UMAP

MODULE 484

Why Do Cells Compete? Some Examples From Visual Perception

Stephen Grossberg
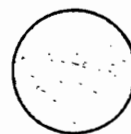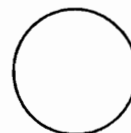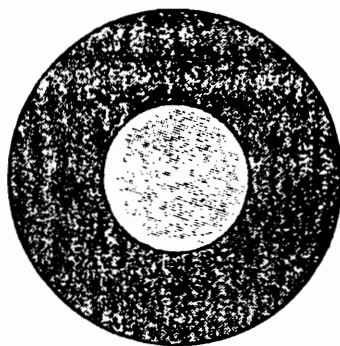
Applications of Algebra and Ordinary Differential Equations to Living Systems

Intermodular Description Sheet: UMAP Unit 484

Title: WHY DO CELLS COMPETE?
SOME EXAMPLES FROM VISUAL PERCEPTION

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equations or mathematical modeling.

Abstract: This unit introduces current data about brightness
constancy and contrast in visual perception, and shows that data of
this kind are a consequence of a principle that holds in all cellular
systems. Variations on this principle imply other visual properties,
such as edge detection, spatial frequency detection, and pattern-
matching properties.

Corequisites: Elementary first-order differential equations.

Related Unit: A Strange Result in Visual Perception (Unit 251)

WHY DO CELLS COMPETE?
SOME EXAMPLES FROM VISUAL PERCEPTION

by

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## MODULES AND MONOGRAPHS IN UNDERGRADUATE
MATHEMATICS AND ITS APPLICATIONS PROJECT (UMAP)

The goal of UMAP is to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications that may be used to supplement existing courses and from which complete courses may eventually be built.

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1. BRIGHTNESS CONSTANCY AND BRIGHTNESS CONTRAST

A mark of a mature science is its ability to explain large amounts of diverse data as manifestations of a few basic principles or laws. Often when a particular empirical phenomenon is explained as an example of a basic law, one then recognizes that the same law helps to explain other data that, on the surface, seem to be unrelated. In this way a basic law may radically reorganize the way we think about and teach data, and even change our ideas about what experiments are interesting and important.

In this unit I will review some data about brightness constancy and contrast (Cornsweet, 1970), and show that data of this kind are a consequence of a principle that holds in all cellular systems (Grossberg, 1978). The visual properties should therefore have analogs in nonvisual cellular systems where the same principle holds. I will then indicate that variations on this principle imply other visual properties, such as edge detection, spatial frequency detection, and pattern matching properties, that on the surface seem to have little to do with brightness constancy and contrast, and that also can be anticipated to occur in nonvisual cellular systems.

An example of brightness constancy is illustrated in Figure 1. A white light of prescribed intensity is shined on the gray circle and its surrounding darker gray annulus. Each point in this picture reflects a fraction of the incident light back to the observer's eyes. The points in the circle reflect a larger fraction of the incident light than do the points in the annulus. The observer's task is to match the apparent brightness of the gray circle with the apparent brightness of one of the comparison circles, which are illuminated separately. Suppose that the comparison circle is chosen that is marked with a star.

Now double the intensity of the white light shining on the circle and annulus. Each point in the picture reflects twice as much light back to the observer's eyes. The points in the circle again reflect more light than the points in the annulus, because each point reflects a fixed fraction, or ratio, of the light that reaches it. These ratios are called reflectances. They are a property of the paper from which the circle and the annulus are made. The observer is again asked to match the apparent brightness of the circle with the apparent brightness of a comparison circle. Although each point in the circle now reflects twice as much light, the observer chooses the same

comparison circle as before!   In fact, the same comparison circle is chosen even if the light illuminating the picture is varied over a surprisingly wide intensity range.
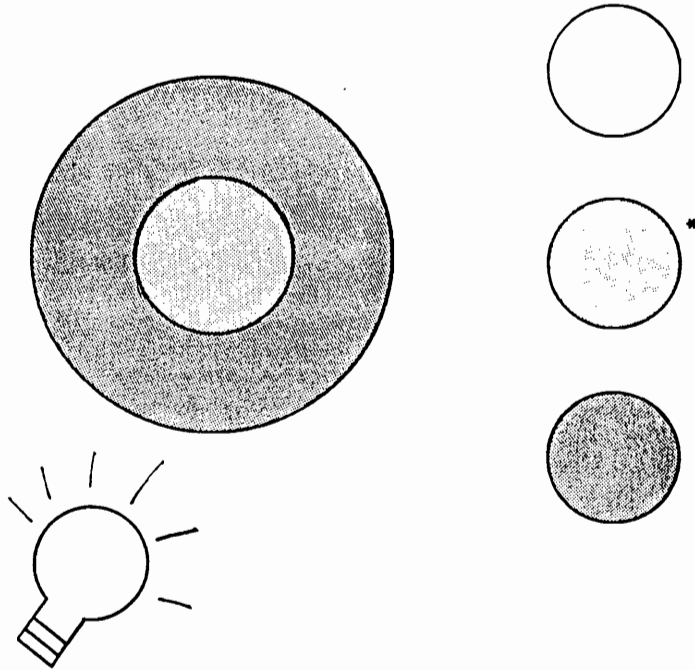

