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SMR/302-25

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

"Modelling the Retina"

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

MODELLING THE RETINA

WHY → UNDERSTAND LIVING SYSTEM (→ brain?)

WHY → BUILD HARDWARE REALISATION (→ connectionism)

HOW → CIRCUIT DIAGRAMS OF (L, R, C) CIRCUITS

(Mead
Mahowald
...)

CIRCUIT DIAGRAMS → Implement in hardware → Obtain response by expt → Compare with living responses

CIRCUIT DIAGRAMS → Mathematical analysis

Mathematical analysis → Noisy nets → Stochastic models

Mathematical analysis → Lattice structures → Continuous models

Stochastic models ⇢ Implement in hardware

Continuous models ⇢ Compare with living responses

Mathematical analysis ⇢ Obtain response by expt

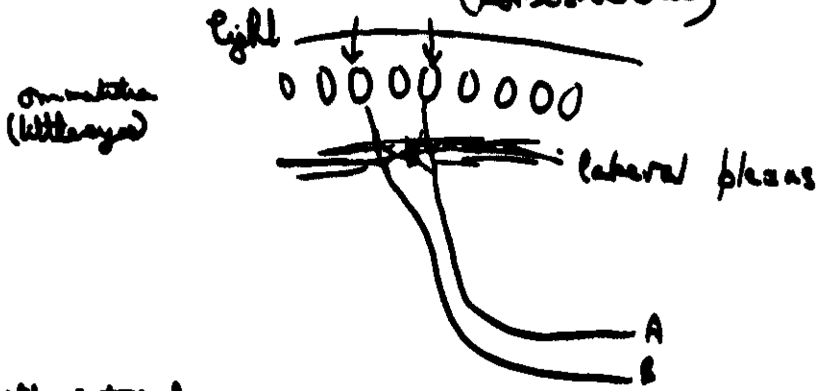
Mathematical analysis

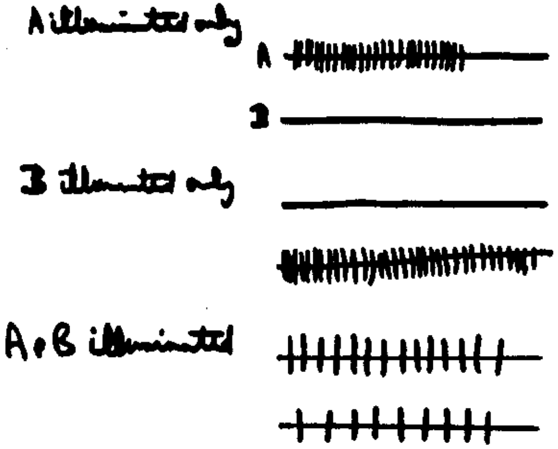
- easier (no hardware to build)

Contents of talk:

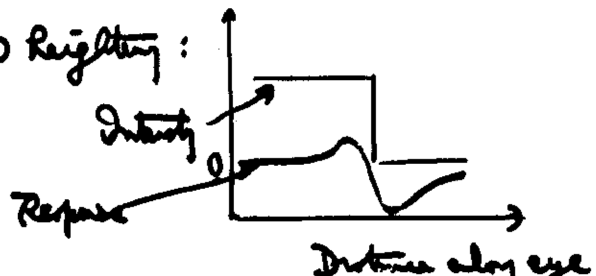
1) Invertebrate retina (lateral inhibition)
2) Math. models of "
3) Vertebrate retina
4) Math. models of "

Mutual inhibition in the compound eye of Limulus (horseshoe crab)





Contrast Reigelting :



~ Mach bands.

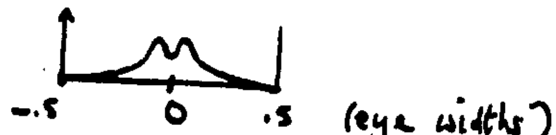
Use sine waves

in t and x, so

$$\tilde{r}(\xi,\omega) = \mathcal{F}(\xi,\omega)\, I(\xi,\omega)$$

$$\mathcal{F} = \frac{E(\omega)\, G(\omega)}{1 + E(\omega) T(\omega) \tilde{K}(\xi)}$$

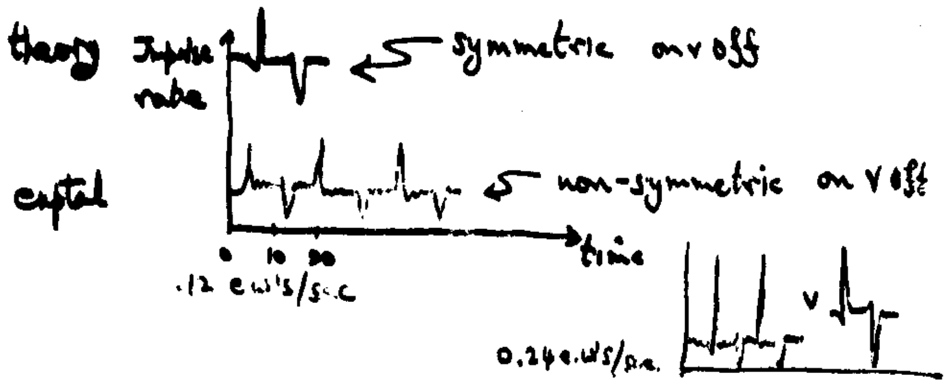
Find $k(x) \sim$



$$\sim A e^{-x^2/a^2} - B e^{-x^2/b^2} \quad \Big\} \text{ D.O.G}$$

$a \sim .17$, $b \sim 0.025$

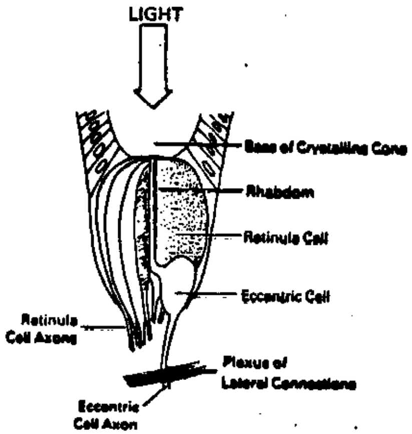
Gives response to moving square-wave stimulus:



9.

