Chapter 8, Our Friend the Limulus

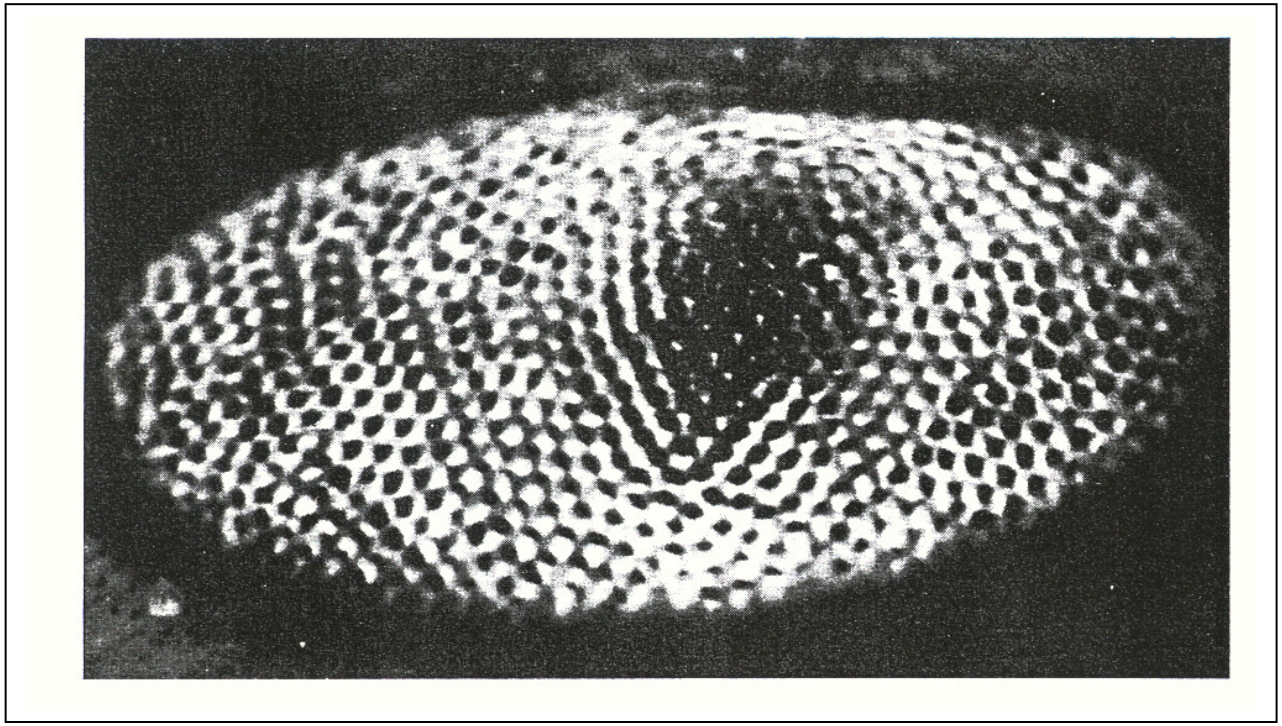
On the beaches of the U.S. North Atlantic Coast you can sometimes see numerous shells of an animal that looks like a crab underneath and like nothing else from above. These are the shells that have been shed by the horseshoe crab, a living fossil – the species has been found fossilized and estimated to be 500 million years old. Quite a biological success story!

The horseshoe crab, or Limulus polephemus, has played an important role in neuroscience and it also provides an undisputable success story for computational neuroscience.

The eyes of the horseshoe crab are aggregates of about 800 ommatidia. Each of these has a small receptive field, but together they cover the hemisphere. Each ommatidium has an axon, signalling the light intensity it receives. The axon is large and it was possible to study the electrical activity inside the axon in the first half of the 1900's. These studies, led by Keffer Hartline, were awarded the 1967 Nobel prize for medicine.

The studies revealed a fundamental principle in sensory processing for enhancement, in this case edge enhancement for the purpose (?) of border detection.

