Chapter 5

Limulus and the Lateral Neural Plexus

We now examine how structure in the (visual) world is reflected in the function of a visual system. This is our first serious integration of outside/inside.

The Limulus visual behavior and possible roles of the two visual systems. Our first neural network; very simple models of neural activity; Question to ponder while reading this lecture: can neural processing predict "what we see"?

5.1 *Limulus polythemus*

We will study, in this (and the next two) lectures the American horseshoe crab, *Limulus*[1]; see Fig. 5.1. It is actually a marine arthropod, and since it evolved hundreds of millions of years ago, it's a living fossil. The shell gives it the appearance of a military tank, which lumbers around in the ocean on the E. coast of the U.S. and the Yukatan. It is clearly an animal with substantial survival skills.

Blood is blue (due to copper); and its blood cells (amoebacytes) contain a substance now used by our pharmaceutical industry to detect certain types of bacterial infection (Limulus amoebocyte lysate, LAL). Because of this the animal is harvested aggressively and its numbers are decreasing.

Behavioural biology of *Limulus*: it swims around in murky water; crawls on the bottom; swims and eats with its legs; mouth surrounds its brain; mates on the shore during a full moon. The mating process is a complex one; Fig. 5.2.

5.1.1 Multiple Visual Systems

Limulus has multiple visual systems distributed over its body. Most are primitive ocelli; prominent are the two lateral compound eyes. These have about 1000 om-

[1]C. N., Shuster, Jr., R. B. Barlow, and J. Brockmann (eds), The Americal Horseshoe Crab, Harvard U.P., 2003

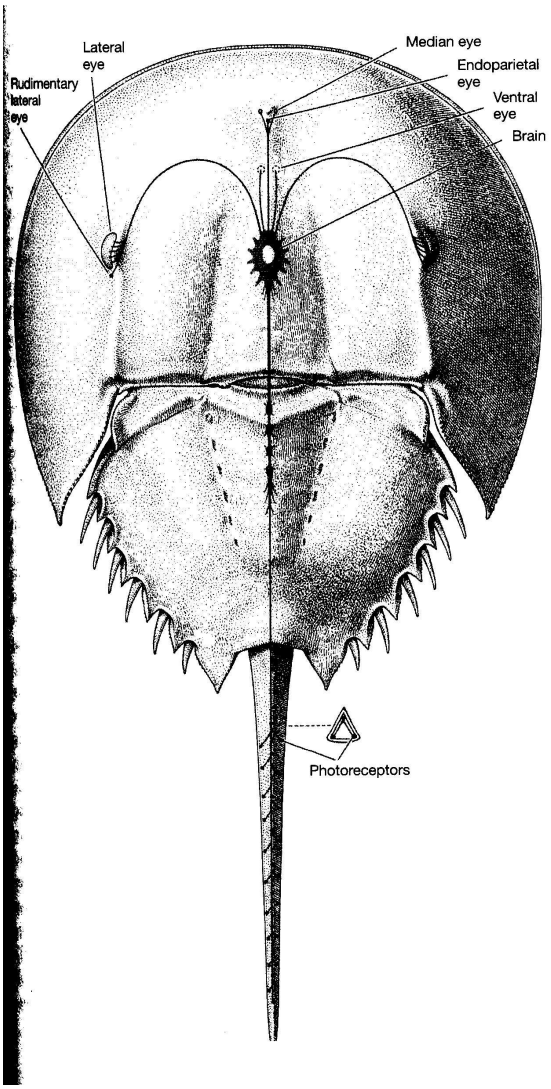


Figure 5.1: The marine arthropod *Limulus* has multiple visual systems. Figure 4.7 from Barlow.

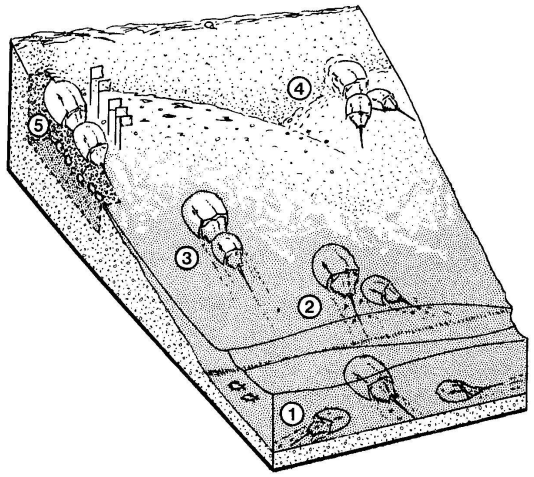


Figure 5.2: Mating behavior in *Limulus* consists of five stages. (1) Males search for females and attempt to attach (2) by gripping with forward claws. Most females arrive on beach with an attached male (3) and other, unattached males attempt to attach (4). A nest with egg clusters buried in the sand (5). From Brockman, Nesting behavior: A shoreline phenomenon, Fig. 2.1.

matidia, or individual receptor units, and are advanced structures that include specialized machinery for light adaptation. This machinery involves both migration of pigment molecules and configural changes. It is controlled by circadian rhythms fed back from its "brain", which in turn is driven by inputs from the ocelli.

Light receptive cells: retinula cells. Graded potential response. Output cells of the ommatidia (eccentric cells) are spiking; we will assume the axons of eccentric cells form the fibres of the optic nerve. This feeds into the lateral plexus, our focus for study.

5.1.2 Image formation and the Compound Eye

Before we can start our development we need to introduce a device for actually forming an image. While we shall consider the physics in more detail later, since light travels in straight lines but bounces in different directions from points on an object's surface, a mechanism is necessary to filter the different combinations away; without this they would superimpose on one another and only a bright mess would result.