Figure 1. Brightness Constancy: Observers match the central gray circle inside the annulus with the starred gray circle over a wide range of illuminating intensities.

Thus the observer does not perceive the absolute amount of light that is reflected from each point. Instead, the observer perceives a quantity that is independent of the illuminating light intensity over a wide range. Such a quantity is the reflectance of the gray circle, or the relative amount of light that is reflected by each point in the circle. The observer's ability to compute this reflectance depends on the fact that the same light illuminates the circle and the annulus. If only the circle were illuminated, it would look brighter as the light intensity increased. The observer's ability to estimate reflectances must therefore be based on a comparison of the relative amounts of light reflected from the circle and the annulus, since this relative quantity does not change when the picture is illuminated at successively higher levels of

illumination.   Brightness constancy refers to the observer's perception that the brightness does not change as the illumination of the picture increases.

Brightness contrast illustrates the same principle as brightness constancy, but in a slightly different experimental paradigm. Brightness constancy teaches us that an observer often overlooks the absolute level of illumination and computes instead a collection of ratios, or reflectances, at each point in a picture. If we interpret this idea literally, and in the simplest way, we might say that the observer computes a collection of ratios θ_i from each point v_i in the picture, and that the sum of these ratios, namely,

$$\sum_{k=1}^{n} \theta_k = 1,$$

is the same no matter what the light intensity.   Another way to say this is as follows: The total brightness of a scene tends to be independent of the light intensity.   The total brightness tends to be "conserved," or is "invariant" under changes in light intensity.

This observation shows why brightness constancy and brightness contrast are related. Consider Figure 2. In Figure 2, the two gray circles are identical, but one annulus reflects much more light than the other. If the total brightness tends to be conserved, then the circle that is surrounded by a lighter annulus should look darker, whereas the circle that is surrounded by a darker annulus should look lighter. This is brightness contrast, and it is easily perceived when the pictures are carefully constructed.
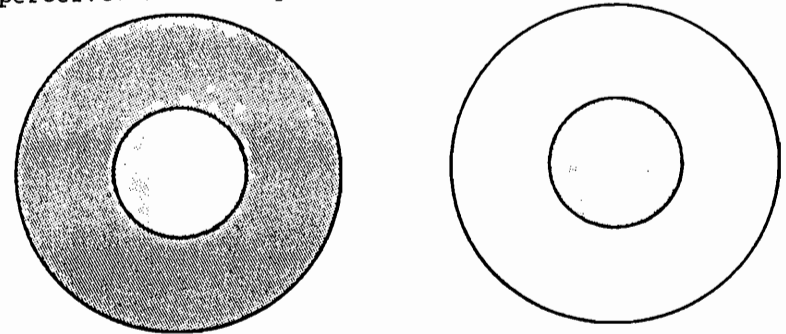

Figure 2. Brightness Constancy: Central gray area on right looks darker than central gray area on left, although the two circles are physically identical.

2. THE NOISE-SATURATION DILEMMA

What causes phenomena like brightness constancy and brightness contrast? I will now show that all cellular systems face a very serious dilemma when they try to react to patterns of incoming signals, and that the mechanism that overcomes this dilemma has formal properties akin to those of brightness constancy and brightness contrast.