Chapter 8, Our Friend the Limulus
Let us look it in the eye



From Ratliff, Mach Bands: *Quantitative Studies on Neural Networks in the Retina*, 1965

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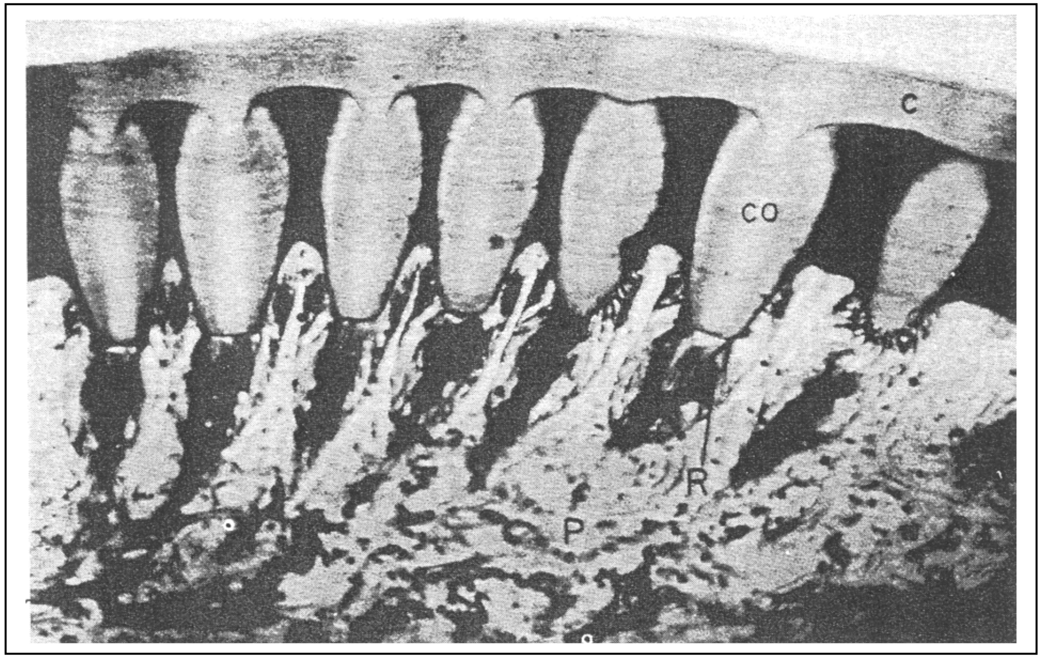
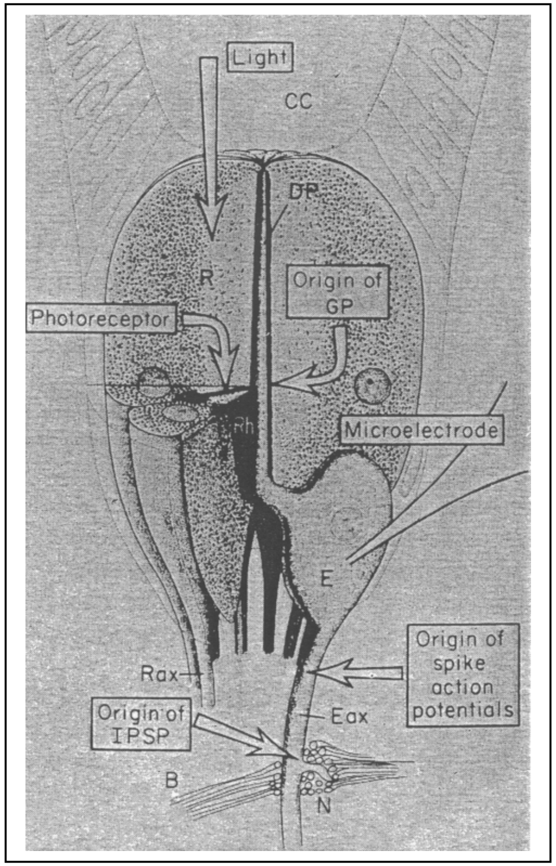
Let us look it in the eye a bit closer



From Hartline et al.,The Peripheral origin of nervous activity in the visual system, *Cold Spring Harbor Symposia on Quantitative Biology, XVII*, 1952, 125-141

Chapter 8, Our Friend the Limulus

The secret is in the ommatidium, more specifically in the box “Origin of IPSP” (Inhibitory PostSynaptic Potential):



From Ratliff et al., The dynamics of lateral inhibition in the compound eye of Limulus.
In Bernhard (Ed.) *The Functional Organization of the Compound Eye*, 1966.