The idea of the compound eye is to provide small guides to block those rays coming from all directions but one; see Fig. 5.3. An interesting trade-off arises here: the small the solid angle through which light can enter, the sharper the image. However, as this angle gets small it limits the amount of light that can enter the ommatidium, which

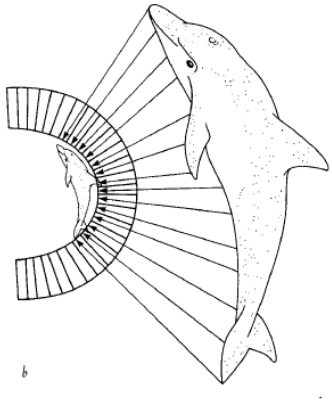


Figure 5.3: (TOP) The geometry of the compound eye shown in cross section. Each ommatidium acts to filter all rays of light except those from a small solid angle. In this way an image is formed, the quality of which is improved with smaller angles. Note: each of the ommatidia has a small lens so the information is not perfect. Figure from Dawkins.

makes detection more difficult. What is the optimal size for each ommatidium?

5.2 The Lateral Plexus as a Neural Network

The structure of the neural plexus is shown in Fig. 5.4

To decipher the structure of the lateral plexus, we begin with a series of experiments. Our first one aims to establish very gross input/output connectivity. We start by recording from the output of the ommatidia.

5.2.1 Neural 'Output' from Neural 'inputs'

We first review the basic idea implied by the "integrate and fire" model of neural processing in the last chapter. Basically we derived the equation:

$$c_m \frac{dV}{dt} = \sum_{\text{sources}} I_{\text{source}} \tag{5.1}$$

where the different input currents I_{source} could be due to leakage across the membrane, synaptic inputs across synapses, and current injected through an electrode. Here we will simplify to the only source being presynaptic activity passing through synapses, and sum across synapses.

$$c_m \frac{dV}{dt} = \sum_{\text{synapses}} I_{\text{synapse}} \tag{5.2}$$

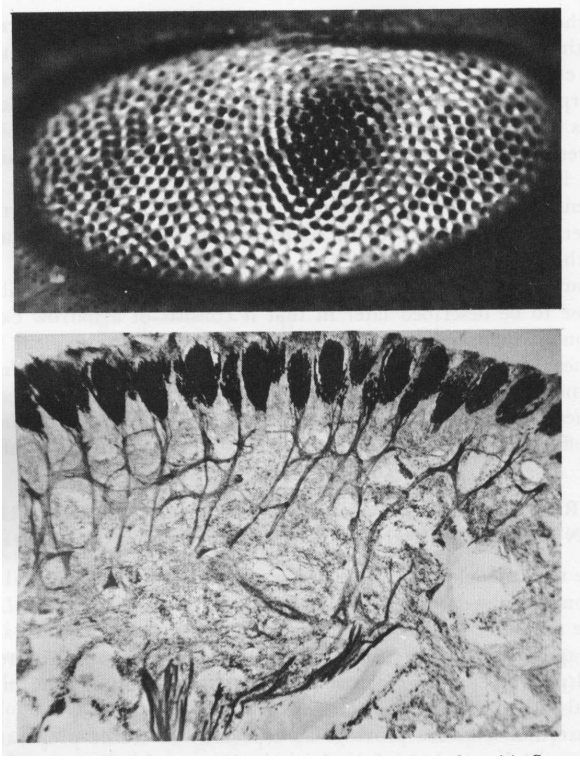


Figure 5.4: (TOP) Compound eye of *Limulus* (approximately 12 mm long by 6 mm wide) contains nearly 1000 ommatidia (center-to-center spacing of optical axes: 0.3 mm). The field of view of each is nearly a hemisphere. (BOTTOM) Section prepared in a direction orthogonal to above. Sensory parts of ommatidia are heavily stained (Samuel's silver stain) showing the output fibres from each one. Note the connections between fibres running laterally - these form the lateral plexus. Taken from Ratliff: fig. 3.24.

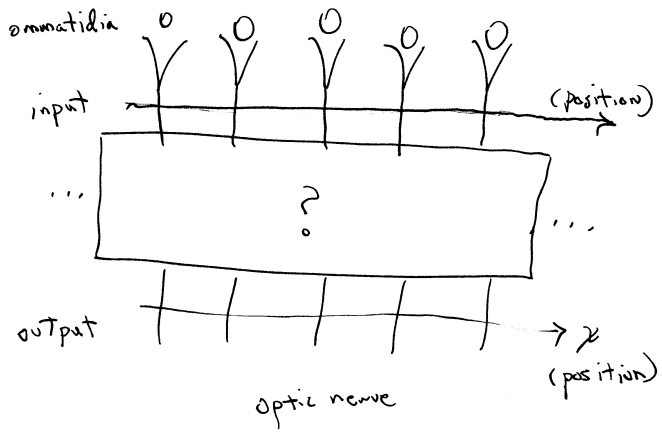


Figure 5.5: Experimental setup

From Ohm's law, we saw that the voltage is a conductance times the current, and from integrate-and-fire we saw that spike frequency is in proportion to how rapidly the voltage integrates to cross the spiking threshold. Conductance ρ is thus a crude version of a synaptic weight. We'll further simplify to say that a *positive ρ corresponds to an excitatory synapse and negative ρ to an inhibitory synapse*. Putting all this together, we have that, loosely, for a given neuron i that receives input from a number N of downstream neurons $j = 1, 2, ..., N$,

$$\left(\text{Output Firing Rate}\right)_i \propto \sum_j \rho_{i,j} \cdot \left(\text{Input Firing Rate}\right)_j$$

We're now ready to flesh this out, using a few experiments to guide us.

5.2.2 Three Experiments

For simplicity, at this point we make a number of **assumptions:**

1. *preparation* We are given a slice through an eye, and the cells in this slice behave as they do *in vivo*.

2. *arrangement* The slice is arranged so that we have access to afferent axons into the lateral plexus and efferent axons from the lateral plexus.

3. *ordering of axonal fibres* agrees between the input and output of the plexus.

4. *spiking neurons*Retinula cell axons spike with frequency in proportion to log(intensity).