Suppose that n cells v_1, v_2, ..., v_n, are given. Let each cell have a finite number of sites that can be in either an excited or unexcited state. For definiteness, suppose that each cell v_i has B excitable sites, of which $x_i(t)$ are excited and $B - x_i(t)$ are unexcited at any time t. Call $x_i(t)$ the _activity_, or _potential_, of v_i. Let each cell v_i be perturbed by a continuously changing input $I_i(t)$ that will excite $x_i(t)$ of v_i's sites (Figure 3). Think of the size of $I_i(t)$ at any time as being the intensity of a coded message to v_i at that time, or alternatively the average intensity of this message in a time interval $[t - \Delta t, t + \Delta t]$ measured from shortly before time t to shortly after time t. For example, $I_i(t)$ might be the intensity of light received at time t by a cell v_i in an idealized retina.
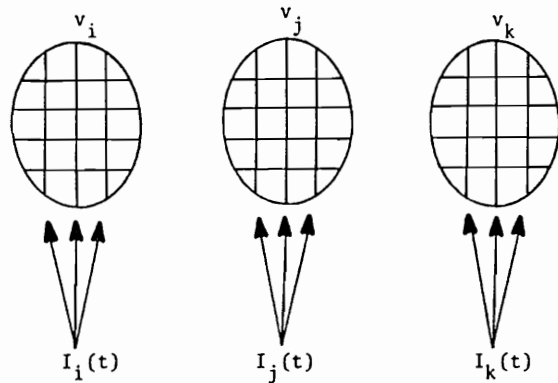

Figure 3. Input I_i activates x_i cell sites at the cell (or cell population) v_i, i = 1, 2, ..., n.

How can the inputs $I_i(t)$ change through time? Two very different types of change can be described in terms of the _total input strength_,

$$I(t) = \sum_{k=1}^{n} I_k(t),$$

and the _relative input intensities_ $\theta_i(t) = I_i(t)/I(t)$ at each v_i. For example, let the v_i represent cells in a retina, and expose the retina to a picture drawn in shades of gray, such as Figure 1 or 2. Changes in I(t) then describe changes in the total illumination of the picture. The picture itself is characterized by the pattern $\theta = (\theta_1, \theta_2, ..., \theta_n)$ of ratios, or reflectances, which do not change through time. Thus it is very important for a system to be able to tell what the pattern weights $\theta(t) = (\theta_1(t), \theta_2(t), ..., \theta_n(t))$ are, whether or not the total input I(t) fluctuates through time. We can say this more generally as follows.
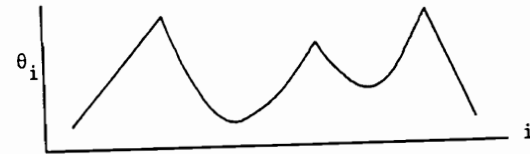

Figure 4a. Let a spatial pattern I_1, I_2, ..., I_n have relative intensity $\theta_i = I_i/I$ at cell v_i, i = 1, 2, ..., n. The figure interpolates a smooth graph of relative intensities through the values θ_i at the discrete integers i = 1, 2, ..., n.

Figure 4b. Noise Contamination: Suppose that the inputs I_i have small overall intensity because $I \simeq 0$. Suppose also that the cells v_i are perturbed by small noisy inputs, either due to their interval metabolism or to extraneous inputs. Then the cell activities x_i can register both the inputs and the noise. The relative intensities θ_i are consequently not accurately registered in the relative sizes of the x_i.

Figure 4c. Saturation: Suppose that the inputs I_i have large overall intensity because $I \gg 0$. Since each cell v_i has only B sites, even the smallest input I_i may be large enough to turn on essentially all the sites of v_i if $\theta_i > 0$. Then all the activities x_i will approximately equal B. Again the relative activities θ_i are not accurately registered by the x_i. The x_i are "insensitive" to the ratios θ_i because each of them has saturated at B.

The inputs $(I_1, I_2, \ldots, I_n)$ form an input _pattern_ at every time t (Figure 4a). How well can a cellular system register an input pattern in its pattern $(x_1, x_2, \ldots, x_n)$ of activities? The ratio θ_i measures the relative importance of the ith input I_i in the pattern $(I_1, I_2, \ldots, I_n)$. How well does the ith activity x_i register the ratio θ_i? In particular, as I is varied (just like the light intensity in Figure 1), do the activities x_i remain sensitive to the ratios θ_i? In other words, can the system discern which inputs are most important as the background activity fluctuates?

In the system of Figure 3, the answer is "no." If I(t) is too small, the inputs can get lost in any noise that disturbs the cells (Figure 4b). If I(t) is too large, the inputs can turn on all the excitable sites in all the cells, thereby saturating the system and rendering it insensitive to input differences across the cells (Figure 4c). This is the noise-saturation dilemma: How do cellular systems overcome insensitivity to input patterns at both low and high input intensities? How do they balance between the equally deadly extremes of noise contamination and saturation in a world where inputs continuously fluctuate through time? Below I indicate how competitive interactions between the inputs allow the cells to retune their sensitivity automatically as I(t) fluctuates, and to avoid saturation as I(t) increases. I will consider only the simplest examples, but they will already possess properties like constancy and contrast.

