

CN510: Principles and Methods of Cognitive and Neural Modeling

Shunting Network: Retinal Processing and Weber's Law

Lecture 8

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Summary to This Point

Network

$$\frac{dx_i}{dt} = -Ax_i + (B - x_i)I_i - (C + x_i)\sum_{j \neq i} I_j$$

Was derived from various considerations

This network has properties:

- automatic gain control
- signal normalization
- adaptation level, which suppresses uniform inputs

Now we will look at some experimental applications of feedforward shunting networks

- Shift property as seen in retinal cells
- Weber's law of difference detection thresholds

Shift Property in the Retina of the *Mudpuppy*

An example of the shift property in a neural system comes from Werblin (1971), who studied the retina of the *mudpuppy*

Werblin studied the effects of background light intensity on photoreceptor and retinal cell properties

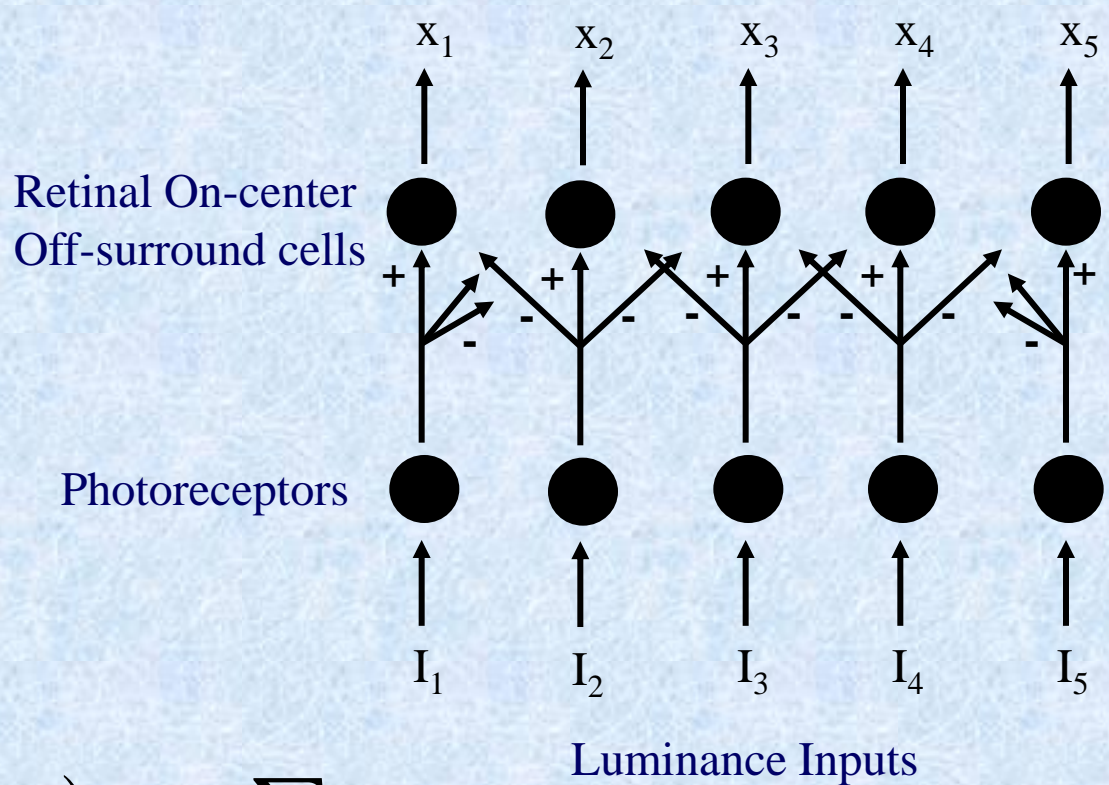
Simple Model of a Retina

For simplicity assume:

- photoreceptor output is linearly related to luminance
- network has full connectivity

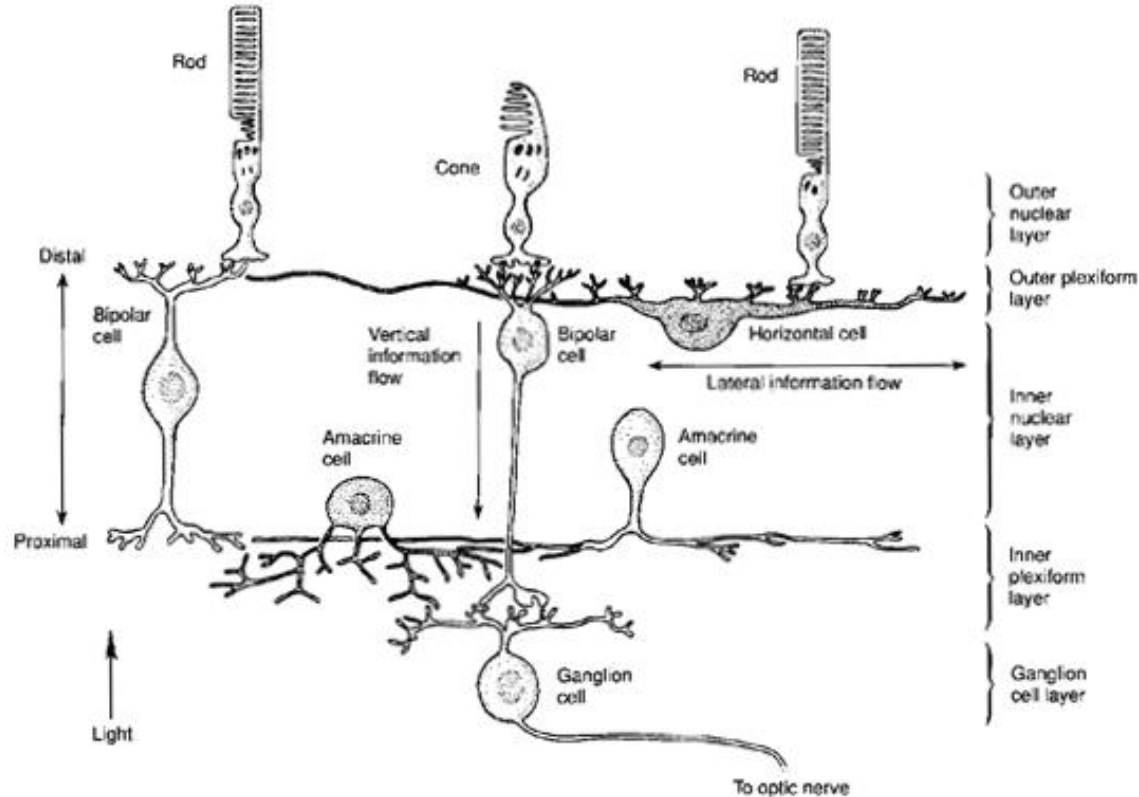
Equation for retinal neurons:

$$\frac{dx_i}{dt} = -Ax_i + (B - x_i)I_i - x_i \sum_{j \neq i} I_j$$



Real Retina and Other Considerations

Real retina is much more complex



Werblin studied reaction to diffuse light, not to stimuli

This is an illustrative example, but both involve shift property

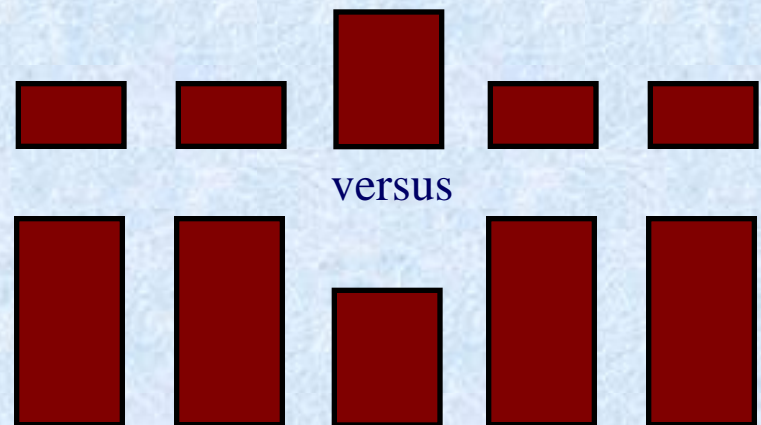
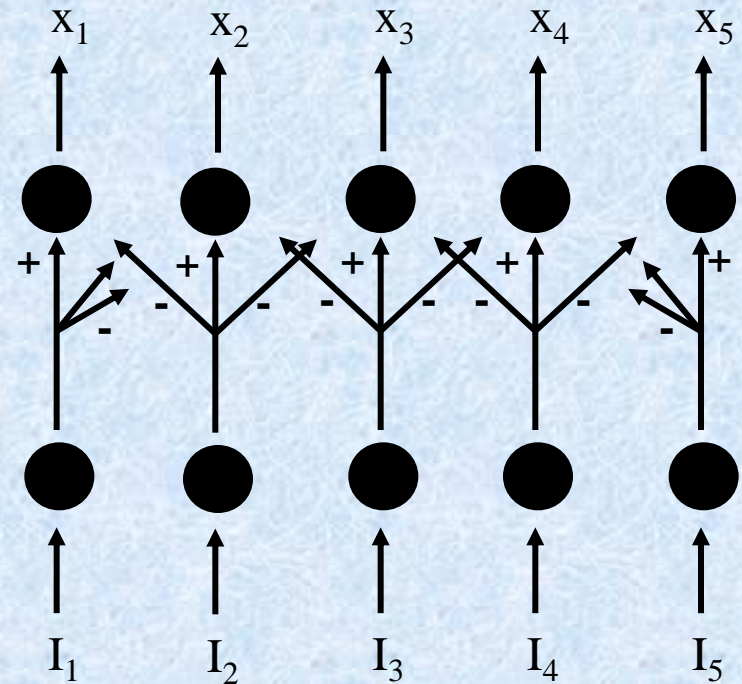
Considering the equation

$$\frac{dx_i}{dt} = -Ax_i + (B - x_i)I_i - x_i \sum_{j \neq i} I_j$$

We can define “background intensity” for cell i as

$$L_i = \sum_{j \neq i} I_j$$

How will the sensitivity of the cell i to its input vary if we vary the background intensity L_i ?