A pRAM APPROACH TO VISUAL PROCESSING IN LIMULUS

(Gorse and Taylor, 1988)



Hartline-Ratliff equations (in 1-D) (1963):

$$x_i(t+1) = \left[e_i(t) - \sum_{i \neq j} K_{ij}\, x_j(t)\right]_+ \quad i = 1..n$$

excitation $\sim \log I$

inhibition due to jth neighbour

- system characterised by fixed point (solution of n linear simultaneous equations)
- uses step function

(from V. Bruce & P. Green, 'Visual Perception', Erlbaum (1985))

Brodie et al (1978): 2D, continuous in space/time. Good fit to data, but still uses step function and 'self-inhibition' (not understood)

pRAM model

$$x_i(t) = K^{-1} \prod_{s=1}^{T} \left(1 + w_s\, r_i(t-s)\right) \times \prod_{j=1}^{N} \left(1 - W_j\, x_{i-j}(t-j-d)\right)\left(1 - W_j\, x_{i+j}(t-j-d)\right)$$

1-D array, each unit receives T time-delayed illumination inputs $\{r_i(t-1), \ldots r_i(t-T)\}$ & inhibitory inputs $x_{i \pm j}(t-j-d)$ from its 2N nearest neighbours

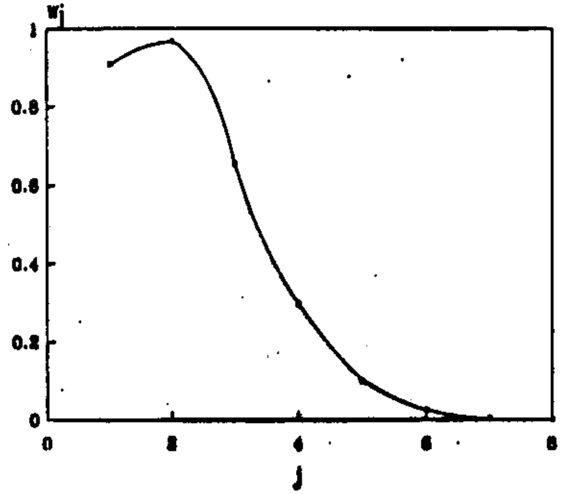
$$K = \prod_{s=1}^{d+1} (1 + w_s)$$

normalisation factor (so that $x_i \in [0,1]$)

$(d+1)$ = number of positive w_s

max/min response $(d+1)$ time units after illumination change

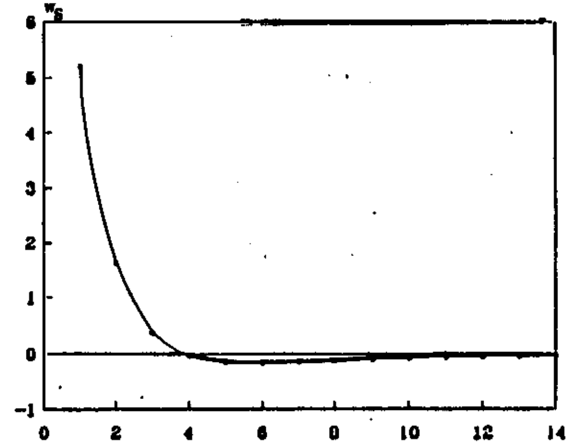
10.



Lateral inhibition falls off with distance of inhibiting unit

DOG form (taken from Brodie et al):

$$W_j = \frac{3}{4}\left[3e^{-j^2/8} - 2e^{-j^2/3}\right]$$



$$w_s = 16e^{-s} - \frac{7}{8}e^{-s/4}$$

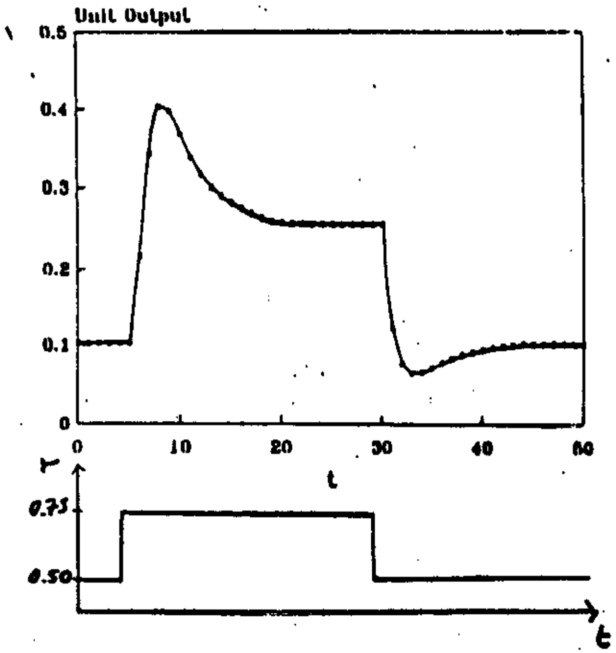
Effect of illumination initially excitatory ($d+1=3$ time steps), then inhibitory

Alternative is self inhibition (Stephens 1964)