Thus we are able to do:

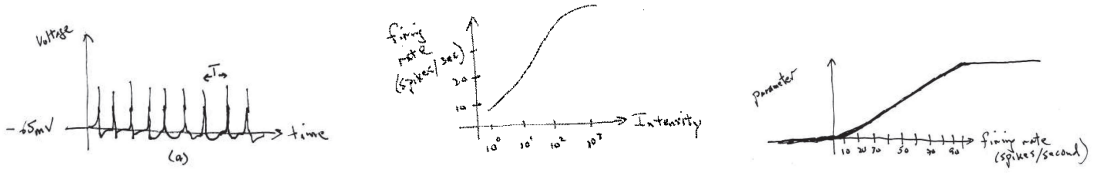


Figure 5.6: Rate code for a regular spiking neuron. (a) Plot of voltage vs time obtained by injecting a constant current into a neuron for some time. This neuron is responding at a regular rate, suggesting a relationship between the input variable (corresponding to the amount of current) and the frequency of firing, T^{-1}, or spikes per second. (b)Coding of the input variable (say, intensity) as a function of the firing rate. For some portion of the scale it seems like the function relating the independent variable (intensity) to the output variable (firing rate) has a graph that is approximately a straight line. This would indicate a (very special) *linear input/output relationship.* (c) Flipping the input/output curve for a neuron provides the inverse view: when neurons are perfect (e.g., linear) individual encoders, the firing rate indicates what the stimulus variable was. Note that there is a lowest (background) firing rate (shown here as about 3 spikes/sec) and a maximum (shown here as about 100 s/s); beyond this the relationship saturates at the max firing rate. Once saturated, is it possible to estimate the value for the input variable? Coding of negative values is essentially impossible, because the full range of (negative) stimulus values would be compressed into the [0,2] spikes range. (It is impossible for a neuron to fire less than 0 spikes/sec.) Normally there is also an initial transient in firing, which is not shown in these illustrations.

Experiment 1: How does the input to a single ommatidium influence the output?

The procedure is to excise the eye/optic nerve/plexus complex from an animal and record from the optic nerve. We shine light to a single ommatidium and record from a number of possible output axons from the plexus; See Fig. 5.7. By scanning across all "output" axons we find activity on only one.

Our first observation relates to the NEURAL CODE for light intensity. An examination of the spike trains suggests a RATE CODE: the neuron fires action potentials at a rate (= frequency = 1/time-between-spikes) that vary in frequency with intensity – the brighter the light, the more rapid the neuron fires. In fact, the actual variation is close to the logarithm of intensity. There are different ways to map the stimulus parameter to neural activity. Rate codes are one example – see Fig. 5.6 – can you think of others?

Note that the activity of the neuron in Fig. 5.7 spans 4 orders of magnitude for light intensity – should this large scale surprise you? Can you guess how much brighter it is outside the entrance to Sterling Library at noon on a clear, sunny day as

compared to how bright it is in your bedroom at night with the lights off at midnight? Some examples of the brightnesses around us are in the table below.

sun illumination	Disk of the sun	10^5 candelas / cm^2
	bright white object	2 candelas / cm^2
	pitch black	4×10^{-2} candelas / cm^2
moon illumination	Disk of the sun	3×10^{-1} candelas / cm^2
	bright white object	5×10^{-6} candelas / cm^2
	pitch black	10^{-7} candelas / cm^2

Based on the data available from this experiment, we conclude that, for our simple network, input to a single ommatidium only effects the output axon in the optic nerve that corresponds to the stimulated ommatidium; see Fig. 5.7,(BOTTOM).

But there is a vague sense that something ought to be happening via interactions with "neighboring" ommatidia in Expt. 1 but somehow we didn't capture it. Even if we record from the output to the "next" neighboring ommatidium we don't see anything. (Question: Can you guess why?) Idea: we need a more complex stimulus to reveal it. So, we are now ready for

Experiment 2: How does the input to two different ommatidia combine to influence the output?

This is a slightly more complex experiment, in which the activity from neighboring positions is revealed by raising the activity level at the active ommatidium. From this we conclude that indeed there is an influence from other ommatidia and that this influence is inhibitory; see Fig.5.8. Does this answer Question above?

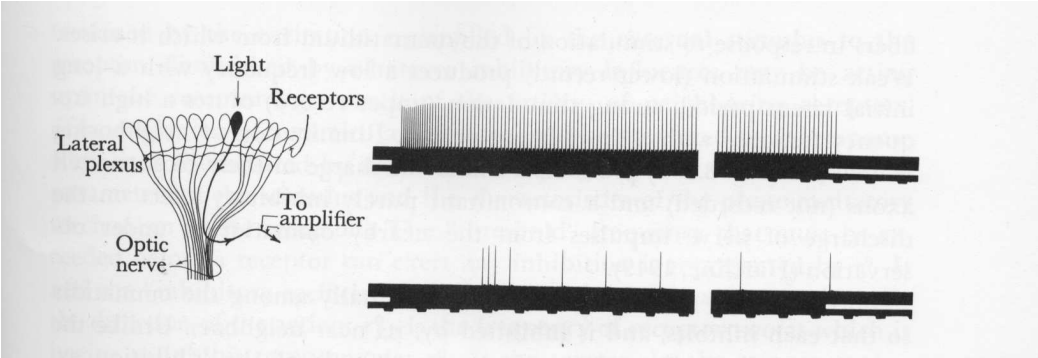
Moreover, careful experimentation further reveals that very low light levels on the inhibiting facet have no effect. This observation will be important for building models.

Experiment 3: How does the input to many ommatidia influence the output?

This extends the results of Expt. 2 to reveal an entire "neighborhood" of interactions—see Fig.5.9. The procedure is to shine light onto the "Active ommatidium (A)" (which indicates the position of the output axon from which we are recording) AND simultaneously onto a Neighboring ommatidium (N_1). The result is a decrease in firing at A. Then we move the putative inhibitory spot onto another neighbor (N_2) and check to see what happens. We continue this procedure until no additional effect is seen.

We observe that there is an inhibitory effect in *Limulus* that extends through about 4 neighboring ommatidia in each direction.

We then check on combinations of inhibitory influences by shining light on the Active ommatidium (A) and on several neighboring ommatidia together. We observe that the inhibitory influence combines as an additive function over the neighborhood.