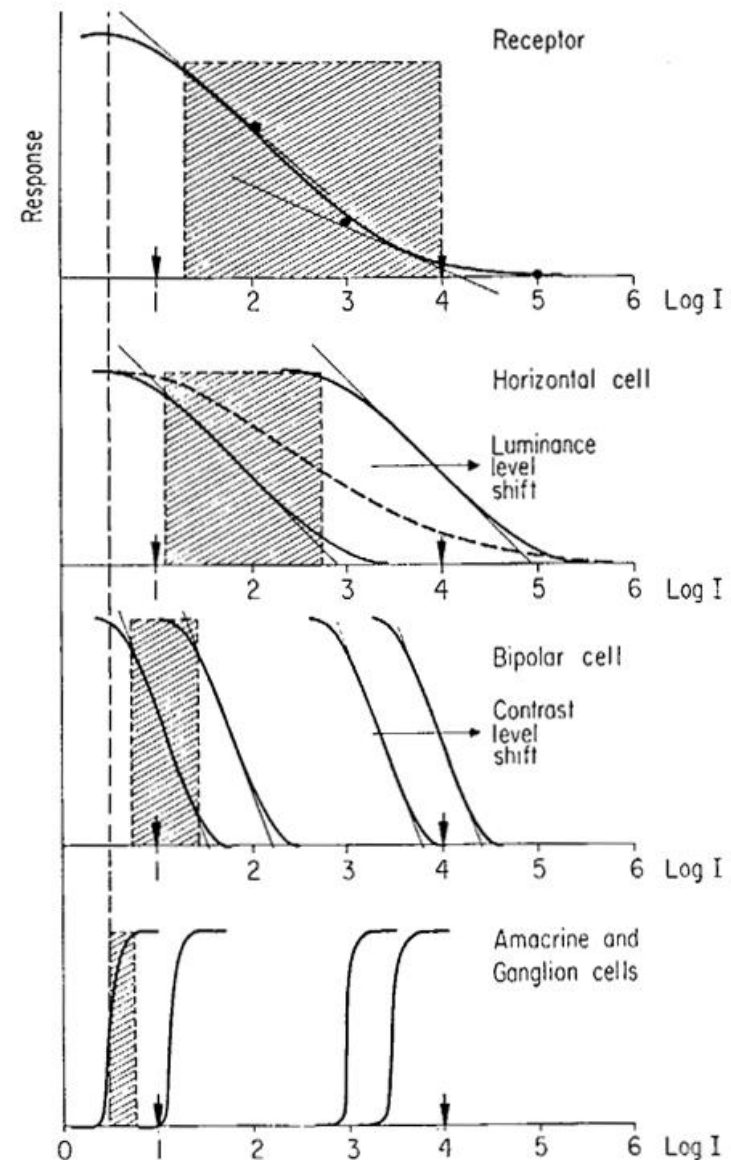


Werblin (1971) Results

Werblin showed that the sensitivity of photoreceptor was unchanged with the change in background input

Consistent with assumption that the response of a receptor depends only on its own input

Note that receptor response is inversely proportional to incoming light



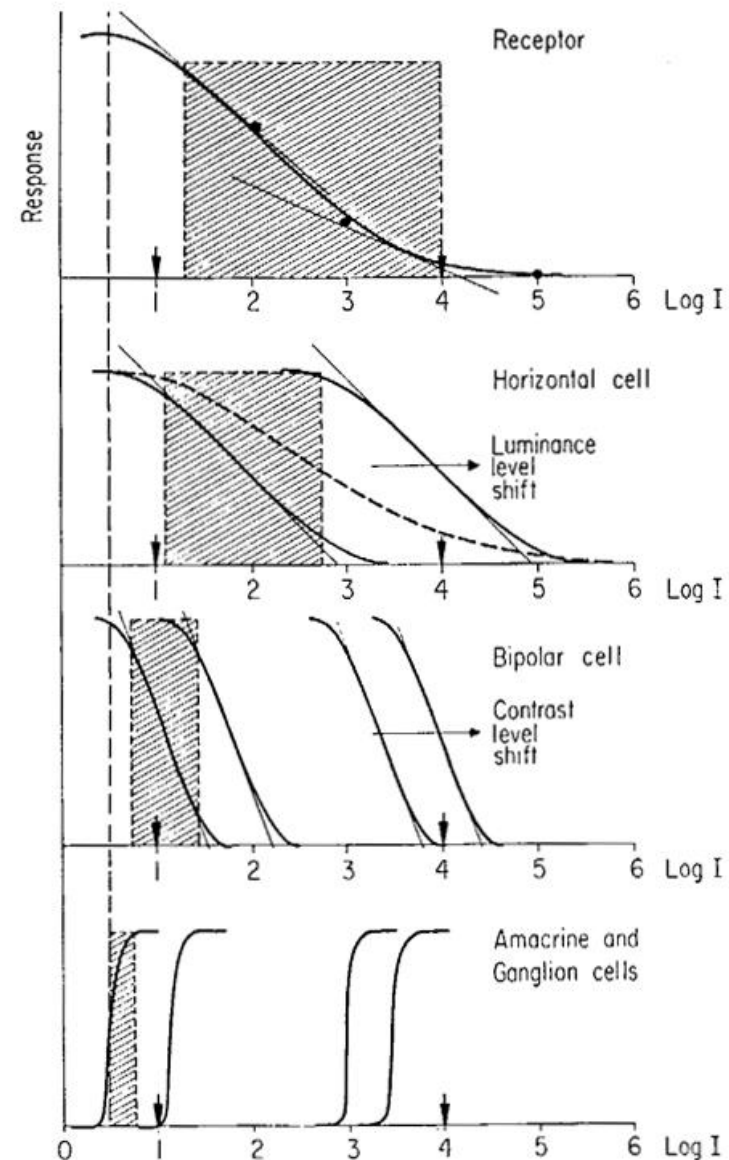
Werblin (1971) Results

Unlike photoreceptor, sensitivity of all other retinal cells shifts as a function of background input

What can be the functional significance of this shift?

Cells with limited and fixed dynamic range can “rescale” their range depending on the input strength