3. COMPETITION IN MASS ACTION SYSTEMS

To understand the saturation problem more precisely, suppose that the ith cell v_i receives an input I_i that can turn on its $B - x_i$ unexcited sites by mass action. In other words, each unexcited site can be turned on at a rate equal to the input intensity I_i, and all the unexcited sites can get turned on independently of one another. Then the total rate of turning on unexcited sites is $(B - x_i)I_i$. In neurophysiology, a multiplicative effect of inputs on activities is said to obey a _shunting_ law.

After the input shuts off, we also need a mechanism whereby the excited sites can shut off, so that the system returns to an equilibrium point from which it can respond to a new input without bias. Suppose that this equilibrium point equals zero, or that all the excited sites can shut off after the input terminates. The simplest hypothesis is

that each excited site can spontaneously become unexcited at a constant rate A, and that excited sites become unexcited independently of each other. Then the total rate at which excited sites spontaneously become unexcited by mass action is $-Ax_i$.

In all, letting $(d/dt)x_i$ denote the _net_ rate at which sites become excited, we find that

(1) $$(d/dt)x_i = -Ax_i + (B - x_i)I_i.$$

Equation (1) provides a more precise model than we had a few moments ago. However, model-building often requires several stages of thinking before a good model is achieved. One way to test our ideas at each stage is to study whether, in reponse to constant inputs I_i, the system outputs x_i approach equilibrium values that substantiate the basic intuitive ideas the model is seeking to represent. In general models, it is not a trivial exercise to prove even that the outputs approach any equilibrium point in response to a constant input. The outputs might, for example, oscillate persistently in response to the input. In the present situation, this does not happen because (1) is a first-order linear equation in the unknown variable x_i, and can be explicitly solved in any of several ways (Boyce and DiPrima, 1977). We do not need this general solution to analyze the equilibrium responses that help us to build our model, but once the model is built, we would need to study its dynamics through time to achieve a complete understanding.

System (1) is inadequate for the following reason. Let the inputs form a spatial pattern $I_i = \theta_i I$. Given a fixed pattern of "reflectances" $\theta = (\theta_1, \theta_2, \ldots, \theta_n)$, choose a background intentity I and let the system reach equilibrium. At equilibrium, $(d/dt)x_i = 0$, so that (1) implies that the equilibrium activities are

(2) $$x_i = \frac{B\theta_i I}{A + \theta_i I}.$$

Now keep θ fixed and increase I. That is, process the same pattern at different background activities, as in Figure 1. By (2), each x_i approaches B as I increases, even if θ_i is small. This is _saturation_ (Figure 4c). How can the system preserve its sensitivity to θ as I increases? In other words, how does the ith cell v_i compute its "reflectance" θ_i in response to a spatial pattern $I_i = \theta_i I$, $i = 1, 2, \ldots, n$, of inputs? Since, by definition,

(3)
$$\theta_i = I_i \left(\sum_{k=1}^{n} I_k \right)^{-1},$$

each cell v_i needs to know what all the inputs I_1, I_2, ..., I_n are in order to compute θ_i.

There exist two general ways for information from all the inputs to reach each cell v_i: Directly or indirectly. Either all the inputs send signals directly to each v_i, or each input I_i influences only v_i after which all the v_i send signals to each other. The former way is said to use a _feedforward_ network, since all the signals move forward from inputs to cells. The latter way is said to use a _feedback_ network, since signals can pass backwards among the cells themselves. In this note, only the simplest feedforward networks will be considered. These networks already display some basic properties on which the study of the much richer and deeper properties of feedback networks can be based (Grossberg, 1981).

In the feedforward case, all the inputs I_k, $k = 1, 2, ..., n$, interact at v_i so that v_i can compute θ_i. What is the nature of this interaction? To understand this, rewrite (3) as:

(4)
$$\theta_i = I_i \left(I_i + \sum_{k \neq i} I_k \right)^{-1}$$

to emphasize that the ith input I_i plays a special role in determining the ith reflectance θ_i. By (4), an increase in I_i increases θ_i, but an increase in any I_k, $k \neq i$, decreases θ_i. In other words, I_i "excites" θ_i but each I_k, $k \neq i$, "inhibits" θ_i (Figure 5). In other words, the
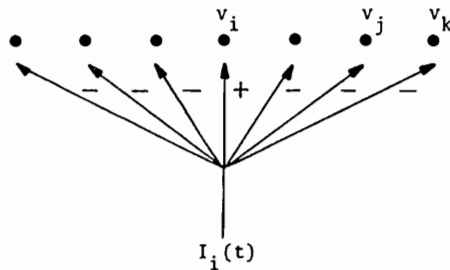