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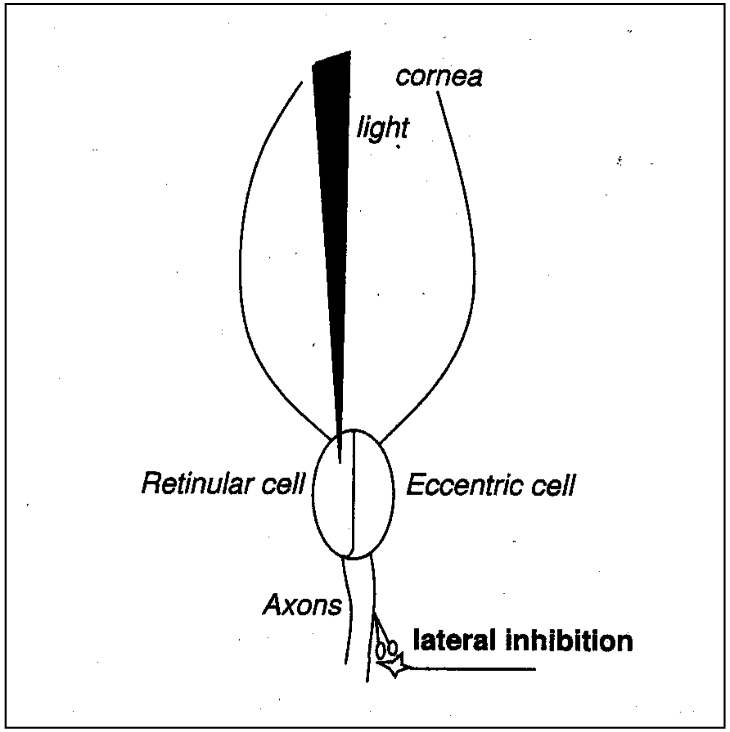
Lytton gives the following schematic image of the ommatidium, he identifies the secret as **lateral inhibition**



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The axon from the neuron of each ommatidium branches out to partially inhibit its neighbours.

This is *lateral inhibition* and is a principle for achieving edge enhancement in vision not only for the Limulus but in our retina as well.

Lateral inhibition has also been shown to be used in the sense of touch for the same purpose.

Lateral inhibition is also a common architectural feature in our cerebral cortex (the Limulus doesn’t have one) but it is more complicated than in the Limulus ommatidium.

In image processing (by computers or digital cameras) there is a similar technique called high pass filtering.

Lateral inhibition is a great invention by the Limulus (or someone even older) and well worth our attention.

Chapter 8, Our Friend the Limulus

Let us see what happens if we have just two neurons inhibiting each other's output.

We call the inputs x_1 and x_2 respectively. The outputs are called y_1 and y_2 respectively.

Let's make it as simple as possible (i.e. linear). Let $y_1 = x_1 - k\, y_2$ and $y_2 = x_2 - k\, y_1$.

k should be "moderate" in size, let us choose $k = 0.1$.
In our first experiment we let $x_1 = x_2 = 1$.

With lateral inhibition, which is one form of lateral feedback, we have a recurrent network. The outputs will keep changing for some time and then settle down to a final state. We can show the development in a table.

Time step	1	2	3	4
y_1	1.00	0.90	0.91	0.91
y_2	1.00	0.90	0.91	0.91

Nothing spectacular so far.

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Now we let $x_1 = 1$ and $x_2 = 0.5$. We will then have the following development:

Time step	1	2	3	4
y_1	1.00	0.95	0.96	0.96
y_2	0.50	0.40	0.41	0.40

The difference between the outputs y_1 and y_2 is larger in the final state than the difference between the inputs, both in absolute and relative terms.

We have achieved an *exaggeration* of the difference between the inputs.