Thus the system as a whole becomes much more sensitive



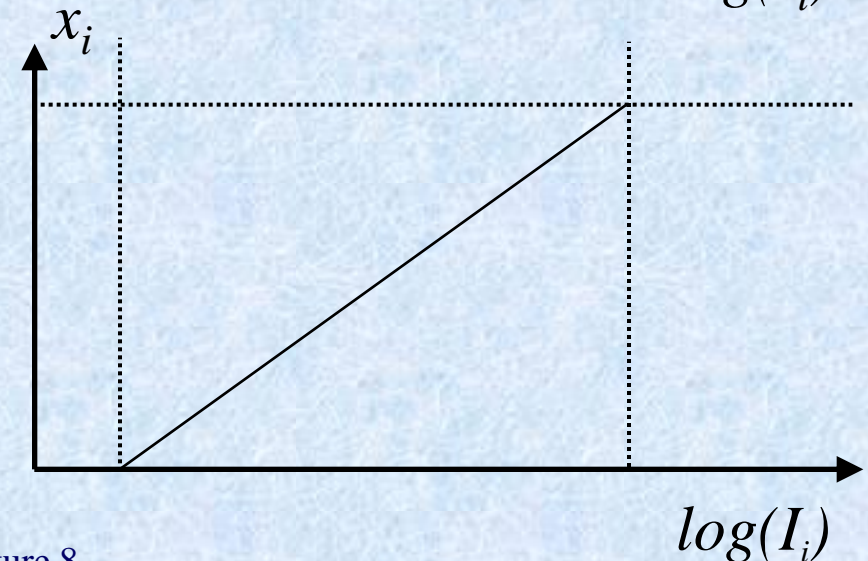
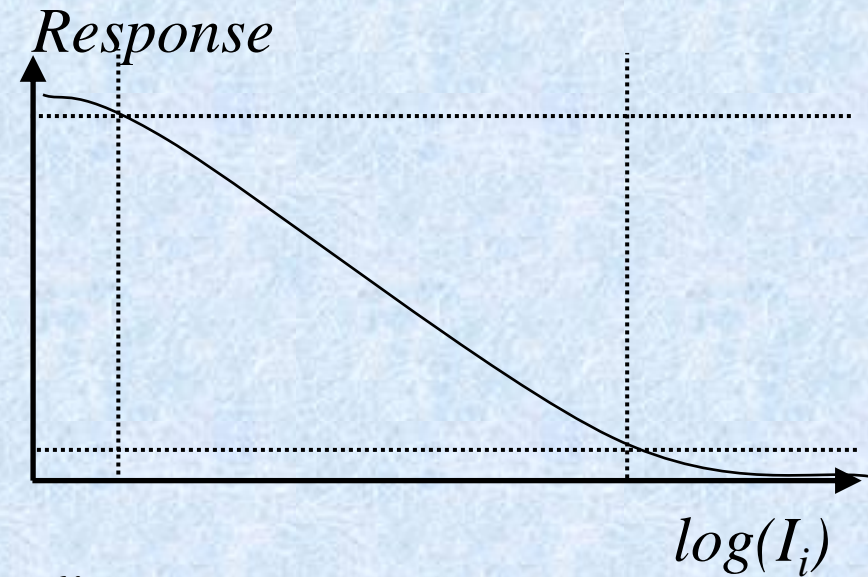
If we define sensitivity as a change in x_i for unit of change in $\log(I_i)$

$$\text{sensitivity} = \frac{x_i}{\log(I_i)}$$

This is just a slope of the plot

We can have a single function for the whole input range

This is what is seen in the photoreceptor

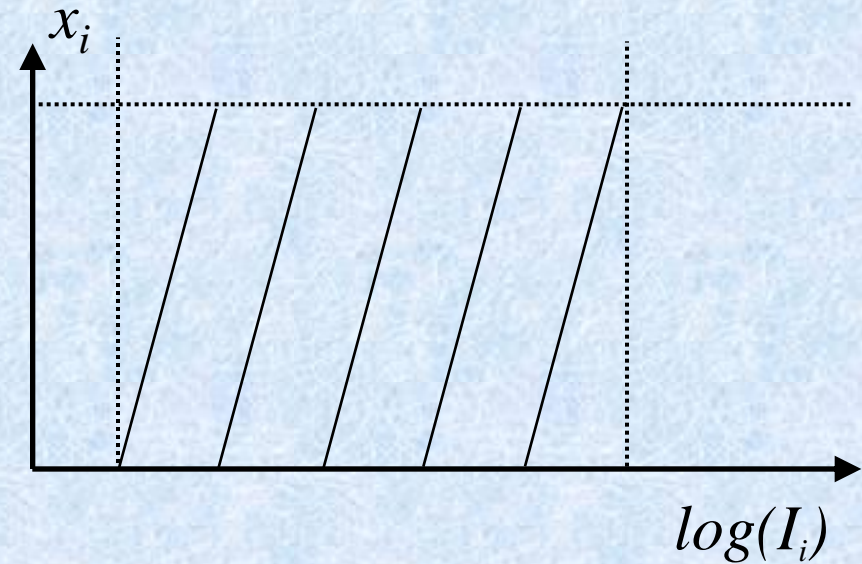


Alternatively we can make our function change depending on the overall input (background intensity)

For a given background intensity we traded some sensitivity to the whole range for a higher sensitivity to a more restricted range

This restricted range depends on the background intensity

This is exactly what Werblin saw in his results



Similar Trade-offs

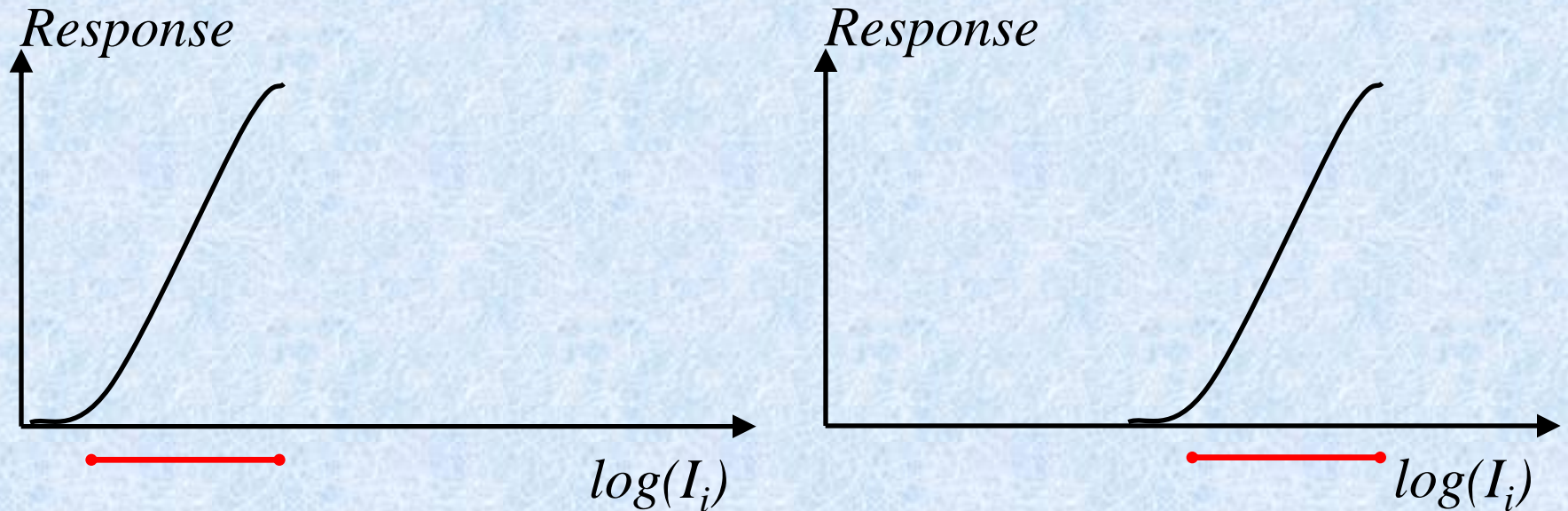
Retina has a region of a very high spatial acuity at the fovea