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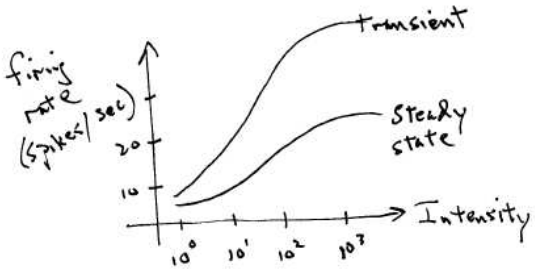

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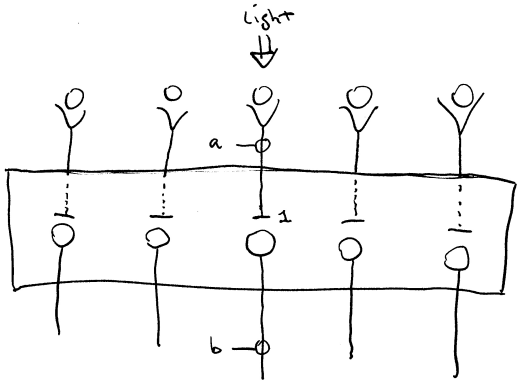


(bottom)

Figure 5.7: Experiment 1: (TOP) Spike trains vary in frequency with the intensity of light. Illustration of spike trains from an actual preparation at two different light intensity levels (upper light is 10^4 times brighter than the lower one.) Note the difference between the initial transient and the sustained portions of the spike train. [Figure from Ratliff, p. 107]. (MIDDLE) Plot of firing rate for the initial (transient) and sustained (steady-state) portions of the spike train. (BOTTOM) Hypothesis about the wiring diagram for the lateral plexus, based in data from Expt. 1.

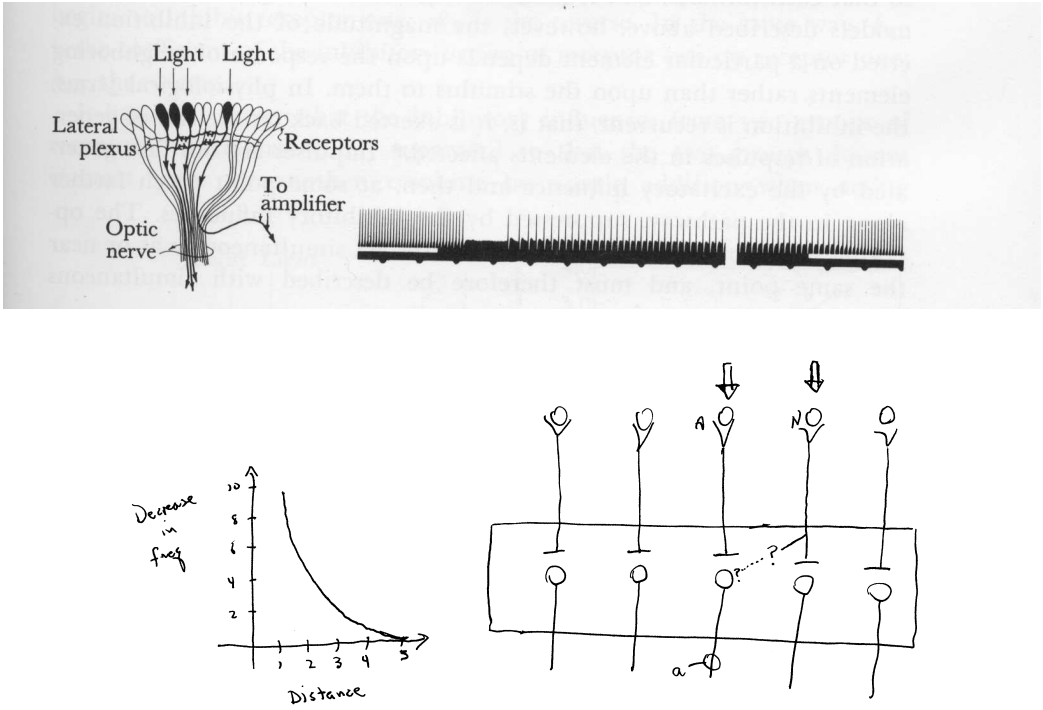


Figure 5.8: Experiment 2: (TOP) Inhibition from neighboring ommatidia. (LEFT) Light is shined on the Active ommatidium (A) and on a Neighboring ommatidium (N). (LEFT) Actual data. (RIGHT) Plot of *decrease* in firing rate measured at A as a function of intensity of light in N. Note that both the transient and the steady-state responses are inhibited, although the initial inhibition greatly exceeds the steady-state inhibition. To generate the data graph, light is shined on the Active ommatidium (A) and on a Neighboring ommatidium (N_1); then on A and another neighbor (N_2), and so on until no effect is seen. Careful study at low light levels reveals that there is no inhibition; rather, the light on a neighboring ommatidium must be sufficently bright to have an effect. This detail at low light levels will be important for our modeling. (BOTTOM) Hypothesis about the wiring diagram for the lateral plexus, based in data from Expts. 1 and 2.

Finally, we confirm that the inhibition is lateral by choosing two neighboring ommatidia and two neighboring outputs, and showing the stimulation to one decreases the other, both ways.

Note: For our modeling we simplify interactions to only nearest neighbors. This results in the "wiring diagram" shown in Fig.5.9. As many of you will recognize, this is a FEEDFORWARD NETWORK with a SINGLE STAGE. So let's see what it can do.

Although we did not repeat all of the above steps explicitly at all positions, we shall now consider this done. The result is that the network works the same way at every position; that is, it is SPATIALLY HOMOGENEOUS. Moreover, remember that we are ignoring boundary conditions; i.e., we are assuming the network is very large and that we're always working far from its endpoints.

5.2.3 An Algebraic Formulation of Lateral Inhibition

Our experiments revealed that the amount of activity in a single neuron in the plexus is a function of the amount of light in the corresponding ommatidium plus the activity from nearby ommatidia. The variable i will move across position; e_i will denote the input activity to the unit at position i; and F_i will denote the firing rate of the output neuron. Observe that e_i denotes the frequency of firing of neuron i if it alone were illuminated. (Unit value for the excitatory synaptic coefficient.)

