 1 - \phi$

(+ more complicated versions: continuous time
no sharp threshold
etc)

$\phi_i(t+1) =$ polynomial of ∂° N in $\{\phi_j(t)\}$

e.g. $N=2$:

$$\boxed{\begin{aligned} \phi_1(t+1) &= \left(\alpha_0\bar{\phi}_1\bar{\phi}_2 + \alpha_1\bar{\phi}_1\phi_2 + \alpha_2\phi_1\bar{\phi}_2 + \alpha_3\phi_1\phi_2\right)(t) \\ \phi_2(t+1) &= \left(\beta_0\bar{\phi}_1\bar{\phi}_2 + \beta_1\bar{\phi}_1\phi_2 + \beta_2\phi_1\bar{\phi}_2 + \beta_3\phi_1\phi_2\right)(t) \end{aligned}}$$

($\alpha_0 = \int_{q_1^c}^{\infty} dq \int dq_1 dq_2\, \delta(q - q_1 - q_2)\,\rho_{11}(q_1)\,\rho_{12}(q_2)$ spont 1 & 2

($\alpha_1 = \int_{q_1^c}^{\infty} dq\, \rho_{11}(q - n_{12} q_{12}^{(0)})$ fire 2, spont 1

($\alpha_2 = \int_{q_1^c}^{\infty} dq\, \rho_{12}(q - n_{11} q_{11}^{(0)})$ fire 1, spont 2

($\alpha_3 = \theta(n_{11} q_{11}^{(0)} + n_{12} q_{12}^{(0)} - q_1^c)$ fire 1 & 2

Natural formulation:

$\underline{\alpha} = (\alpha_1, \dots, \alpha_N) \qquad \alpha_i = 0 \text{ or } 1$

$P_{\underline{\alpha}}(\underline{p}) = \prod_{i=1}^{N} p_i^{\alpha_i} \bar{p}_i^{\bar{\alpha}_i}$

$$\boxed{p_i(t+1) = \sum_{\underline{\alpha}} u_{\underline{\alpha} i} \, P_{\underline{\alpha}}(\underline{p}(t))}$$

$0 \leq u_{\underline{\alpha} i} \leq 1$

$(\bar{x} \equiv 1-x)$

Can be implemented in hardware by

p-RAM nets

probabilistic

(→ D. Gorse

e.g. $N=3$:

$p_1(t+1) = (\alpha_0 \bar{p}_1\bar{p}_2\bar{p}_3 + \alpha_1 \bar{p}_1\bar{p}_2 p_3 + \dots + \alpha_7 p_1 p_2 p_3)(t)$

$p_2(t+1) = (\beta_0 \bar{p}_1\bar{p}_2\bar{p}_3 + \beta_1 \bar{p}_1\bar{p}_2 p_3 + \dots + \beta_7 p_1 p_2 p_3)(t)$

$p_3(t+1) = (\gamma_0 \bar{p}_1\bar{p}_2\bar{p}_3 + \dots$

$0 \leq \alpha_i, \beta_i, \gamma_i \leq 1$

- In general

$p_1(t+1) = (\alpha_0 \bar{p}_1 \dots \bar{p}_N + \dots + \alpha_{2^N-1} p_1 \dots p_N)(t)$

$\vdots$

$p_N(t+1) = (\delta_0 \bar{p}_1 \dots \bar{p}_N + \dots + \delta_{2^N-1} p_1 \dots p_N)(t)$ →

- Maps $[0,1]^N \longrightarrow [0,1]^N$

- Changes in α's, β's ... ~ changes in $t_{dues}, q_{ij}^{(0)}, n_{ij}, \dots$ ~ training ~ exptal input

- Use of noise in learning

IV. Properties of Noisy Net Eqns. (I.N. Model)

- Dynamical system

$$\phi(t+1) = P_N(\phi(t)) \; : \; [0,1]^N \to [0,1]^N$$

Well defined

- Always $\exists$ one fixed point (Brouwer)

No analytic form of f.p. for $N > 2$.