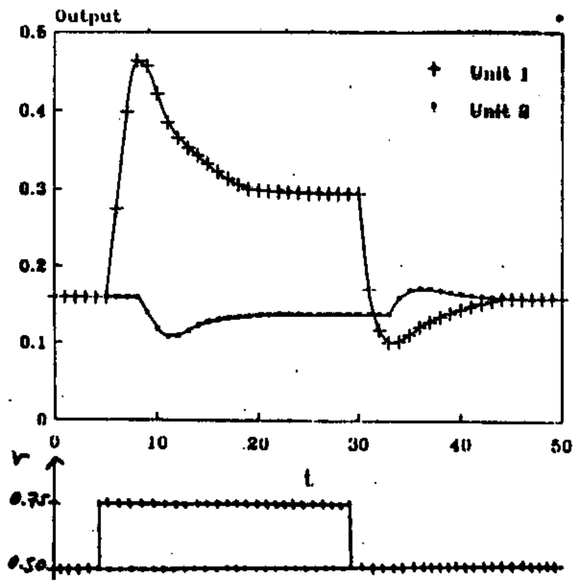
- less pronounced transients
- oscillations

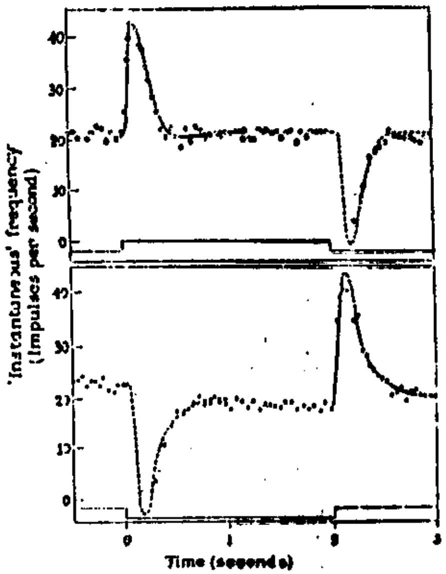
- too many back-connections for hardware implementation
- evidence against (Fahrenbach 1985)

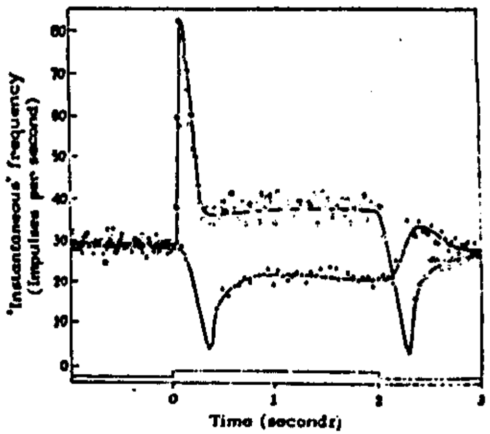
convergence if $|x_i(t) - x_i(t-j)| < 0.0001 \quad i = 1..64, \; j = 1..8$