Inhibition is also modeled in the simplest way: the activity of a unit i firing at rate e_i is inhibited by a function of the firing rate e_j for neighboring unit j: Think of $\alpha_{i,j}$ as an inhibitory synaptic coefficent.

$$F_i = e_i - \alpha_{i,j} e_j. \tag{5.3}$$

Moreover, from our simplified experiments we would like to say that all units $j = 1, 2, \ldots, K$ within the neighborhood of influence of i combine as a sum:

$$F_i = e_i - \sum_{j \in neigh(i)} \alpha_{i,j} e_j. \tag{5.4}$$

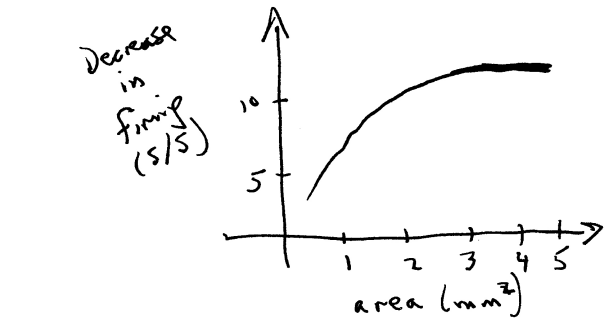
Finally, taking the "threshold" for inhibition discovered in Expt. 2 into account, we obtain:

$$F_i = e_i - \sum_{j \in neigh(i)} \alpha_{i,j} \lfloor e_j - \theta \rfloor. \tag{5.5}$$

where we have introduced the THRESHOLD FUNCTION

$$\lfloor e_j - \theta \rfloor = \begin{cases} e_j - \theta & \text{if } e_j \geq \theta \\ 0 & \text{if } e_j < \theta \end{cases} \tag{5.6}$$

In words: unless the excitation on the neighbor j exceeds the threshold there is no inhibition from that neighbor.



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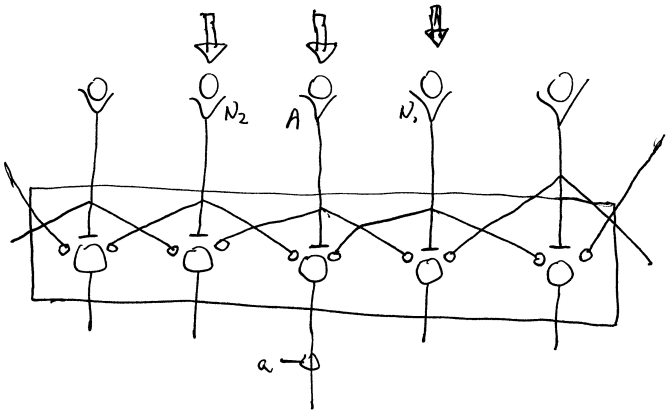

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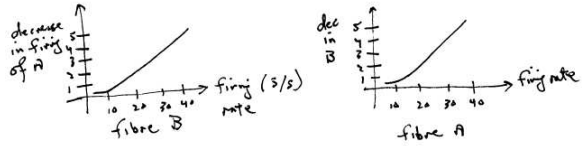

(c)

Figure 5.9: Experiment 3: (A) Inhibition from a neighborhood of ommatidia to check whether the inhibitory influences combine and, if so, how they combine. This is accomplished by shining light on the Active ommatidium (A) and on several neighboring ommatidia together. Plot of *decrease* in firing rate measured at A as a function of area of inhibitory illumination. These data imply that inhibitory influences combine additively. (B) Hypothesis about the wiring diagram for the lateral plexus, based in data from Expts. 1, 2, and 3. (C) Final confirmation data, obtained by checking that, for two neighboring ommatidia A and B, light at A inhibits B AND light at B inhibits A.

For now, let's assume that the firing rate is well above the threshold, $e_j \gg \theta$, so we can concentrate on eq. 5.4.

It is important to realize that the algebraic version of the model in Fig. 5.9 places additional structure on what was an intuitive model. It has two important roles:

- It enables us to do computations with the network. These simulations can provide insight into further experiments by providing hypotheses - in effect, conjectures about what the network is doing.

- It forces us to be precise about what we mean by the different notations; the algebraic terms are models for the different components. Whether they are biophysically accurate needs to be checked.

We shall deal with each point in turn.

We also note that the algebraic formulation above is sensible precisely in the context of the integrate-and-fire model for neurons in the previous Chapter. Recall the plot of input current vs. output firing rate as a linear function.

5.2.4 Experiments with the feed-forward model

To do these experiments, we need to specify the synaptic weighting parameters. For simplicity, we assume the feedforward excitation is unity and the inhibitory parameters are uniformly $\alpha_{i,j} = .2$. (Note that since we used a minus sign directly in the equation, this number should be positive.)

Which input light distribution, or equivalently, which input excitation levels, should we focus on? Now that we have a full model to experiment with, the temptation to use distributions that span many positions is irrestible. So we begin with a constant distribution:

input	20	20	20	20	20	20	20	20	20	20
output	12	12	12	12	12	12	12	12	12	12

This is rather boring. The first suggestion in class was to use a ramp, say from a low value to a high value:

input	...	10	10	12	14	16	18	20	20	...
output	...	6.0	5.6	7.2	8.4	9.6	10.8	12.4	12	...

Now, this is much more interesting, and it seems like something is happening here. Perhaps if we increase the slope of the ramp to infinity ...

input	...	10	10	10	10	20	20	20	20	...
output	...	6	6	6	6	4	16	12	12	...

Sketches of these experiments are in Fig. 5.10.

Indeed, edges – boundaries of objects – are extremely important to our visually-mediated behaviours, and it looks like lateral inhibition has succeeded in enhancing the distribution of light around them.

This enhancement of light was fundamental to Ernst Mach.

(This calculation is tediously repetitive – is there some way to think about it not just as multiplications and additions of numbers? Is there something more basic going on here?)