Figure 5. The input I_i excites v_i and inhibits all v_k, $k \neq i$, in order to enable the activities x_i to compute the ratios θ_i. This anatomy is called a nonrecurrent (or feedforward) on-center off-surround network.

inputs compete to determine the reflectance θ_i. In neurophysiology, the inhibitory effect of an input I_k on a cell v_i in a different input pathway is often called "lateral inhibition." Our way of rewriting the ratio θ_i in (4) thus suggests that lateral inhibition helps to solve the noise-saturation dilemma.

We need more, however, than the idea of lateral inhibition to model this intuition dynamically. We need to marry the ideas suggested by (4) to mass action, or shunting, laws for the activities x_i. The excitatory effect of I_i on v_i's unexcited sites is already cast as a mass action rule in the $(B - x_i)I_i$ term of (1). To translate our insight about lateral inhibition into mass action terms, we need to understand how the sum

$$\sum_{k \neq i} I_k$$

of inputs in (4) can shut off v_i's excited sites. The simplest mass action network that models this property differs from (1) by adding a term that expresses the lateral inhibitory effect in mass action terms. This network is defined by the system

(5)
$$\frac{d}{dt} x_i = -A x_i + (B - x_i) I_i - x_i \sum_{k \neq i} I_k$$

$i = 1, 2, ..., n$. In (5), I_i excites v_i via the term $(B - x_i)I_i$ just as in (1). The new term,

(6)
$$-x_i \sum_{k \neq i} I_k,$$

describes how the inputs I_k, $k \neq i$, inhibit (note the minus sign) the excited sites of v_i (which number x_i) by mass action.

The _gain_ of x_i is its decay rate. The gain of x_i is found in (1) and (5) by grouping together all the terms that multiply x_i. In (1), the sum of these terms is $A + I_i$; in (5), it is $A + I$. The two gains differ by the sum

$$\sum_{k \neq i} I_k$$

of inhibitory signals. In both (1) and (5), the inputs automatically change the gain of x_i, but in (5), these inputs include inhibitory inputs. We now note how automatic gain control by the inhibitory signals overcomes the saturation problem.

Present a spatial pattern $I_i = \theta_i I$ to (5) and let each x_i reach equilibrium. Setting $(d/dt)x_i = 0$, we find that

(7) $$x_i = \frac{BI_i}{A+I} = \theta_i \frac{BI}{A+I} .$$

In (7), x_i remains proportional to θ_i no matter how intense I is, and thus estimates θ_i up to a positive constant. The saturation problem is solved! Furthermore, the positive constant $BI(A+I)^{-1}$ depends on the total input intensity, so that the feedforward network is sensitive to the overall brightness of the input field. This brightness effect has a form that is familiar in visual studies. Indeed, term $BI_i(A+I)^{-1}$ in (7) has the form of a Weber-Fechner law (Cornsweet, 1970). Finally, the total activity,

(8) $$x = \Sigma_k x_k = \frac{BI}{A+I},$$

is independent of the number n of active cells. This is the conservation law that we used to motivate brightness contrast. Note, however, that x is not independent of the total input I, although $BI(A+I)^{-1}$ does approach B as I increases. The saturation problem is hereby overcome by competitive mass action interactions. These interactions imply properties of constancy and contrast as automatic consequences.

4. NOISE SUPPRESSION AND INSENSITIVITY TO ZERO SPATIAL FREQUENCY

Equation (5) illustrates a general principle in its simplest form, and instructs us to study mass action competition as a major problem of cellular design. Our task is now to classify how more complex competitive systems solve the saturation problem while accomplishing other tasks as well. Some illustrations of this classification are described below.

In (5), each activity x_i can fluctuate between B and O. The inhibitory term

$$-x_i \sum_{k \neq i} I_k$$

cannot drive x_i below its passive equilibrium point O. This is not always true in vivo, where a cell potential can sometimes be inhibited below the passive equilibrium point. How does this fact alter pattern processing? The simplest example is the system

(9) $$\frac{d}{dt} x_i = -Ax_i + (B-x_i)I_i - (x_i+C) \sum_{k \neq i} I_k,$$

which differs from (5) only in that x_i can fluctuate between B and -C, rather than B and O, where -C < 0. Often in vivo B represents the saturation point of a sodium channel, -C the saturation point of a potassium channel, and B is much larger than C (Kuffler and Nicholls, 1976).