- No energy function

$$\begin{pmatrix} x \to & \text{lin} & + xy \\ y \to & " & + xy \end{pmatrix}$$

- Region in parameter space with P_N contractive

e.g. $N = 2$ $\quad \phi_1(t+1) = \alpha_0 \bar{\phi}_1 \bar{\phi}_2(t) + \ldots$

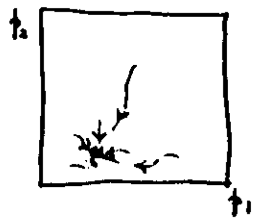
$$\phi_2(t+1) = \beta_0 \bar{\phi}_1 \bar{\phi}_2(t) + \ldots$$

with

$$\left. \begin{array}{l} |\alpha_1 - \alpha_0| + |\alpha_2 - \alpha_0| + 2|\alpha_3 + \alpha_0 - \alpha_1 - \alpha_2| \\ |\beta_1 - \beta_0| + |\beta_2 - \beta_0| + 2|\beta_3 + \beta_0 - \beta_1 - \beta_2| \end{array} \right\} < 1$$

$\sim$ $\alpha_1, \alpha_2, \alpha_3 \sim \alpha_0$ & β's

$\sim$ spontaneous region



- May have wide range of dynamical behaviour as increase α's, β's, ...

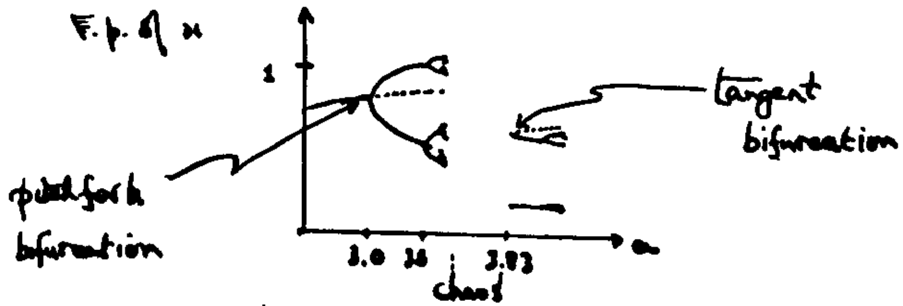
e.g. $\phi_1(t+1) = \bar{\phi}_1 \bar{\phi}_2 + \phi_1 \phi_2 = 1 - \phi_1 - \phi_2 + 2\phi_1 \phi_2$

$$\phi_2(t+1) = \bar{\phi}_1 \phi_2 + \phi_1 \bar{\phi}_2 = \phi_1 + \phi_2 - 2\phi_1 \phi_2$$

$\Rightarrow \quad \phi_1(t) + \phi_2(t) = 1$

$\Rightarrow \quad \phi_1(t+1) = 2\phi_1(t)(1 - \phi_1(t))$

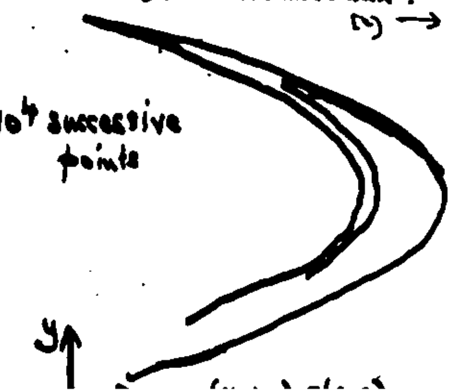
$x \to a x(1-x)$ (logistic map)



(destruction of KAM tori, integrable $\to$ non integrable system — but no Hamiltonian.)

- Henon map in [2]

$$\left. \begin{array}{l} x \to 1 - \mu x^2 + y \\ y \to bx \\ b = 0.3, \mu > 1.06 \end{array} \right\} 10^4 \text{ successive points}$$



- $(x, y) \longrightarrow (y, ay(1-x))$ (Aronson et al

f.p. $(0,0)$ stable $0 < a < 1$ $\left(\frac{a-1}{a}\right)(1,1)$ stable $1 < a < 2$

$a \uparrow 2$: invariant circle

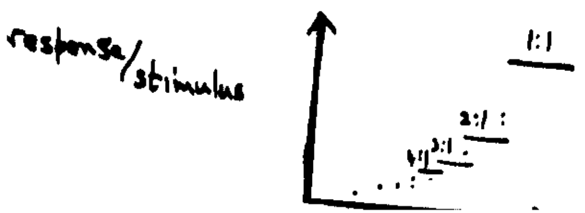
then breaks up as $a \uparrow 2.27$

$a^* = 2.27$

Chaos in living systems (excitable cells) :