Temporal response of model

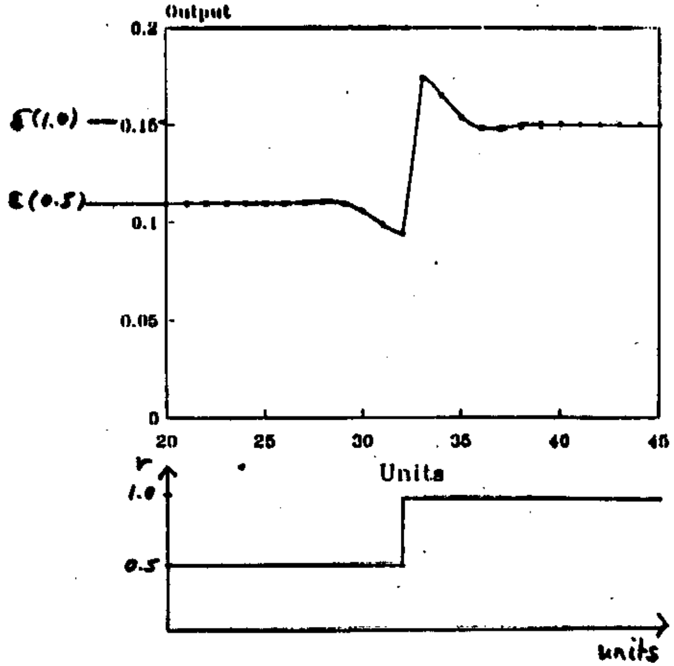




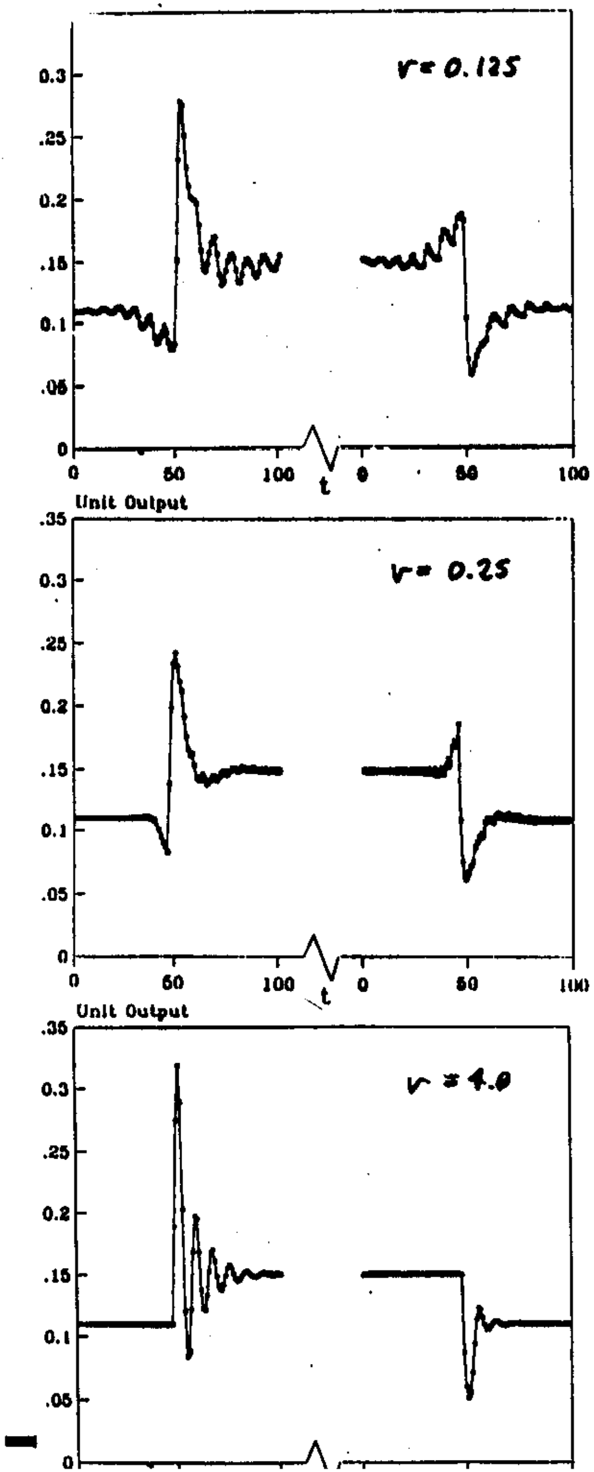


F. Ratliff, H.K. Hartline & W.H. Miller, J. Opt. Soc. Am. 53 (1) (1963), 110

Spatial response (Mach bands)



enhancement ~ 50% of ε(1.0) − ε(0.5)



Spatiotemporal behaviour

Response of central unit as illumination step r=0.5→r=1.0 passes over it

Low velocity (retinal units/time step).

Anticipatory Mach bands contain oscillations due to neighbour-neighbour (second order) interactions

Intermediate velocity:

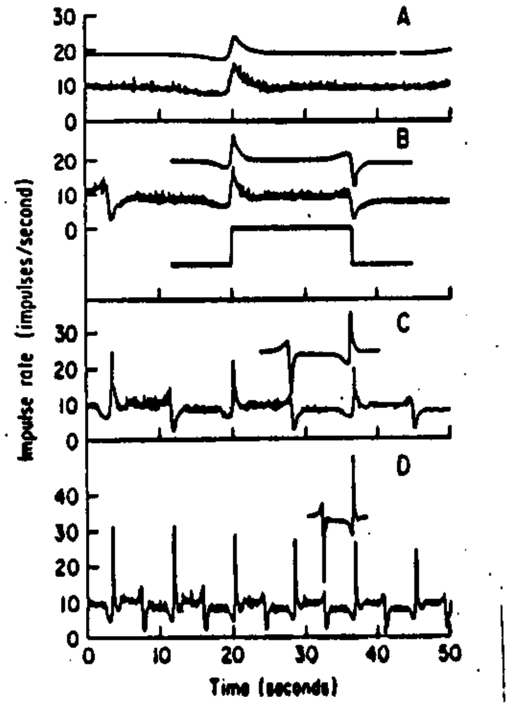
Inhibition from neighbours, but more distant ones now have no time to contribute inhibitory surges

High velocity (v>1):

No time for anticipatory inhibition to be felt before maximum associated with the arrival of the step

Damped oscillations arise from time-delayed lateral inhibition from excited neighbours

Data from S.E. Brodie, B.W. Knight & F. Ratliff, J. Gen. Physiol. 72 (1978), 129



velocities in eyewidths per second

u = 0.03

u = 0.06

u = 0.12

u = 0.24

Data comparable with pRAM-net results for intermediate velocities (Brodie model predicts on- and off-transients of equal magnitude)

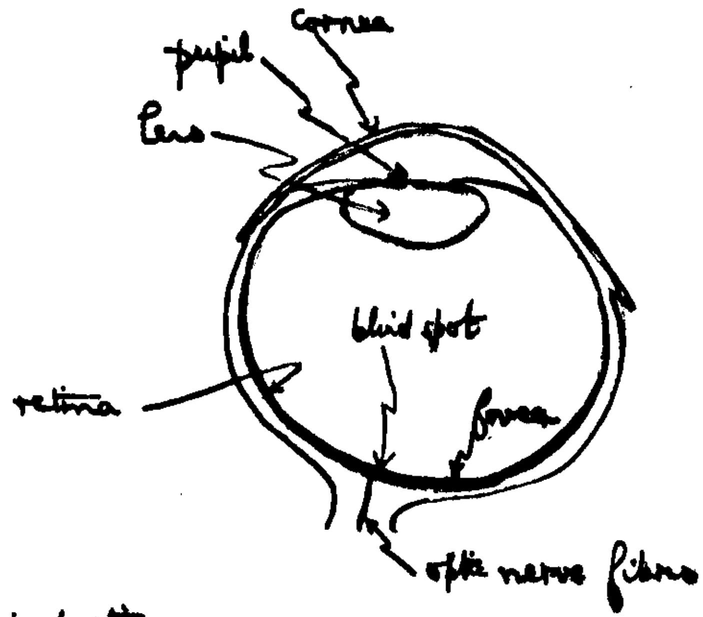
Low velocities : discrepancy could be due to the small no. of units used in the simulation

High velocities : finite speed of information transmission (v=1) – anticipatory Mach bands impossible for v > 1