It can be moved around by pointing the eyes to the area of interest thus providing maximal resolution where it is needed

Roger and Schwartz (1990) estimated that uniform sensor array with the sensitivity equal to that in the fovea would require 400 times more cells

Thus for the fixed amount of circuitry maximal overall sensitivity is obtained by a region of high sensitivity that can be moved around

Similarly, for the fixed dynamic range maximal overall sensitivity can be obtained by having a region of high sensitivity that can be shifted along the input range



Moving window of sensitivity

Does the network

$$\frac{dx_i}{dt} = -Ax_i + (B - x_i)I_i - x_i \sum_{j \neq i} I_j$$

possess this property?

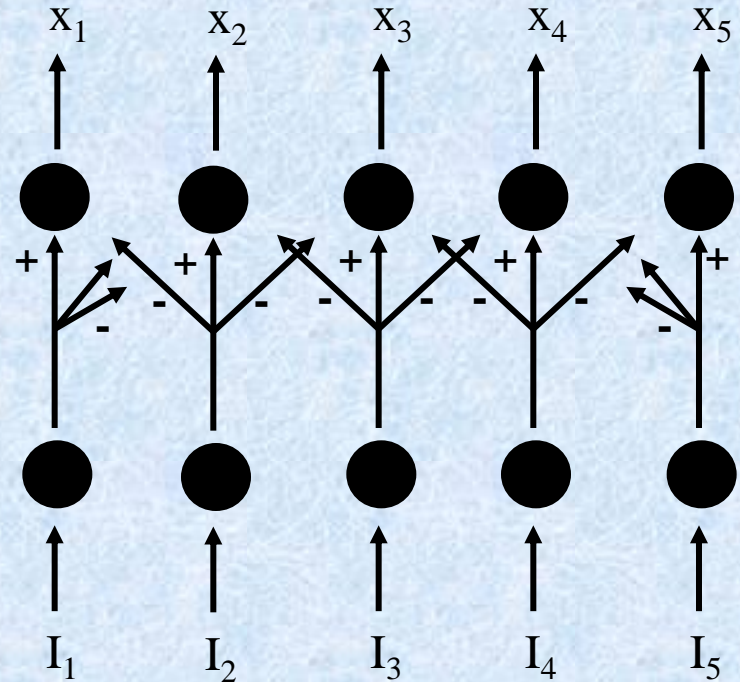
At equilibrium

$$x_i = \frac{BI_i}{A + I_i + \sum_{j \neq i} I_j}$$

or

$$x_i = \frac{BI_i}{A + I_i + L_j}$$