To see how the inhibitory saturation point influences pattern processing, let (9) process the spatial pattern $I_i = \theta_i I$. At equilibrium,

(10) $$x_i = \frac{(B+C)I}{A+I} (\theta_i - \frac{C}{B+C}).$$

By (10), $x_i > 0$ only if $\theta_i > C(B + C)^{-1}$. The constant $C(B + C)^{-1}$ is an _adaptation level_ that θ_i must exceed to excite x_i. To see how the inequality B > C influences pattern processing, consider the simplest case: Suppose that the ratio CB^{-1} matches the ratio of the number of cells excited by each I_i, namely 1, to the number of cells inhibited by I_i, namely (n - 1). If $CB^{-1} = (n - 1)^{-1}$, then $C(B + C)^{-1} = 1/n$.

Now, let a uniform pattern $I_i = (1/n)I$ perturb the system. No matter how intense I is, all $\theta_i = 1/n$, and thus, by (10), all $x_i = 0$. In other words, the network suppresses uniform patterns, or patterns with "zero spatial frequency." This is a familiar property in vision (Cornsweet, 1970), and its physical usefulness is obvious: By suppressing "noise" or the "uniform part" of input patterns, the network can focus on informative differences in input intensities across space. This example illustrates how a classification theory can illuminate the importance of each aspect of network design by showing how it alters the transformation from input pattern to activity pattern.

5. EDGE ENHANCEMENT, SPATIAL FREQUENCY DISTRIBUTION, AND PATTERN RECOGNITION

The noise suppression property generalizes to systems whose excitatory and inhibitory interactions can depend on intercellular distances, as in the system

(11) $$\frac{d}{dt} x_i = -Ax_i + (B-x_i) \sum_{k=1}^{n} I_k C_{ki} - (x_i+D) \sum_{k=1}^{n} I_k E_{ki},$$

where $C_{ki}(E_{ki})$ is the excitatory (inhibitory) coefficient from v_k to v_i (Figure 6). Noise suppression at v_i (that is $x_i \leq 0$) occurs in response to a uniform pattern (all $\theta_i = 1/n$) in (11) if
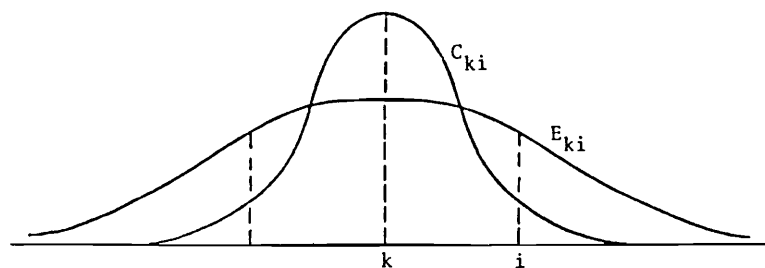
Figure 6. The excitatory intercellular coefficients C_{ki} often decrease more quickly than the inhibitory intercellular coefficients E_{ki} as a function of the distance between v_i and v_k.

$$(12) \qquad B \sum_{k=1}^{n} C_{ki} \leq D \sum_{k=1}^{n} E_{ki},$$

which generalizes $CB^{-1} = (n - 1)^{-1}$ in (10). If the interaction coefficients C_{ki} and E_{ki} decrease as the distance between v_k and v_i increases, then several other important properties prevail.

To illustrate the property of edge enhancement, suppose that a rectangular pattern perturbs such a network (Figure 7a). Then a cell's activity x_i will be suppressed either if its interactions fall so far outside the rectangle or so far inside it that the pattern looks uniform to its interaction coefficients C_{ki} and E_{ki}. Consequently,
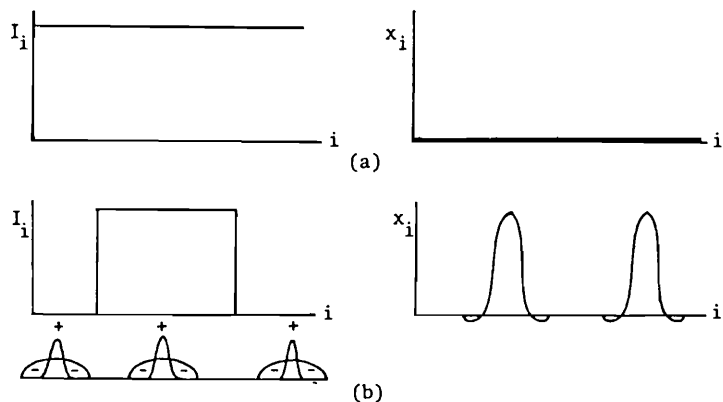

(a)

(b)

Figure 7a. The cells suppress activity patterns that they perceive as uniform.