5.2.5 Recurrent Networks

In the transition from experiments to network structure, we made implicit assumptions about "where" in the network the connections were made. Another possibility is shown in Fig. 5.11 in which inhibition is a function of (possibly) inhibited neurons.

$$F_i = e_i - \sum_{j \in neigh(i)} \alpha_{i,j} \lfloor F_j - \theta \rfloor. \tag{5.7}$$

Can you spot the difference from equation 5.5?

Such networks implement a feedback between different units that leads to different temporal dynamics. For the earlier, non-recurrent network, to get such effects we would have to "stack up" several "layers". The input to the n^{th} layer of the network would be the output from the $(n-1)^{st}$ stage, implementing a kind of *iteration* in algorithmic terms. The number of iterations would then be comparable to the number of times the network was repeated.

5.3 Mach Bands: Sensation vs Perception

The emergence of "edge enhancing" phenomena from this neural network is a remarkable next-step in a story that began almost a century before Hartline's Nobel-prize-winning work on the lateral plexus in *Limulus*. In the middle 19^{th} century Ernst Mach discovered that perceived brightness patterns in the neighborhood of edges were caused by, but were not identical with, the actual physical stimulus. This phenomenon today is called: Mach Bands; see Fig. 5.12.

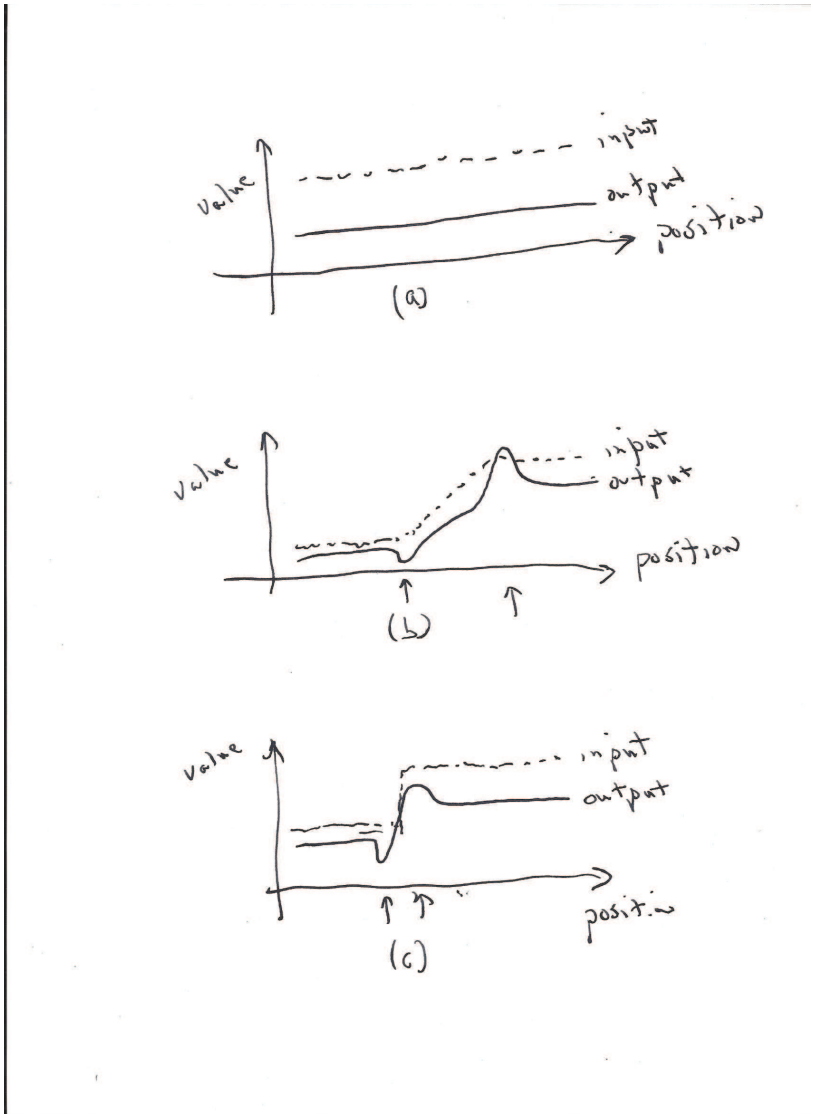

Figure 5.10: Sketches of our experiments with the model of the lateral plexus for Limulus. (a) When a constant input pattern is given, the output remains constant (but reduced in amplitude). (b) When a ramp is given as input, small bumps (see arrows) arise; overall contrast is reduced. (c) When a step input is given, roughly analagous to an 'edge' in a visual image, the overall contrast is reduced except for a tight region spanning the step. These bright/dark bumps are called Mach bands and are thought to emphasize edge-like structures in images.

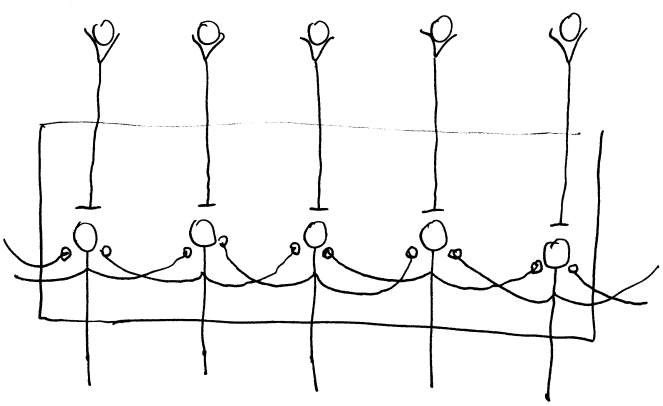

Figure 5.11: An alternative network structure for the lateral inhibitory network in which the inhibition is taken from neurons within the network rather than from input neurons. While many aspects of these two networks are qualitatively similar, such as their production of Mach-band-like phenomena, the temporal dynamics are different. Data from *Limulus* suggests that this recurrent network model is more realistic; see [Ratliff].

> The deviation of a sensation from the mean of the adjacent sensations is always noticable, and exacts a special effort on the part of the sense-organ.
> E. Mach, p. 97.