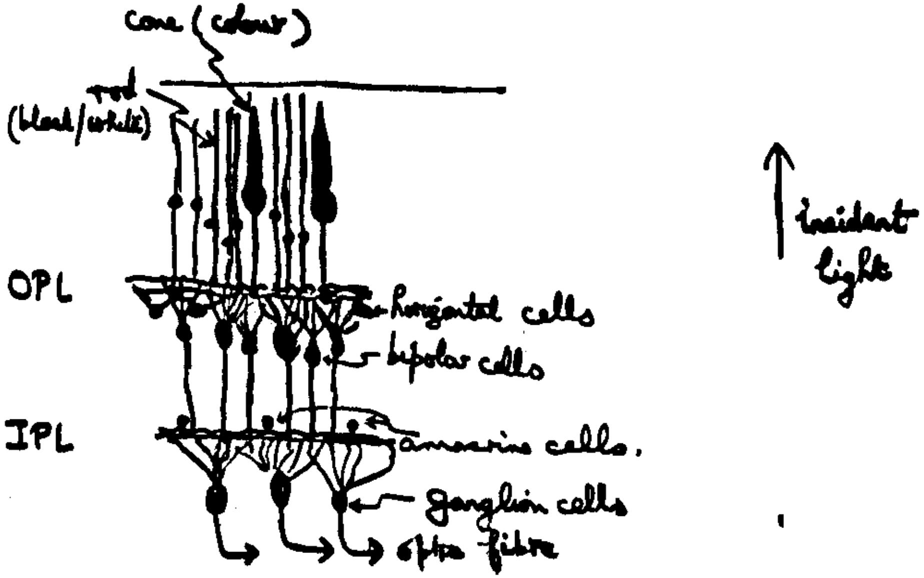
v = 1 ⇔ u = 2-20

(≥ 8 × faster than max velocity so far used)

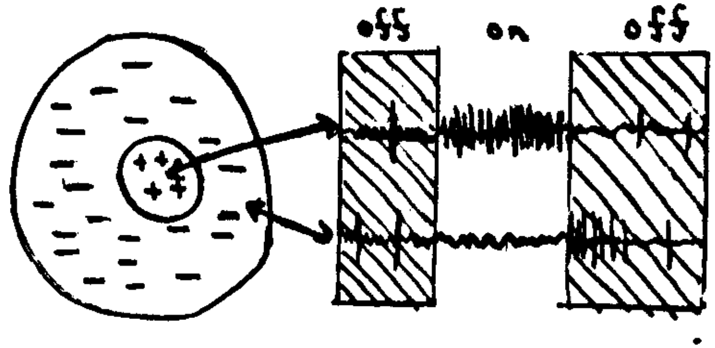
3 Vertebrate Retina.



Primate retina



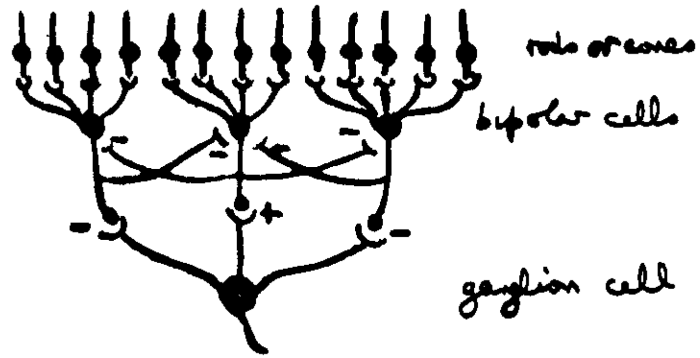
Receptive field of ganglion cell:



On-centre off-surround

Also have off-centre on-surround

Neuronal connections to achieve this:



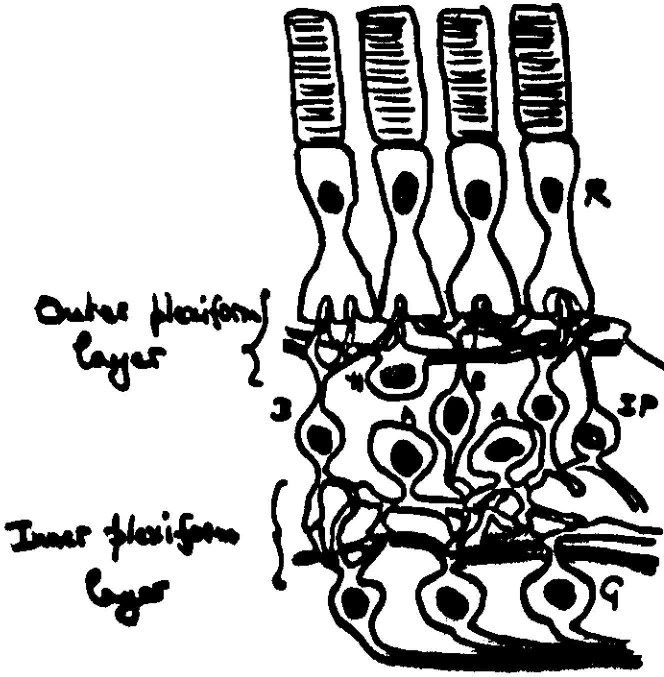
But (a) what are horizontal cells + amacrine cells for?

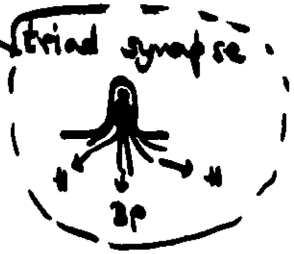
(b) can have more complicated ganglion cell responses — 'moving spot' detectors

(c) need to describe quantitatively.