Figure 7b. Hence they generate suprathreshold reactions only at the edges of the input rectangle.

only activities near the edge of the rectangle will be enhanced (Figure 7b). More generally, the spatial gradients of activity in any input pattern are matched against the spatial gradients in each cell's interaction coefficients to enhance the activity of only those cells to whom the input pattern looks non-uniform. Such cells have some properties of spatial frequency detectors (Robson, 1976).

Pattern matching is illustrated as follows. Suppose in (10) that each input I_i is a sum of two inputs J_i and K_i whose patterns $J = (J_1, J_2, \ldots, J_n)$ and $K = (K_1, K_2, \ldots, K_n)$ are to be matched. In many learning and developmental situations, one of the patterns (say J) is a learned feedback template, or expectancy, against which the other pattern (say K) of afferent data is to be matched (Grossberg, 1980a). In these examples, one seeks the property that a match between J and K will amplify the activity pattern $(x_1, x_2, \ldots, x_n)$, whereas a mismatch between J and K will suppress the activity pattern. To see why this happens, suppose that J and K are maximally mismatched, as in Figure 8a. Then their peaks and troughs are out of phase and add up to form an almost uniform total pattern $(I_1, I_2, \ldots, I_n)$. By (10), any uniform pattern is suppressed. Thus pattern mismatch attenuates network activity. By contrast, if the two patterns match, then there exists a parameter $\alpha > 0$ such that $J_i = \alpha K_i$, $i = 1, 2, \ldots, n$. Equation (10) implies that
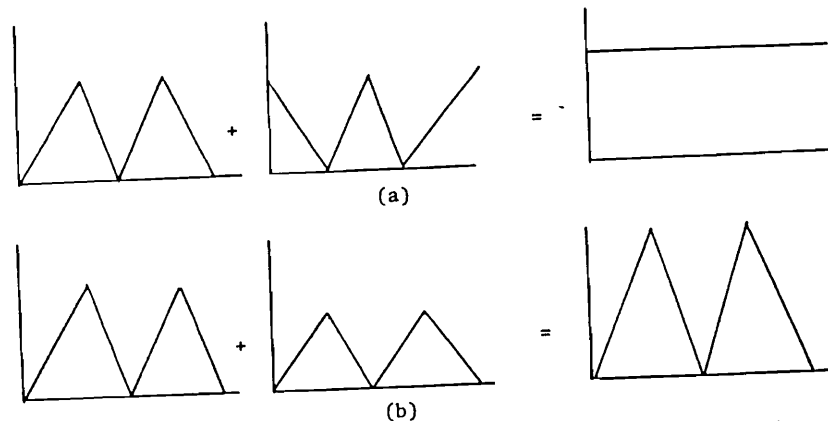

(a)

(b)

Figure 8a. The two patterns are mismatched. Hence their sum is more uniform than either one of them, and tends to be quenched as noise.

Figure 8b. The two patterns are matched, and hence their sum produces a more vigorous reaction than either one of them would produce alone.

$$x_i = \frac{(B + C)(1 + \alpha)\overline{K}}{A + (1 + \alpha)\overline{K}} \left(\theta_i - \frac{C}{B+C}\right),$$ (13)

where

$$\overline{K} = \sum_{i=1}^{n} K_i$$

and $\theta_i = I_i/I$. In other words, a match between J and K amplifies each x_i, as comparison with (10) shows, without changing the pattern θ.

6. CLASSIFICATION OF COMPETITIVE CELLULAR SYSTEMS

The examples above show how solving the noise-saturation dilemma leads us to study mass action competitive systems, and that formal properties of these systems help to explain and to interrelate visual phenomena from a fundamental viewpoint. After a while, one notices that the visual phenomena are special cases of cellular properties that occur in nonvisual systems as well, and one begins to realize that the classification of competitive properties is a major biological problem. In this module, some of the most basic properties have been described, but the module does not even begin to discuss how competitive feedback signals between the cells themselves can transform input patterns and store them in a short term memory.