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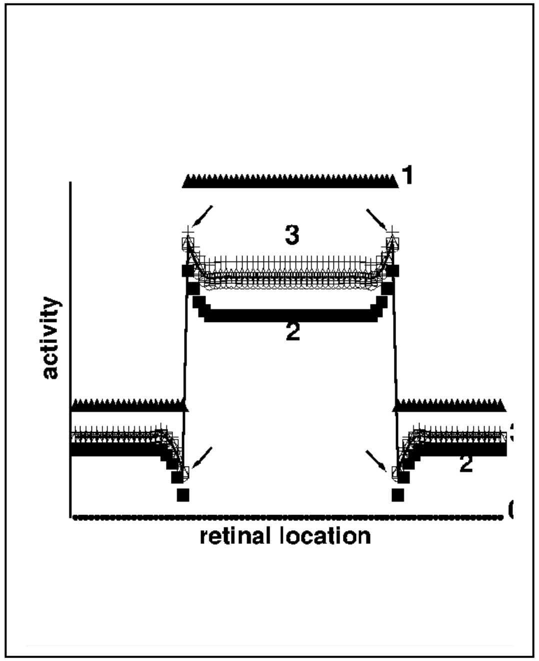
A scene can be seen as many inputs in a two-dimensional array. An edge in the scene will mean abrupt changes in inputs. With lateral inhibition we will exaggerate these changes. We will have *edge enhancement*. Edge enhancement is in turn useful for *border detection* which in turn has an obvious survival value.



A one-dimensional “image” (marked 1) and edge enhancement according to Lytton
:

Chapter 8, Our Friend the Limulus

A few words of tribute to Ernst Mach:

The enhancement of the edges are seen as bands on both sides of the abrupt changes.
These bands are called Mach bands in honour of Ernst Mach 1838-1916, an Austrian physicist, psychologist and philosopher, who discovered them.

If you experience a sonic boom when a supersonic jet plane goes through the “sound barrier” you experience something that Ernst Mach discovered in his laboratory before there were any supersonic jet planes (or any other planes for that matter). That’s why we talk about Mach 2 when we mean twice the speed of sound.

William James (the psychologist who preceded Hebb by some fifty years) about Ernst Mach:

> I don’t think anyone ever gave me so strong an impression of pure intellectual genius. He apparently has read everything and thought about everything …

From Frank, *Modern Science and its Philosophy*, 1949, p. 79

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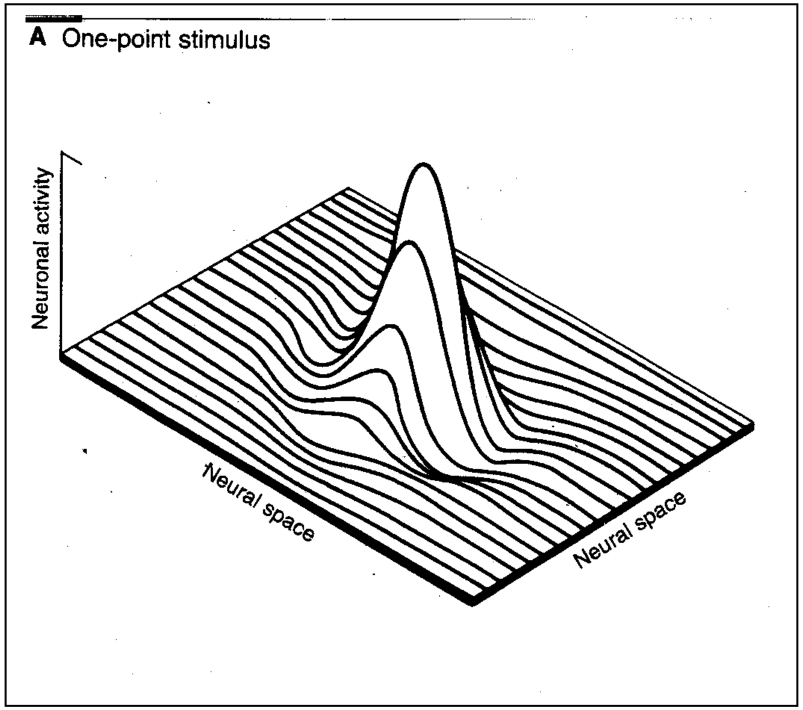
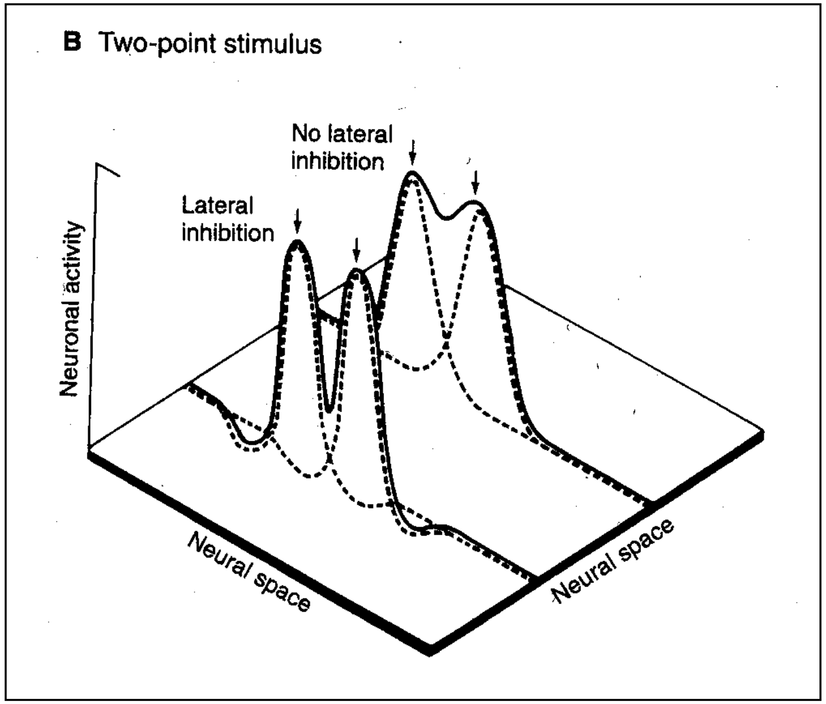
Tactile discrimination is enhanced much the same way as visual:





From Kandel et al. Eds., Principles of Neural Science, 1991, p. 377
Originally from Mountcastle and Darian Smith, 1968

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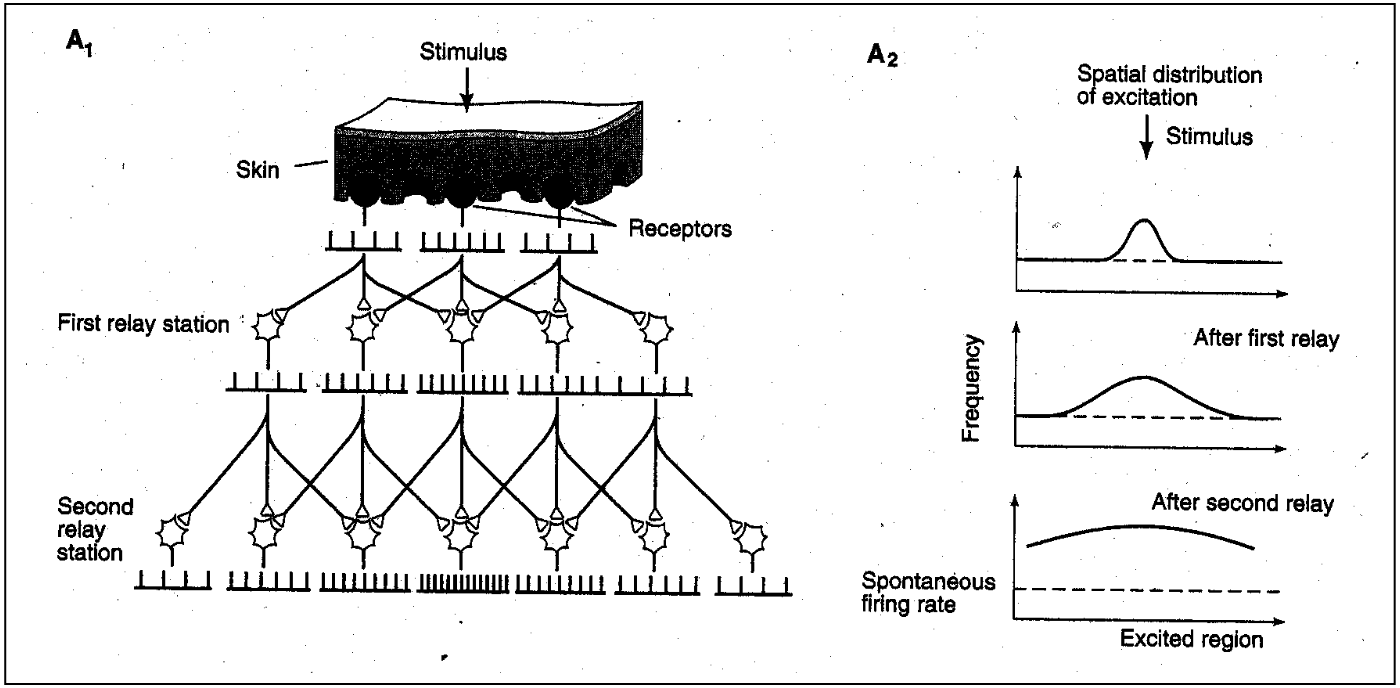
Tactile discrimination is enhanced much the same way as visual.
Here how it would – or rather wouldn't - work without lateral inhibition:



From Kandel et al. Eds., Principles of Neural Science, 1991, p. 376
Originally from Dudel, 1983

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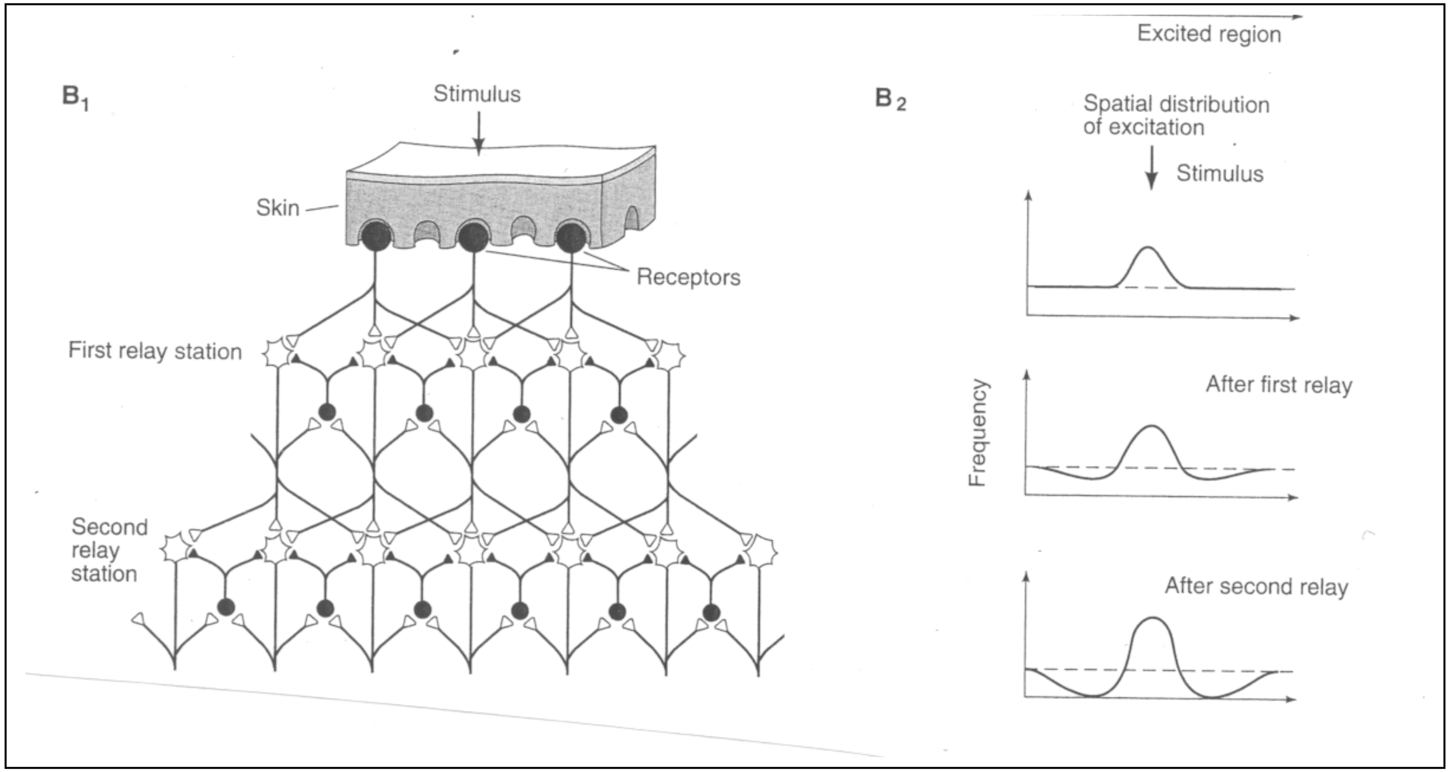
Tactile discrimination is enhanced much the same way as visual.
Here how it does work with lateral inhibition:

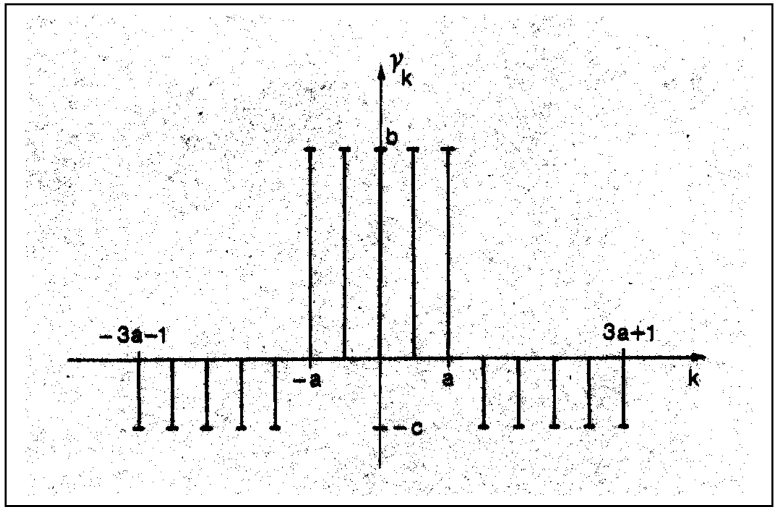


From Kandel et al. Eds., Principles of Neural Science, 1991, p. 376
Originally from Dudel, 1983

Chapter 8, Our Friend the Limulus
An extension of the basic principle

The Limulus eye uses lateral inhibition. A common architecture in neocortex is a combination of lateral excitation of the closest neighbours and lateral inhibition of more distant neighbours (and, although that has not been fully investigated, again lateral excitation of even more distant neighbours).

For a linear array of neurons we may model weights for lateral feedback to one neuron as shown below.



From Kohonen, Self-Organization and Associative Memory, 1984, p. 130

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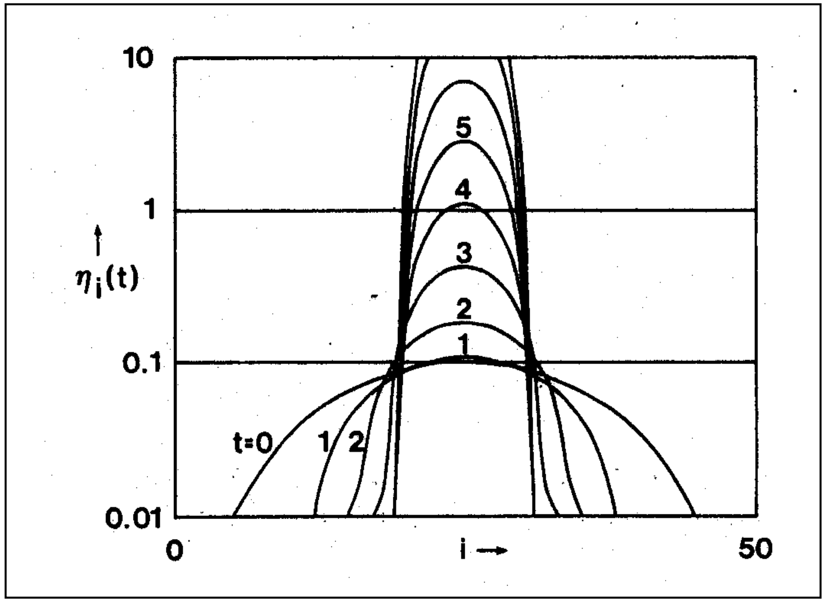
An extension of the basic principle and its effects

If a linear array of neurons with such lateral excitatory and inhibitory feedback is subjected to a “broad” stimulus, as shown for t = 0 in the figure below, a dynamic process will start, which ends in a concentrated and more intense activity.