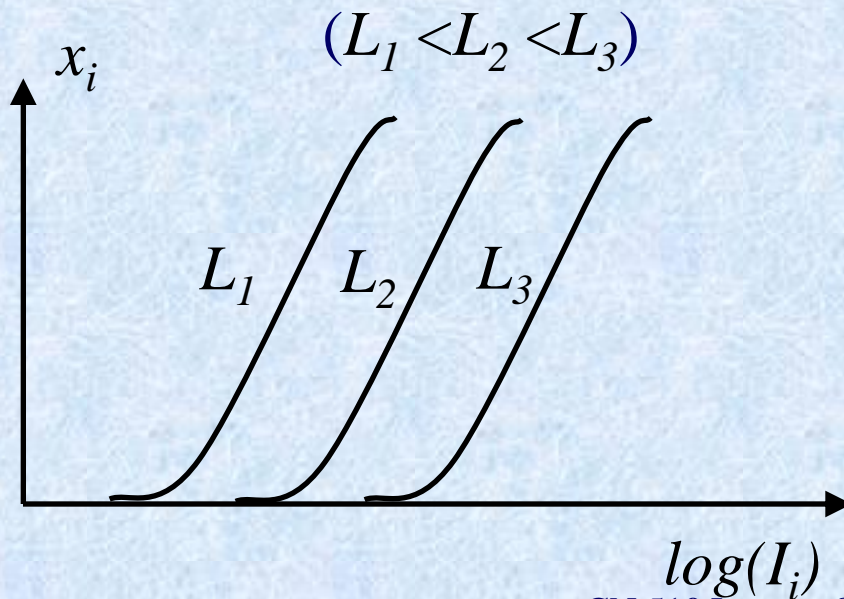
where L_j is background intensity



Switching to logarithmic coordinates $M_i = \log(I_i)$

$$x_i(M_i, L_j) = \frac{B \exp(M_i)}{A + \exp(M_i) + L_j}$$

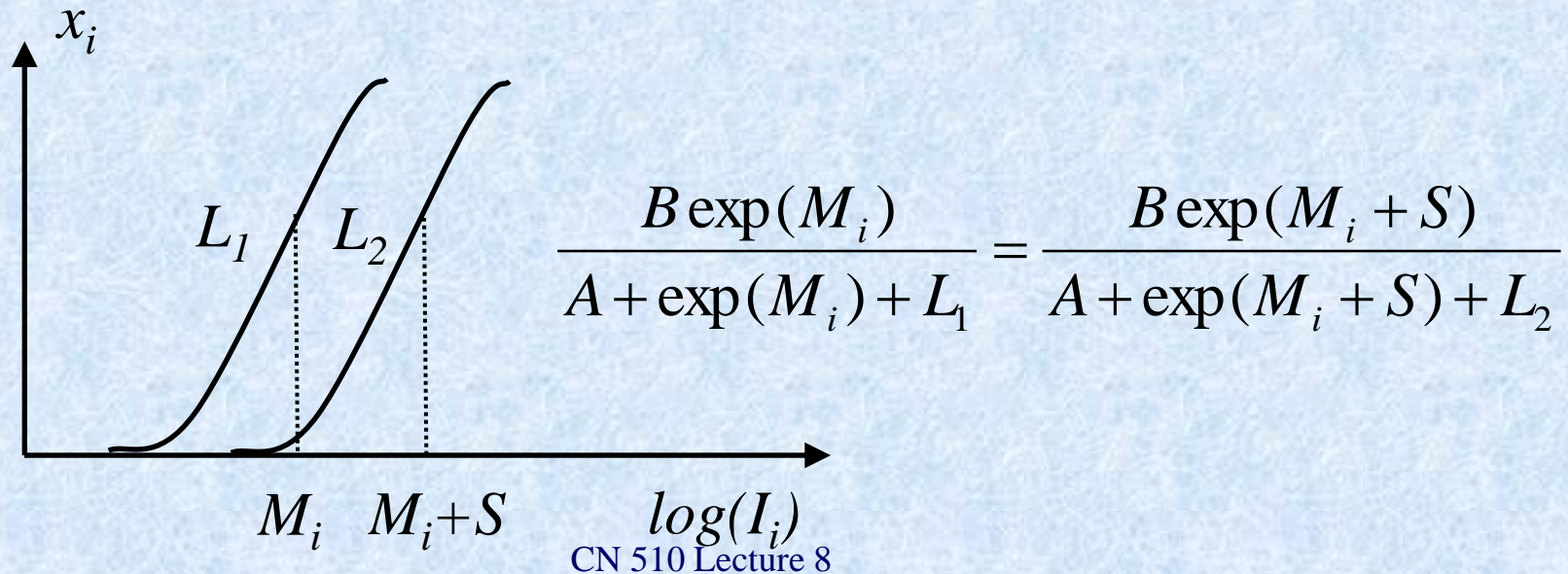
If we plot this function for different L_j we get the shift property



In other words the size of surround inhibition shifts the input range over which a cell's output remains sensitive

We already saw this property and called it automatic gain control

To verify it mathematically we can solve for input change S :



$$\frac{\cancel{B} \exp(M_i)}{A + \exp(M_i) + L_1} = \frac{\cancel{B} \exp(M_i + S)}{A + \exp(M_i + S) + L_2}$$

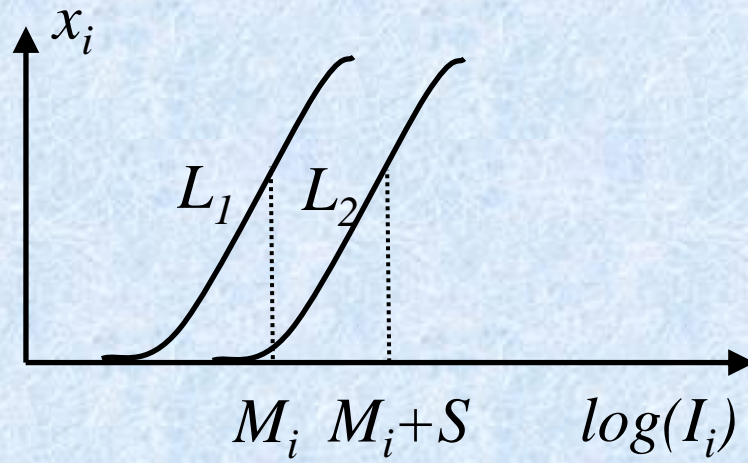
$$\cancel{\exp(M_i)}(A + \exp(M_i) \exp(S) + L_2) = \cancel{\exp(M_i)} \exp(S)(A + \exp(M_i) + L_1)$$

$$A + \cancel{\exp(M_i)} \exp(S) + L_2 = \exp(S)A + \cancel{\exp(S) \exp(M_i)} + \exp(S)L_1$$