More detailed structure of retina:

R = receptor
B = bipolar
H = horizontal
IP = interplexiform
G = ganglion
A = amacrine

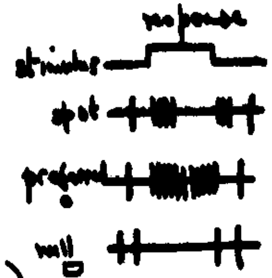


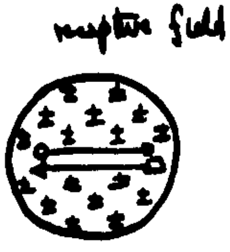


Frogs, pigeons : Bipolar ⟶ Amacrine ⟶ Ganglion

Primates : Bipolar ⟶ Ganglion

more complicated ; G-cell responses



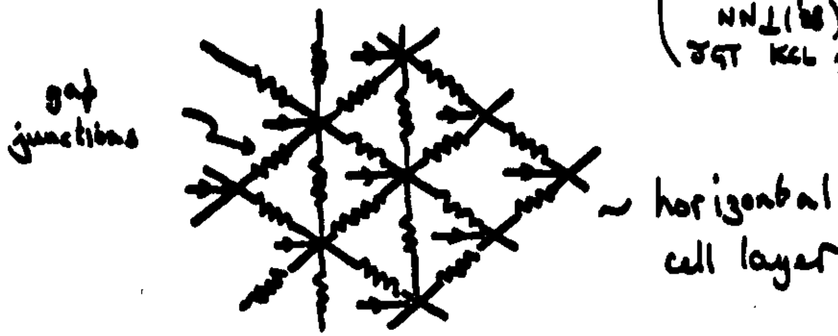


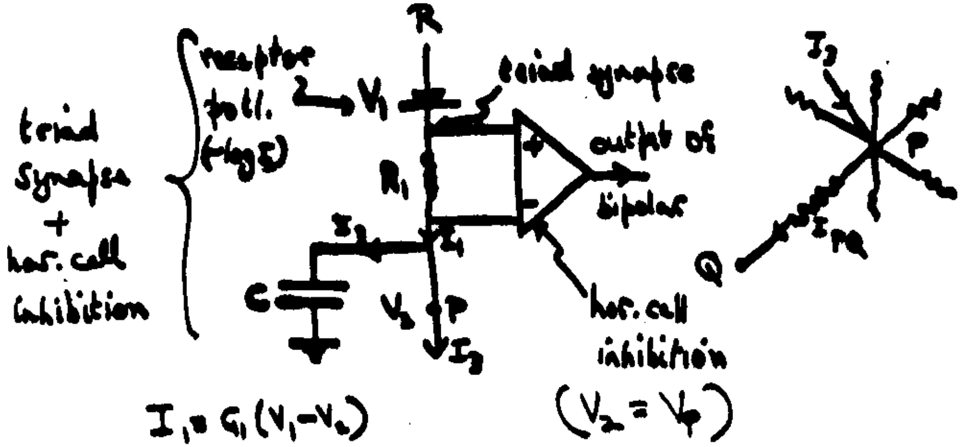
(± ~ response at onset & offset.)

18\. 4. Mathematical Modelling

Attempt to model hor. cell layer by resistive network (G are connected electrically)

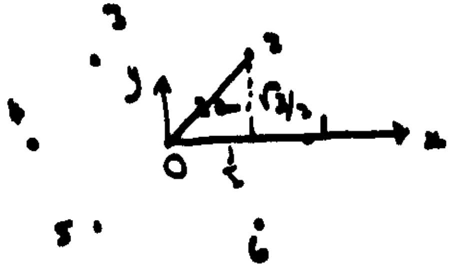
(Mead & Mahowald NN 1 ('88) 91; JGT KCL preprint)





$$I_1 = G_1(V_1 - V_2)$$
$$I_2 = C\dot{V}_2$$
$$I_3 = \sum_{\langle Q,P\rangle} I_{PQ} = \sum_{\langle Q,P\rangle} G_2(V_P - V_Q) = I_1 - I_2$$

$$\Rightarrow \quad G_1[V_1(P) - V(P)] - C\dot{V}(P) = G_2\Big[N V(P) - \sum_{\langle Q,P\rangle} V(Q)\Big]$$



For a small, $V(1)-V(0) = aV_x + \frac12 a^2 V_{xx}$

$V(2)-V(0) = \frac12 aV_x + \frac{\sqrt3}{2} aV_y + \frac{a^2}{2}\left(\frac14 V_{xx} + \frac{\sqrt3}{4}V_{xy} + \frac34 V_{yy}\right)$

$V(3)-V(0) = - \quad + \quad + (\quad - \quad)$

$V(4)-V(0) = -aV_x + \frac12 a^2 V_{xx}$

$V(5)-V(0) = - \quad - \quad (\quad + \quad)$

$V(6)-V(0) = + \quad - \quad (\quad - \quad)$

$\sum V(Q) - 6V(P) = \frac{3a^2}{2}(V_{xx}+V_{yy}) + O(a^4)$

$\Rightarrow \quad \dot V + (G_1/C)V - (3G_2a^2/2C)\nabla^2 V = (G_1/C)V_1$

Use F.T. $\tilde V = \int dt\, d^2\underline{r}\, e^{-i(\omega t + \underline{k}\cdot\underline{r})} V(\underline{r},t)$

$\Rightarrow \quad \tilde V = [(i\omega C/G_1) + 1 + k^2(G_2 a^2/G_1)]^{-1}\tilde V_1$

$\Rightarrow \quad V(\underline{r},t) = (2\pi)^{-3}\int d^2\underline{k}\, d\omega\, [(i\omega C/G_1)+1+k^2\lambda^2]^{-1}\tilde V_1(\underline{k},\omega)\, e^{i(\underline{k}\cdot\underline{r}+\omega t)}$

with $\lambda^2 = (\frac32 G_2 a^2/G_1)$

Take small spots: $\tilde V_1 = f(\omega)e^{-k^2d^2}$

$V_1(\underline{r}) \sim e^{-r^2/d^2}$ size $\sim d$.