Is there a general way to start a classfication theory for competitive systems? The answer is "yes," and it is summarized in the articles by Grossberg (1980b, 1981). Whether or not you pursue this classification, I hope that I have made clear the need to find a principled explanation of our data, and the conceptual power that such principles bring when we are lucky enough to find them.

7. EXERCISES

1. Prove that (2) is the steady-state response of (1). Can you solve (1) at all times $t \geq 0$ given any initial value $x_i(0)$? How does the rate with which $x_i(t)$ approach its steady-state depend on I_i?

2. Prove that (7) is the steady-state response of (5).

3. Prove that (10) is the steady-state response of (9).

4. Prove that (12) guarantees noise suppression by (11).

5. Prove that (13) is the steady-state response of (9) to the sum of two matched patterns.

6. In (11), by contrast with (5), the steady-state activities x_i are not proportional to θ_i at all background intensities I. Study how each ratio

$$X_i = x_i \left(\sum_{k=1}^{n} x_k\right)$$

deviates from θ_i as I increases. Read Cornsweet (1970) to compare how this deviation is related to changes in perceived colors at high luminances. Why does this deviation occur in (1) but not in (5)?

7. Philosophical exercise: Is competition good or bad? Discuss in terms of a dialectic that tries to balance between the two equally deadly, but complementary, extremes of noise and saturation.

8. General question: Can you think of other biological systems where competition occurs? What is the analog of constancy? contrast? edge detection? etc.

8. REFERENCES

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9. ANSWERS TO EXERCISES

1. Set $(d/dt)x_i = 0$ in (1). Then

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

Since $I_i = \theta_i I$, (2) is immediate.

To solve (1), rewrite the equation as

$$\frac{d}{dt} x_i + (A + I_i) x_i = I_i.$$

If I_i is constant, then

$$\frac{d}{dt}\left[e^{(A+I_i)t} x_i \right] = e^{(A+I_i)t} \left[\frac{dx_i}{dt} + (A+I_i)x_i \right].$$

Consequently,

$$\frac{d}{dt}\left[e^{(A+I_i)t} x_i \right] = e^{(A+I_i)t} I_i.$$

Integrate this equation from $t = 0$. Then

$$e^{(A+I_i)t} x_i(t) - x_i(0) = I_i \int_0^t e^{(A+I_i)v} dv.$$

Thus

$$x_i(t) = x_i(0)e^{-(A+I_i)t} + \frac{I_i}{A+I_i}\left[1 - e^{-(A+I_i)t} \right].$$

The rate is $A+I_i$.

2. Set $(d/dt)x_i = 0$ in (5) and use the fact that

$$I = \sum_{k=1}^{n} I_k$$

to find (7).

3. Set $(d/dt)x_i = 0$ in (9) to find

$$x_i = \frac{BI_i - C \sum_{k \neq i} I_k}{A + \sum_{k=1}^{n} I_k}.$$

$$x_i = \frac{BI_i - C(I - I_i)}{A + I},$$

$$x_i = \frac{(B+C)\theta_i I - CI}{A + I},$$

$$x_i = \frac{(B+C)I}{A + I}\left[\theta_i - \frac{C}{B+C} \right].$$

4. The steady-state response of x_i to $I_i = \theta_i I$ is

$$x_i = \frac{I \sum_{k=1}^{n} \theta_k (BC_{ki} - DE_{ki})}{A + I \sum_{k=1}^{n} \theta_k (C_{ki} + E_{ki})}.$$

If all $\theta_k = 1/n$, then by (12) all $x_i \leq 0$.

5. Since $J_i = \alpha K_i$, the reflectances of patterns J and K are the same, namely θ_i. However the total activity of the pattern sum

$$I = \sum_i (J_i + K_i) = (1 + \alpha)\overline{K}.$$

When these two facts are substituted into (10), (13) results.

6. The equilibrium value of x_i found in Exercise 4 supplies the tool. Form the ratios

$$X_i = x_i \left(\sum_k x_k \right)^{-1},$$

and differentiate X_i with respect to I. In particular, note how the maximal and minimal ratios X_i change as I increases. These changes are due to the fact that the interactions C_{ki} and E_{ki} in (11) depend on intercellular distance in a nontrivial way.

7. On the cellular level, competition is needed to process patterns at all. Many different competitive rules can all solve the noise-saturation dilemma. Some rules are good for some purposes but cannot achieve other purposes. Also the competitive rules can break down to destroy the balancing act. For example, formal seizures and hallucinations can be traced to shifts of competitive parameters in neural networks.

8. See Grossberg (1978).