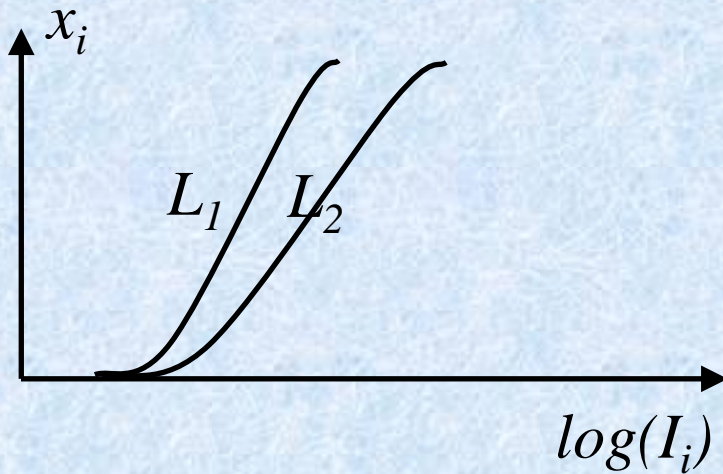
$$A + L_2 = \exp(S)(A + L_1)$$

$$S = \ln \frac{A + L_2}{A + L_1} = \ln(A + L_2) - \ln(A + L_1)$$

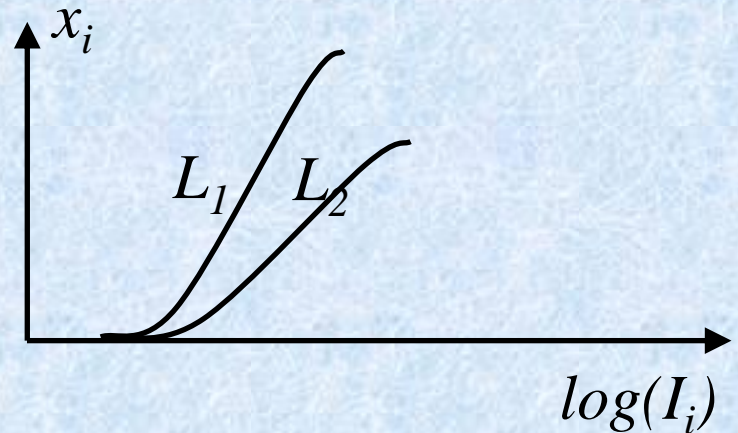
Note that the size of the shift does not depend on input, meaning that for a change from L_1 to L_2 shift is the same no matter what M_i is



not



or



Weber's Law

Psychophysics – refers to studies that attempt to correlate quantitative aspects of physical stimuli with the sensations that they evoke

e.g., we could get a measure of tactile sensation by testing how close together two simultaneous pin pricks can be before they are sensed as a single pin prick

Just Noticeable Difference (JND) – the minimum difference in intensity between two stimuli that can be detected

Weber's law: the just noticeable difference ΔJ for distinguishing the intensities of two inputs is directly proportional to the intensity J

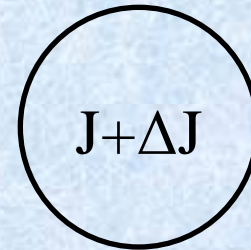
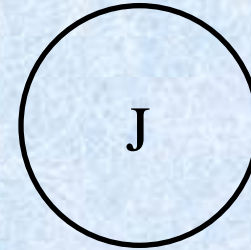
Two discs flashed simultaneously
Subject is reporting whether they
have the same intensity

Mathematically Weber's law is
stated as

$$\Delta J = kJ$$

or in other words the ratio $\Delta J/J$
is constant

Automatic gain control again?



Weber's Law from Shunting Equation

Solving $\frac{dx_i}{dt} = -Ax_i + (B - x_i)I_i - x_i \sum_{j \neq i} I_j$

At equilibrium $x_i = \frac{BI_i}{A + \sum I_j}$

Then

$$x_2 - x_1 = \frac{BI_2}{A + \sum I_j} - \frac{BI_1}{A + \sum I_j}$$

Since we can write $I_2 = I_1 + \Delta J$

$$x_2 - x_1 = \frac{B(I_1 + \Delta J)}{A + \sum I_j} - \frac{BI_1}{A + \sum I_j} = \frac{B\Delta J}{A + 2I_1 + \Delta J + \sum_{j \neq 1,2} I_j}$$

Weber's Law from Shunting Equation

$$x_2 - x_1 = \frac{B\Delta J}{A + 2I_1 + \Delta J + \sum_{j \neq 1,2} I_j}$$

Lets assume detection threshold as $\Gamma = x_2 - x_1$ and solve for ΔJ

$$\Gamma A + 2\Gamma I_1 + \Gamma \Delta J + \Gamma \sum_{j \neq 1,2} I_j = B\Delta J$$

$$\Delta J = \frac{\Gamma(A + 2I_1 + \sum_{j \neq 1,2} I_j)}{B - \Gamma}$$

here if we assume small decay ($A \ll 2I_1$) and low background intensity ($I_j \ll 2I_1$ for j other than 1 and 2) we get

$$\Delta J = \frac{2\Gamma I_1}{B - \Gamma} = kI_1$$

Shunting Network and Weber's Law

For small I_1 the model predicts that

$$\Delta J = \frac{\Gamma(A + 2I_1 + \sum_{j \neq 1,2} I_j)}{B - \Gamma} = \frac{\Gamma(A + \sum_{j \neq 1,2} I_j)}{B - \Gamma} + \frac{2\Gamma}{B - \Gamma} I_1$$

This actually does make sense if we consider no background (sum of other inputs is 0) and the dimmer input $I_1 = 0$

The model predicts that there is a non-zero JND, while a strict Weber's law $\Delta J = kJ$ predicts $\Delta J = 0$

“The data have been plotted on this figure only for intensities high enough that the dimmer disk is always seen. The curve must necessarily depart from a straight line at lower intensities for statistical reasons not relevant to the present discussion”

Additive Network and Weber's Law

Solving $\frac{dx_i}{dt} = -Ax_i + BI_i - \sum_{j \neq i} I_j$

At equilibrium:

$$x_i = \frac{BI_i - \sum_{j \neq i} I_j}{A}$$

Then

$$x_2 - x_1 = \frac{B(I_1 + \Delta J) - \sum_{j \neq 2} I_j - (BI_1 - \sum_{j \neq 1} I_j)}{A}$$

And

$$x_2 - x_1 = \frac{(B+1)\Delta J}{A}$$

Does not depend on I_1 , therefore does not account for Weber's law

Summary

We discussed feedforward shunting competitive network

Investigation of **noise-saturation dilemma** highlighted several closely related feedforward shunting network properties:

- Factorization of pattern and energy
- Total energy normalization
- Automatic gain control

Shunting network interpretations elucidate the possibility that **Weber's law** and the **shift property** of retinal neurons are the result of the same shunting network property of **automatic gain control**