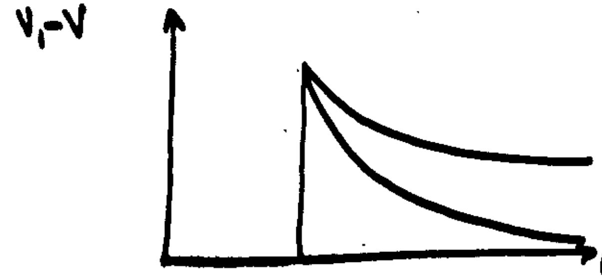
1) Step fn. in time

$V_1(t) = a + b\,\theta(t)$

$\tilde\theta(\omega) = \int_0^\infty e^{-i\omega t}dt = \frac{1}{i(\omega - i\varepsilon)}$

Can show

$V_1(0,t) - V(0,t) = \frac{1}{2\pi} b\,\theta(t)\, e^{-tG_1/C} + V_1\frac{\lambda^2}{d^2} + O\left(\frac{\lambda^4}{d^4}\right)$



$\downarrow \frac{\lambda}{d}\to 0$ (patch size $d\to\infty$)

increases inhibition from surroundings

2) Step fn. in space ($\dot V_1 = 0$)

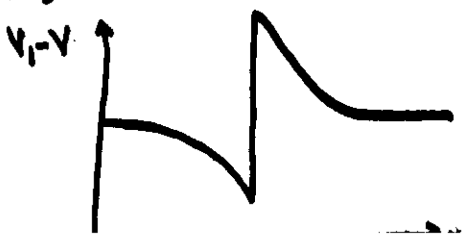
$V - \lambda^2\nabla^2 V = V_1(\underline{r})$

In 1D:

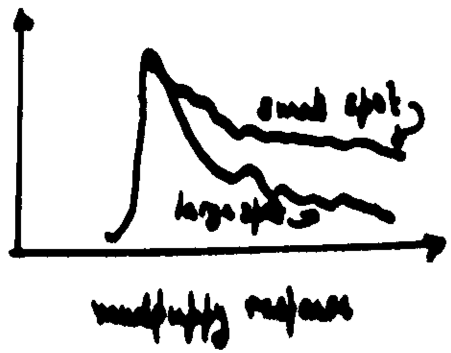
$V = b - \frac12 b e^{-x/\lambda} \qquad x>0$

$\;\;\; = \frac12 b e^{x/\lambda} \qquad x<0$

$\Rightarrow \quad V_1 - V = \frac12 b[e^{-x/\lambda}\theta(x) - e^{x/\lambda}\theta(-x)]$



(~ Mach bands)



3) Moving edge

$$V_1 = a + f\,\theta(x - vt)$$

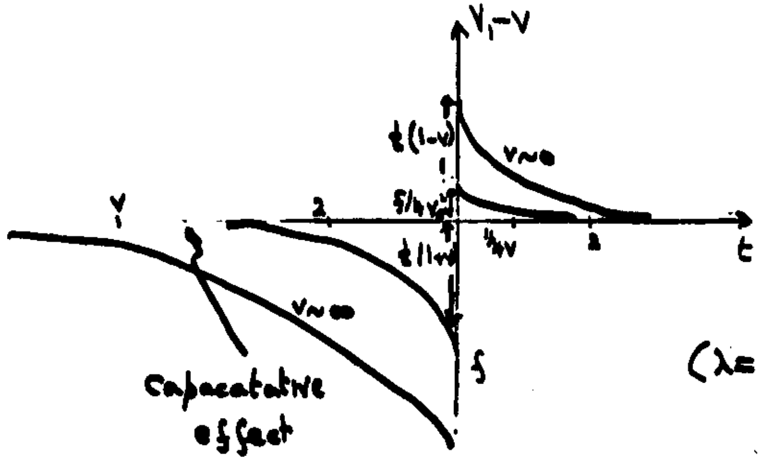
$$\Rightarrow \quad \tilde{V}_1 = (2\pi)^3 a\, \delta^2(\underline{k})\,\delta(\omega) + (2\pi)^2 f\, \delta(k_y)\left(\frac{1}{ik_x}\right)\delta(\omega + k_x v)$$

$$\Rightarrow \quad V_1 - V = \frac{f}{\sqrt{4\lambda^2 + \frac{v^2c^2}{q_1^2}}}\left[\frac{e^{+k_-(vt-x)}}{k_-}\theta(vt-x) + \frac{e^{-k_+(x-vt)}}{k_+}\theta(x-vt)\right]$$

$$k_\pm = \frac{1}{2\lambda^2}\left[\left(\frac{vc}{q_1}\right) \pm \sqrt{4\lambda^2 + \left(\frac{vc}{q_1}\right)^2}\right]$$

$v \sim 0: \quad V_1 - V \approx \frac{f}{2}\left[-\left(1 + \frac{vc}{2q_1\lambda}\right)e^{-(vt-x)/\lambda}\theta(vt-x) + \left(1 - \frac{vc}{2q_1\lambda}\right)e^{-(x-vt)/\lambda}\theta(\ )\right]$

$v \sim \infty: \quad V_1 - V \approx f\left[-e^{q_1(vt-x)/vc}\theta(vt-x) + \frac{q_1^2\lambda^2}{v^2c^2}e^{-\frac{vc}{q_1\lambda^2}(x-vt)}\theta(\ )\right]$



$(\lambda = \frac{1}{2},\ c = q_1 = 1)$

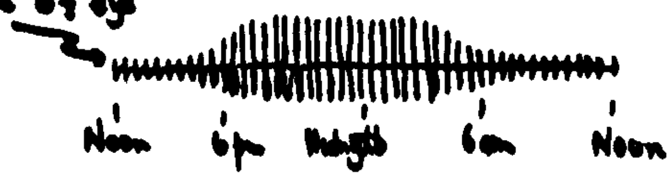
So v. asymmetric for large v.