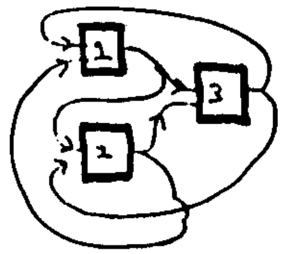
driven heart cells (period doubling)
(phase locking)

- cardiac tissue (chaos) (Chialvo & Jalife Nature Dec'87)

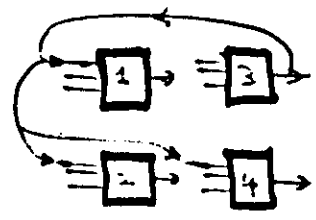


~ devils staircase

- To find dynamics : compute iterations



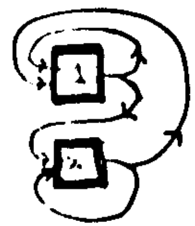
3×2RAM Net



4×3RAM Net

50,000 runs (cgence to .001)

→ only 1 fixed point (& stable)

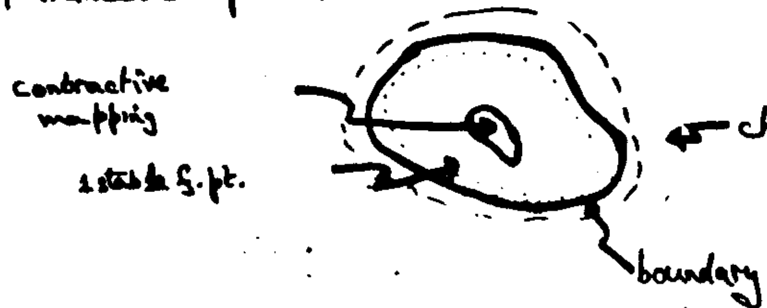


2×2RAM Net

10^6 runs :

→ only 1 fixed point (& stable)

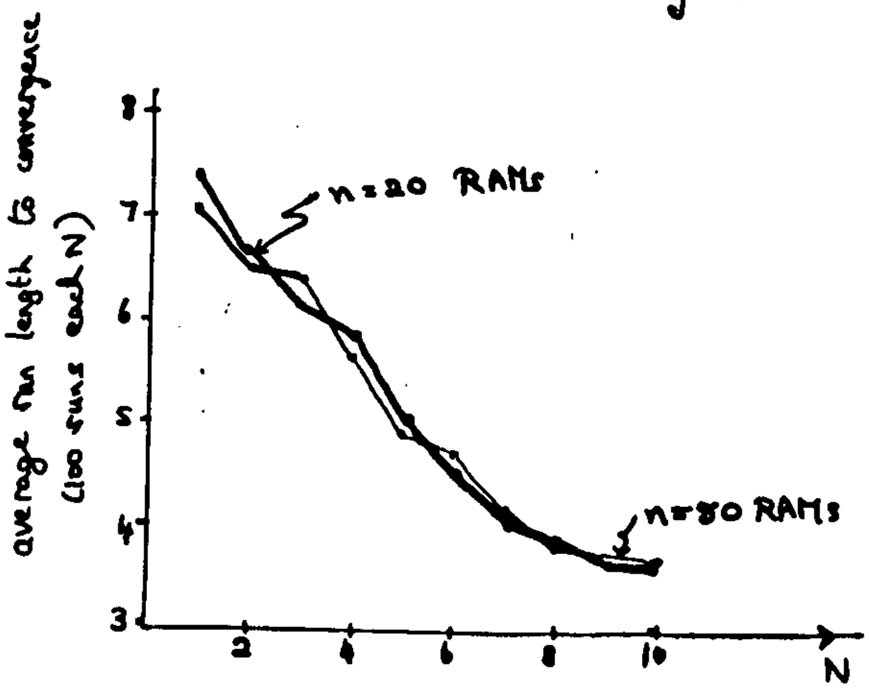
Paramater space:



(with possible cycles)

for small nets

• For large nets : n N-RAMs
randomly connected webs



V. fast convergence : '3 and a bit'

• Conjectures : • no chaos for $\forall N$

• only 1 stable f.p. $n \times N$ with $n \gg N > 10$

• 3 cycles at boundary

} ~ behaviour of Markov model

• Expect robust (asynchrony, etc)

↳ have similar polynomial maps

(Compare all Kohonen ---

• linearised version:

$$\phi_i(t+1) = A_i + A_{ij}\,\phi_j(t)$$

$$A_i = \langle (\rho_s)^N \rangle_i = \int dq \prod dq_j\, \delta(q - \Sigma q_j)\, \rho_R(q) \prod \rho_s(q_j)$$

$$A_{ij} = \langle (\rho_s)^{N-1} (\Delta\rho)_j \rangle_i \;, \quad \Delta\rho_j = (\rho_d - \rho_s)(q_j)$$

Needs

$$A_{ijk} = \langle (\rho_s)^{N-2} (\Delta\rho)_j (\Delta\rho)_k \rangle_i \ll A_{ij}$$

etc $\Rightarrow \rho_d \sim \rho_s$

(or restrict ϕ's $\ll 1$ artificially)

• deterministic limit :

$$q_0 \to 0 \Rightarrow \rho_s \to \delta(q)$$

$$\phi_i(t) = u_i(t) = 0 \text{ or } 1$$

≡ Caianiello equations

(most non-linear limit)

I. MARKOV ⟷ I.N.

I.N. : variables $\{p_p(t)\}_{1 \le p \le N}$

Markov : variables $\{p_i(t)\}_{1 \le i \le 2^N}$

Markov ≡ IN

$\Leftrightarrow \ \exists\ 2^N - N - 1$ identities between p_i's

e.g. $N=2$: $p_{00}p_{11} = p_{01}p_{10}$

$N=3$:

$$\left.\begin{aligned} p_{110}p_{101} &= p_{100}p_{111} \\ p_{101}p_{011} &= p_{001}p_{111} \\ p_{110}p_{011} &= p_{010}p_{111} \\ p_{110}p_{101}p_{011} &= p_{000}p_{111} \end{aligned}\right\} 4$$

<u>Question</u>: Are IN identities satisfied <u>at all times</u> by Markov model $\left\{\begin{array}{l}\text{cattle} \\ \text{hop field}\end{array}\right.$

<u>Answer</u> : Never (unless $M < 1$)

<u>Question</u>: Are asymptotic f.p.'s of Markov and IN identical?

<u>Answer</u> : Only 'd $(2^N - N - 1)$ ← reduce to IN at all times identities satisfied

or $N(2^N - N - 1)$ ← linear

⇒ only in linear case (never?)

VI. LEARNING RULES.

Incorporation of synaptic parameters

⇒ can model learning in detail

← synaptic efficiency parameter ε etc

$\Rightarrow$ $\Delta \alpha^{i}_{\pm}$ details

e.g. $p_i(t+1) = A_i + A_{ij}\, p_j(t)$

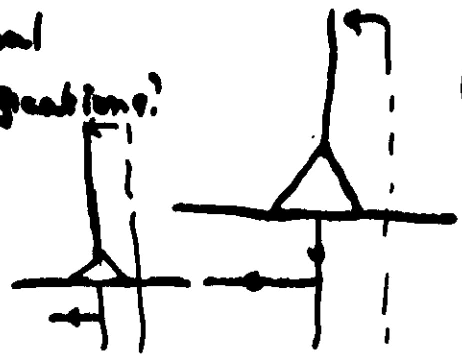
$\Delta A_{ij} \propto p_i p_j$

$\Delta A_i \propto p_i (\Sigma p_j)$

} especially affected by 'pseudo-potentials' – Ca^{++} mediated

Questions about learning:

apical v basal dendritic modifications?



(Braitenberg

CONCLUSIONS.

1) I.N. model of synaptic noise presented

→ linear model ($\langle \Delta q \rangle \ll 1$)

→ Caianiello model (spont. → 0)

→ 1.§.p.

2) I.N ≢ Markov

dubious neurophysiologically

3) Can apply I.N. to learning nets.

4) But $\boxed{\text{how to use nets with 1.§.p.?}}$

PL 131A (88) 326 (Limulus? → D. Gorse
Retina ? → JGT