Mach bands are a type of visual illusion–they indicate that perceived brightness is not the same as physical brightness. Mach performed a series of psychophysical experiments in which he characterized the mapping between a *light surface*, the objective light intensity as a function of position, and the *sensation surface*, or the perceived, subjective intensity surface. An insightful series of psychophysical experiments (see Fig. **; e.g. Ratliff, 254, 256) enabled him to deduce that it was the "curvature", not the slope or the magnitude, of the light surface that was key to understanding the relationship between them. He actually derived the formula:

$$e = a \log\{i/b \pm k\frac{(\frac{d^2 i}{dx^2}}{i}\}.$$

It's important to notice that Mach introduces the Laplacian, or second-derivative operation, here. This has the effect of enhancing changes in the intensity array, which are clearly important in enhancing the "edges" of objects. Technically it can be viewed as a filtering operation, a point to which we shall return shortly.

Do you think that artists understood lateral inhibition?

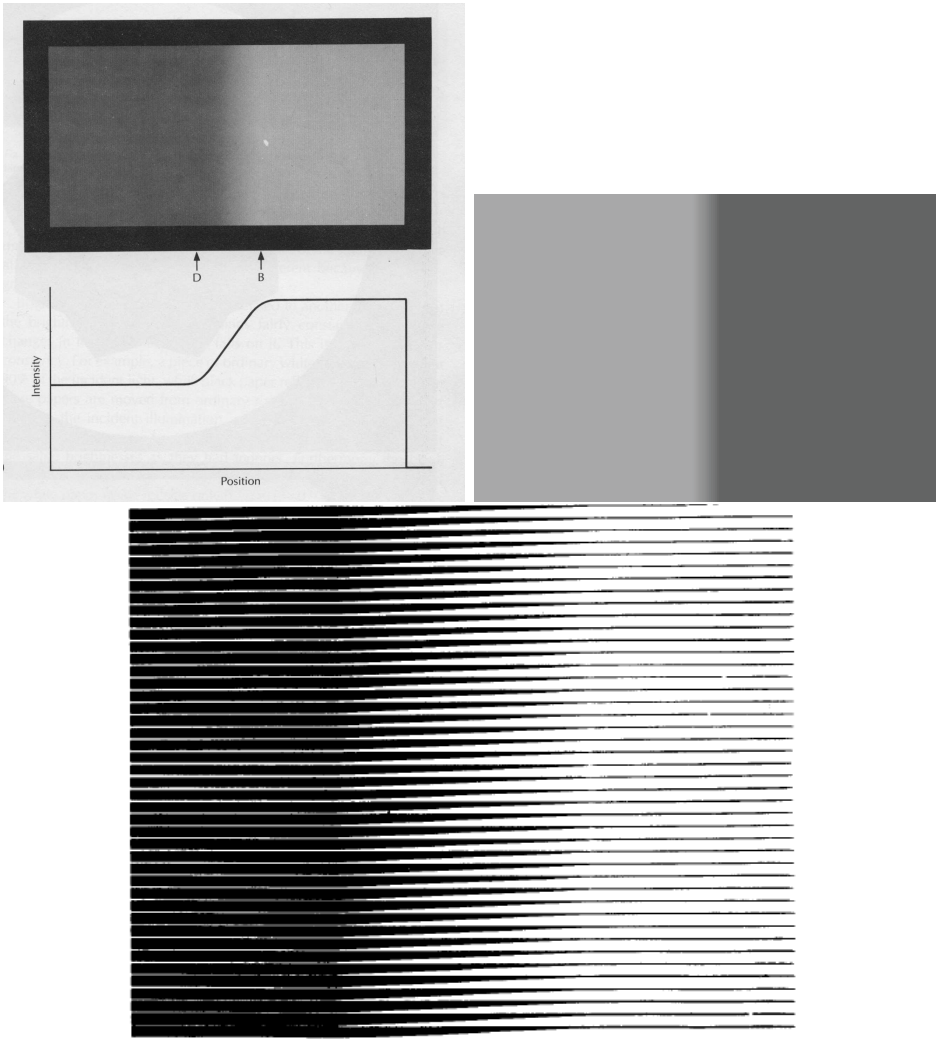

Figure 5.12: Illustration of Mach Bands (middle from Wikipedia). Bottom from Baxandall

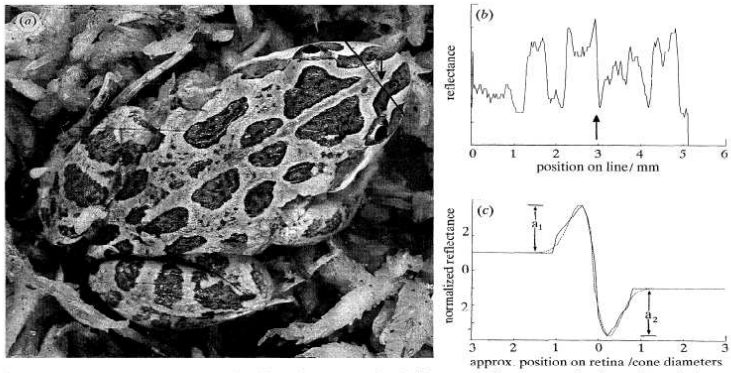

Figure 1. (*a*) A small (20 mm long) frog *Limnodynastes tasmaniensis* with a camouflage pattern showing enhanced edges. The bands that demarcate the borders of the spots on the frog are each about 0.3 mm wide. The line drawn across the snout shows the path of the intensity scan in (*b*), which was digitized from a negative using a computer-controlled frame grabber. The speckle in the scan is due to specularities on the moist skin and digitization noise. (*c*) The solid curve is a normalized version of the arrowed edge profile in (*a*) and (*b*). Reflectance has been scaled to normalize the amplitude of the step component, and position calibrated in units approximating the cone receptive field diameter for a garter snake viewing the frog at a distance of 90 cm. The dashed curve shows a quantitative approximation to the reflectance profile by the function:

Figure 5.13: Various animals have developed camophlage patterns that have Mach-like profiles. What does this say about the visual systems of their predators? see Osorio and Srinivasan, 1991.

5.4 Conclusions

Neural processing effects what we "see". Context plays a fundamental role.