2.3. Central Pattern Generators (CPG's)

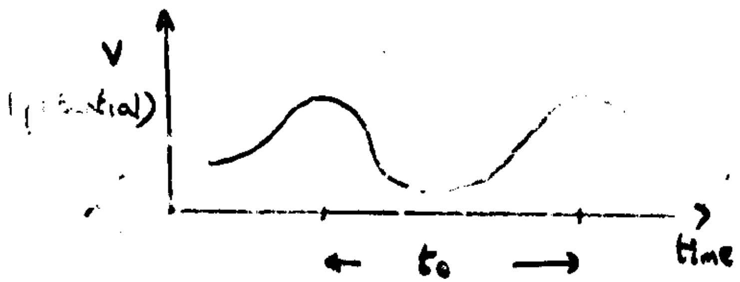
(Leech : Science 200, 1348, '78
lobster : TINS April '83, 120

- Small #'s of neurons controlling
  rythmic muscular contractions :
  in walking, flying, swimming — insects, leech
  stomach muscles — lobster
- Circadian rythm generators — crab eye response

response of eye to light flash



- cockroach limb movement :



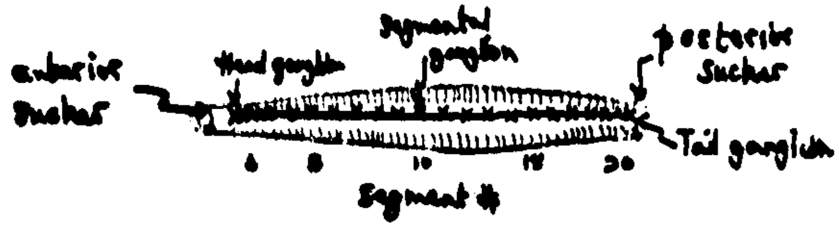
non-spiking interneurons v. important

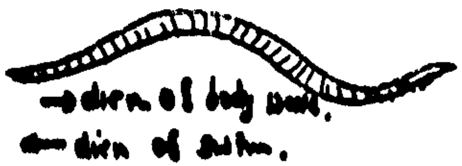
May be due to either

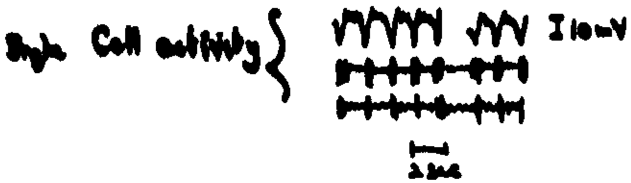
(a) endogenous oscillator

(b) oscillatory network

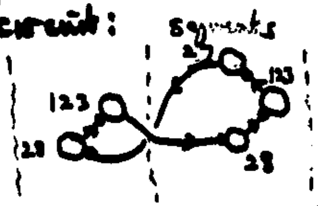
e.g. (b) : leech swimming movement







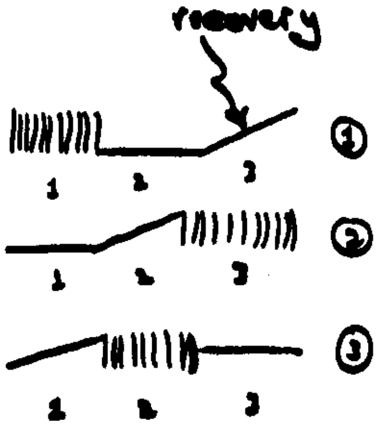
Caused by
5-neuron circuit :



all synapses inhibitory

eg. 3 cell network:

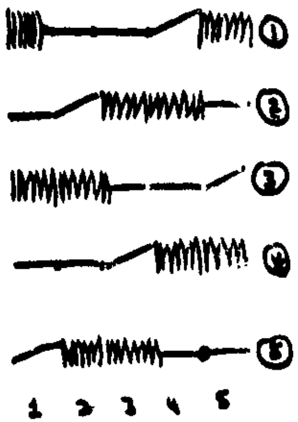
phase 1	1	0	0_r
2	0	0_r	1
3	0_r	1	0



odd # of recurrently inhibitory cells

eg. 5:

	a28	a13	p18	p188	p97
phase 1	1	0	1	0	0_r
2	0	0_r	1	0	1
3	0	1	0	0_r	1
4	0_r	1	0	1	0
5	1	0	0_r	1	0

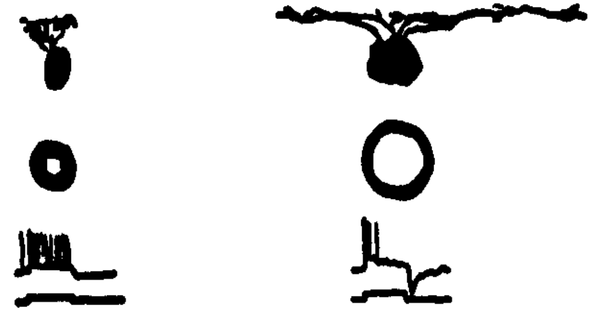


(need cell in recovery phase for $(01)^n$)

(→ "The Crustacean Stomatogastric System" ed Selverston & Moulins, Springer '87

Inner Plexiform Layer:

Ganglion cells: on β   on α



small convergence

16 cones → 4 CBP's → 1 on β

Sterling et al TINS 9(1986)

high convergence

200 CBP's → 1 on α

gives transient + steady

continuous limit:

$$\int (V_1 - V)(x)\, dx = 0$$

so only transient.

Rods: 1500 rods → 1 on β (no hor. effects: only on-centre)
(thro' amacrines)

Conclusions:

- can model invertebrate retina by noisy neurons, or by linear model (to within self-inhibition?)
- can model vertebrate IPL by R-C network
- can obtain analytic solutions in continuum limit ([z] - field theory)
- can model ON or OFF α- and β- ganglion cells (without details of amacrines, no motion detection)