Adding Local Kernels

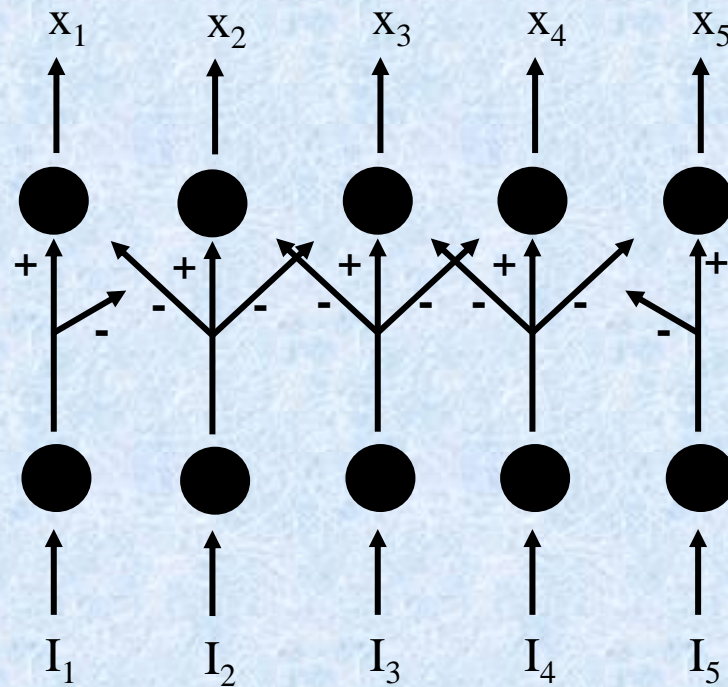
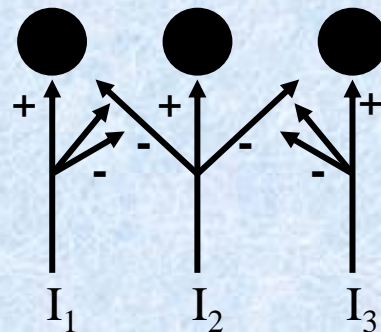
Network

$$\frac{dx_i}{dt} = -Ax_i + (B - x_i)I_i - (C + x_i)\sum_{j \neq i} I_j$$

has global feed-forward inhibition

This is not realistic for large networks

Much more realistic version for on-center off-surround network would be to have local excitation and inhibition

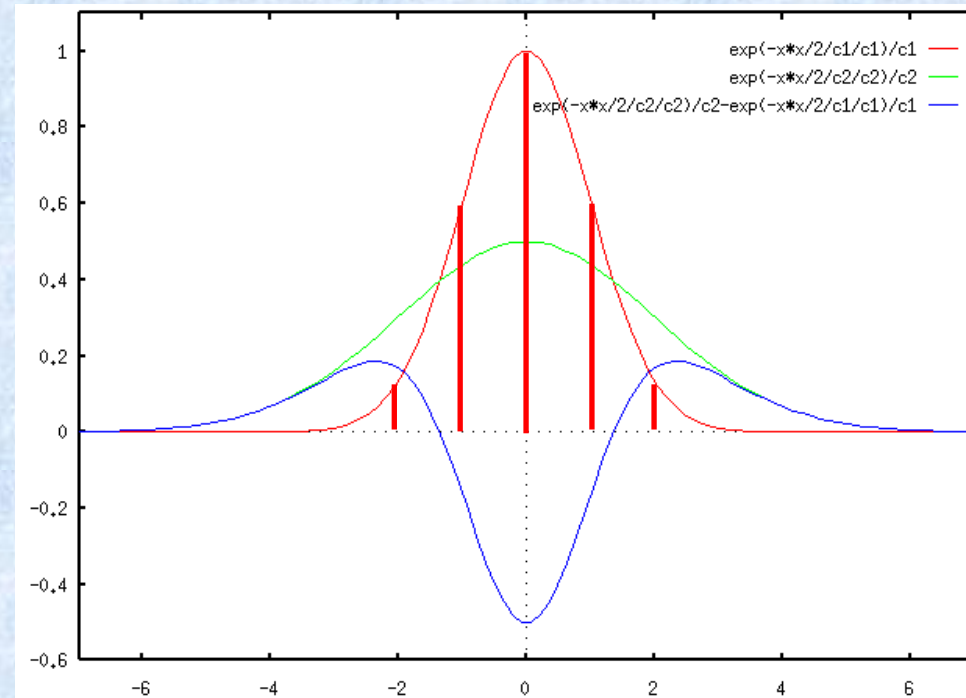


Local Excitation and Inhibition

For off-center on-surround network example Gaussian kernels are shown

Vertical bars show the inhibitory weights for $i-2$, $i-1$, i , $i+1$, and $i+2$ cells

Set the cut-off for small weights



$$\frac{dx_i}{dt} = -Ax_i + (B - x_i) \sum_{k \in E} E_{ki} I_k - (C + x_i) \sum_{j \in F} F_{ji} I_j$$

It is important to take care of the boundary conditions: pad with 0s, pad with boundary value, wrap around...

Properties of Distant-Dependent Network

Unfortunately, the automatic gain control becomes local, so it is not as effective in adaptation to global stimulus energy

As the gain changes through the network the pattern becomes distorted

That does not make this network useless, as you will see in the homework, it allows new interesting features to emerge

This is a general trend in network modifications: often a simple change in the architecture entails a new (and sometimes totally unexpected) behavior

Next Time

Pattern preservation and transformations in recurrent competitive fields (RCFs)

Properties associated with linear, faster-than-linear, slower-than-linear, and sigmoid feedback signal functions

Readings

- Appendix D of Grossberg, S. (1980). How does the brain build a cognitive code? *Psychological Review*, **87**, pp. 1-51.
- Grossberg, S. (1973). Contour enhancement, short term memory, and constancies in reverberating neural networks. *Studies in Applied Mathematics*, **LII**, pp. 213-257. [SMB Chapter 8.]

Izhikevich neuron assignment is due!