We also are at the beginning of a deeper look into modeling. With *A. coli* we were able to leap from a model of movement under a food distribution to an abstraction. This illustrated how models should be simplifications, but not simpler (in the words of Einstein). That is, they need to capture the "essentials" without all of the confusing detail. Gradient ascent emerged naturally.

With the barnacle, the behavior was simple but the biophysics complicated. We illustrated how the type of thinking in physics provides a key abstraction.

In this lecture we also developed an abstraction of the lateral plexus, which was simple enough to avoid the extra complexity of many lateral connections but rich enough to reveal lateral inhibition. The diagram and its algebraic formulation permitted computational experiments, and these were suggestive.

But many questions remain: how should inhibition correspond to excitation? Should they be balanced? What happens if they are not? In the next two lectures we show how more more can be obtained by studying the abstraction and then feeding it back to the biology.

5.5 Notes

If you're interested in fossil eyes, the trilobyte is a beautiful example. See the classic book: Levi-Setti, R. 1993. *Trilobites* (2nd Ed.). University of Chicago Press, or the

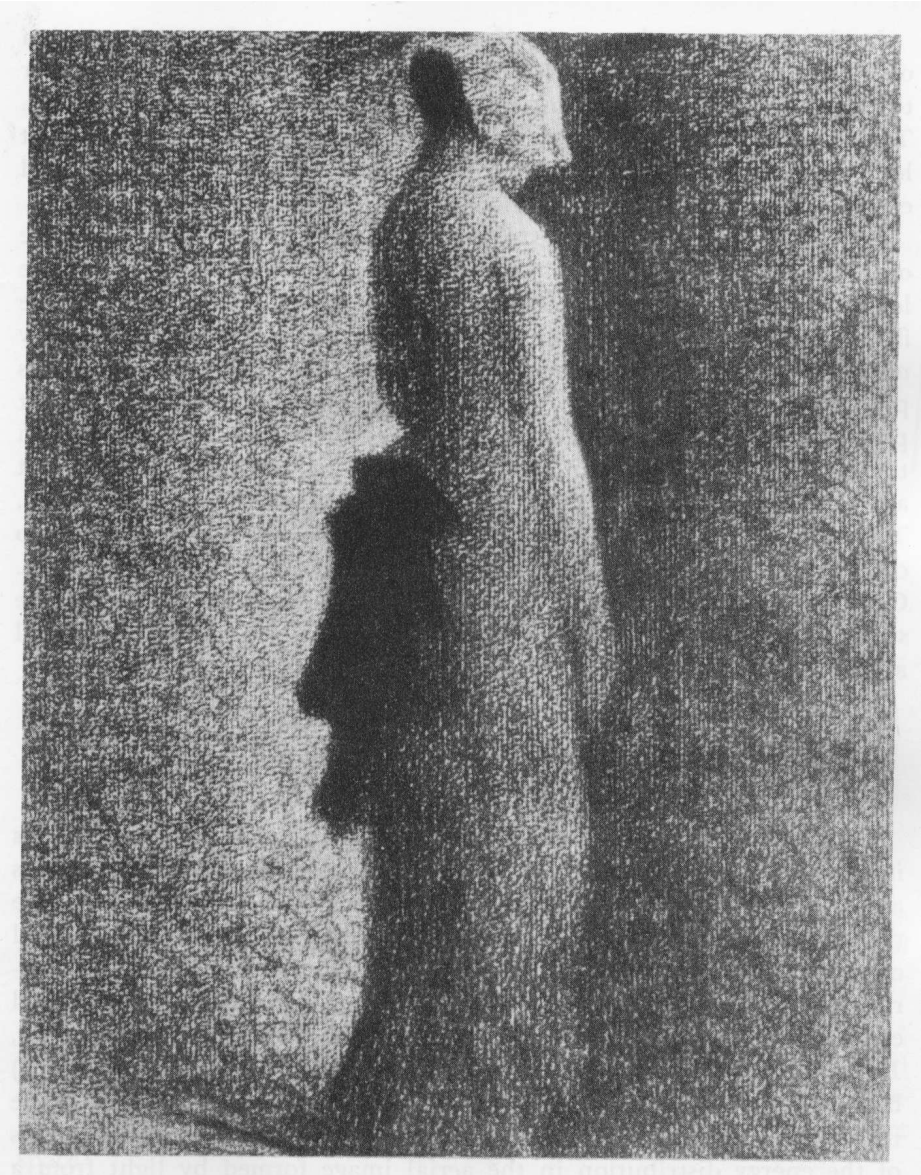

Figure 5.14: Do you think G. Seurat understood lateral inhibition? Mach bands? The manner in which physical intensities related to perceived brightness?

Figure 5.15: Do you think Chinese artists from the early Ming dynasty understood lateral inhibition?

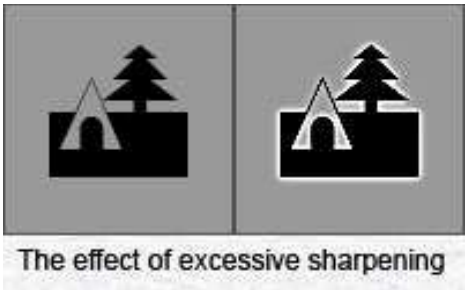

Figure 5.16: Even graphics artists have understood that tremendous emphasis can be placed on visual patterns that have an interesting cross-section in certain neighborhoods.

website: `http://www.trilobites.info/eyes.htm`.

The primary discussion of Limulus is F. Ratliffe, *Mach Bands: Quantitative Studies of neural networks in the retina*, Holden-Day, 1965. The three experiments are taken from the discussion in: T. Cornsweet, *Visual Perception*. Both books are classics.

Beautiful discussion of *Light and Color in the Outdoors* by M.G.J. Minnaert, Springer, 1993; the table of brightnesses comes from this book.

The frog example comes from D. Osorio and M. V. Srinivasan, Camouflage by edge enhancement in animal coloration patterns and it implications for visual mechanisms, *Proc. Roy. Soc. (Lond.)*, 1991, **244**(1310), 81 - 85.