From Kohonen, Self-Organization and Associative Memory, 1984, p. 130

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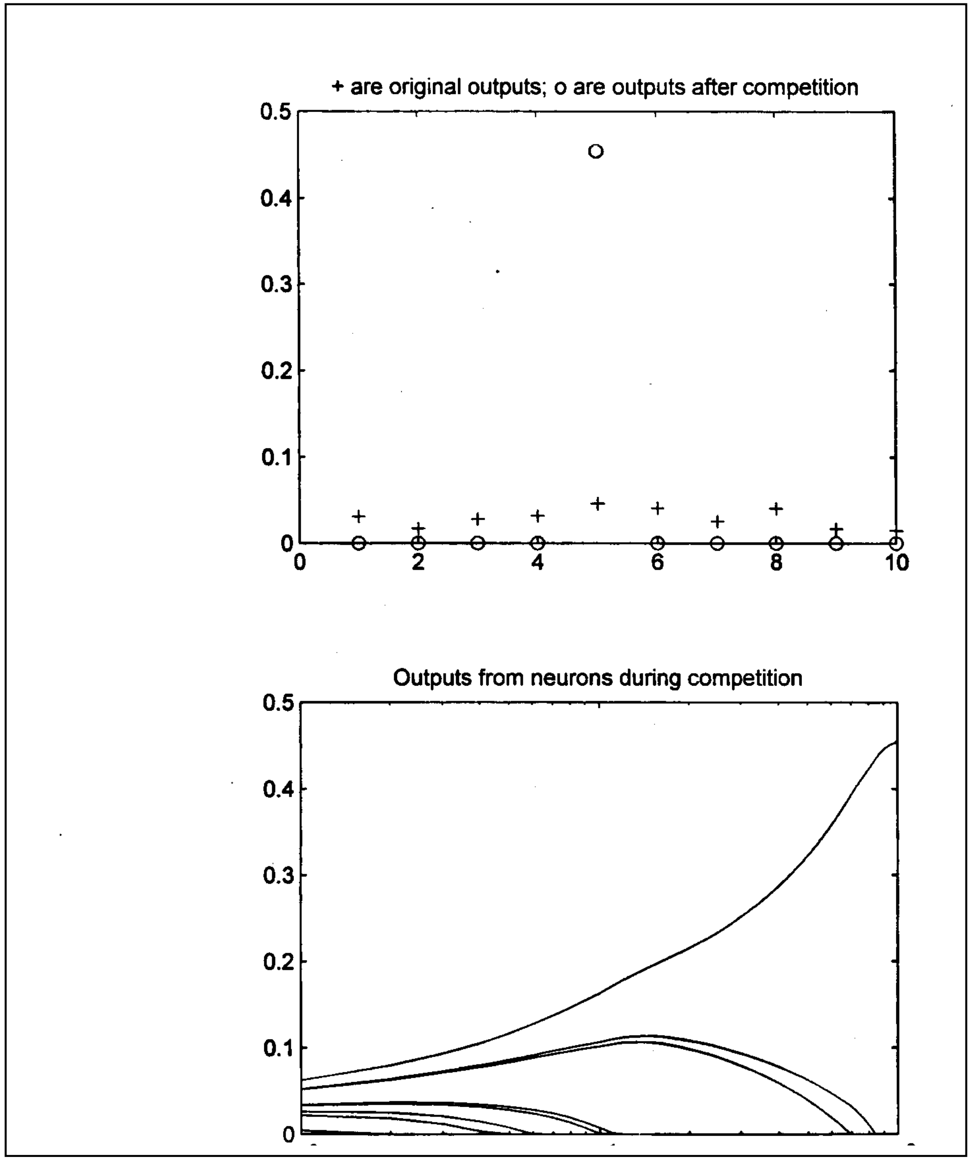
A winner-take-all network (Lytton, page 140)

In a linear array of neurons with self-excitatory feedback and lateral inhibitory feedback one “winning” neuron may emerge. This will enhance one input and totally suppress all others.



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