

pattern  $\theta$ . On later performance trials, a CS input to  $v_0$  activates  $x_0$ , which in turn activates the signal B. Signal B reads the pattern Z into STM via the terms  $Bz_{0i}$  in A4. Since  $Z \cong \theta$ , A4 shows that the  $x_i$ s that are activated in this fashion are proportional to the  $\theta_i$ s, as desired.

Many aspects of associative learning can be understood using these STM and LTM laws

in more complex anatomies. In particular, the  $Z_i$ s are stimulus sampling probabilities whose properties explain in a neural setting the partial successes of statistical learning models. The distributions of STM and LTM traces also mimic and predict various data about serial learning, paired associate learning, and free recall experiments. See Grossberg (1974, 1978a, 1978e) for additional discussion.

### Appendix C

This section summarizes how feedforward competitive interactions solve the saturation problem using automatic gain control by inhibitory signals, and how properties such as noise suppression, pattern matching, edge enhancement, and spatial frequency sensitivity follow as special cases.

#### Noise-Saturation Dilemma

All cellular systems face the following dilemma. If their inputs are too small, they can get lost in noise. If the inputs are too large, they can turn on all excitable sites, thereby saturating the system and rendering it insensitive to input differences across the cells. For example, suppose that the  $i$ th cell  $v_i$  receives an input  $I_i$  that can turn on some of its B excitable sites by mass action. Let  $x_i(t)$  be the number of excited sites and  $B - x_i(t)$  be the number of unexcited sites at time  $t$ . The simplest mass action law for turning on unexcited sites and letting excited sites spontaneously turn off is

$$\frac{d}{dt}x_i = -Ax_i + (B - x_i)I_i, \quad (A10)$$

$i = 1, 2, \dots, n$ . Term  $(B - x_i)I_i$  says that the input  $I_i$  turns on unexcited sites  $B - x_i$  by mass action. Term  $-Ax_i$  says that excited sites spontaneously becomes unexcited by mass action at rate A. Hence, when  $I_i \equiv 0$ ,  $x_i$  can decay to the equilibrium point 0.

System A10 is inadequate for the following reason: Let the inputs form a spatial pattern  $I_i = \theta_i I$ . Given a fixed pattern  $\theta = (\theta_1, \theta_2, \dots, \theta_n)$ , choose a background intensity  $I$  and let the system reach equilibrium. This equilibrium is found by setting  $(d/dt)x_i = 0$  and solving for  $x_i$ :

$$x_i = \frac{B\theta_i I}{A + \theta_i I}. \quad (A11)$$

Now keep  $\theta$  fixed and increase  $I$ . That is, process the same pattern with different background activity. Then all  $x_i$  in A11 approach B even if the relative input intensity  $\theta_i$  is small. This is saturation. How can the system preserve its sensitivity to  $\theta$  even as  $I$  increases? In other words, how does the  $i$ th cell  $v_i$  compute its "reflectance"  $\theta_i$  in response to a spatial pattern  $I_i = \theta_i I$ ,  $i = 1, 2, \dots, n$ , of inputs? Since

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

cell  $v_i$  needs to know what all the inputs  $I_1, I_2, \dots, I_n$  are in order to compute  $\theta_i$ . Since

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

increasing the  $i$ th input  $I_i$  "excites"  $v_i$  (increases  $\theta_i$ ), whereas increasing any input  $I_k$ ,  $k \neq i$ , "inhibits"  $v_i$  (decreases  $\theta_i$ ). When this intuition is most simply modeled by a cellular mass action network, we find the system

$$\frac{d}{dt}x_i = -Ax_i + (B - x_i)I_i - x_i \sum_{k \neq i} I_k, \quad (A12)$$

$i = 1, 2, \dots, n$ . In Equation A12,  $I_i$  excites  $v_i$  via term  $(B - x_i)I_i$ , just as in A10. The new term

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

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. This is found by grouping together all the terms that multiply  $x_i$ . The sum of these terms is  $A + I$ , where

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

Thus the inputs automatically change the gain of  $x_i$ . In A10 the gain of  $x_i$  is  $A + I_i$ . The two gains differ by the sum

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

of inhibitory signals. 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 A12 and let each  $x_i$  reach equilibrium. Setting  $(d/dt)x_i = 0$ , we find

$$x_i = \theta_i \frac{BI}{A + I}. \quad (A13)$$

In A13,  $x_i$  remains proportional to  $\theta_i$  no matter how intense  $I$  is, and  $BI(A + I)^{-1}$  has the form of a Weber-Fechner law. The saturation problem is hereby overcome using automatic gain control by inhibitory signals.

#### Noise Suppression

In A12, the passive equilibrium point, due to term  $-Ax_i$ , and the inhibitory saturation point, due to term

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

are both zero. This is not always true in vivo, where a cell potential can sometimes be actively inhibited below the passive equilibrium point. How does this fact alter pattern processing? Consider the system

$$\frac{d}{dt}x_i = -Ax_i + (B - x_i)I_i - (x_i + C) \sum_{k \neq i} I_k, \quad (A14)$$

which differs from A12 only in that  $x_i$  can fluctuate between  $B$  and  $-C$ , rather than  $B$  and  $0$ , where  $-C < 0$ . Often in vivo  $B$  represents the saturation point of a  $\text{Na}^+$  channel,  $-C$  represents the saturation point of a  $\text{K}^+$  channel, and  $B$  is much larger than  $C$ .

To see how the inhibitory saturation point  $C$  influences pattern processing, let A14 equilibrate to the spatial pattern  $I_i = \theta_i I$ . Setting  $(d/dt)x_i = 0$ , we find the equilibrium activities

$$x_i = \frac{(B + C)I}{A + I} \left( \theta_i - \frac{C}{B + C} \right). \quad (A15)$$

By A15,  $x_i > 0$  only if  $\theta_i > C(B + C)^{-1}$ . The constant  $C(B + C)^{-1}$  is an *adaptation level* that  $\theta_i$  must exceed in order to excite  $x_i$ . For simplicity, 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  $C(B + C)^{-1} = 1/n$ . Since, in response to a uniform spatial pattern of inputs, all  $\theta_i = 1/n$ , no matter how intense  $I$  is, it then follows by A15 that all  $x_i = 0$ . This is noise suppression in its simplest form. It is due to a matched symmetry-breaking between the intracellular excitatory versus inhibitory parameters ( $B, C$ ) and the intercellular spread of off-surround versus on-center pathways.

#### Edge Enhancement, Spatial Frequency Detection, and Pattern Matching

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

$$\frac{d}{dt}x_i = -Ax_i + (B - x_i) \sum_{k=1}^n I_k C_{ki} - (x_i + D) \sum_{k=1}^n I_k E_{ki}, \quad (A16)$$

where  $C_{ki}$  ( $E_{ki}$ ) is the excitatory (inhibitory) coefficient from  $v_k$  to  $v_i$ . Noise suppression at  $v_i$  (i.e.,  $x_i \leq 0$ ) occurs in response to a uniform pattern (all  $\theta_i = 1/n$ ) in A16 if

$$B \sum_{k=1}^n C_{ki} \leq D \sum_{k=1}^n E_{ki}, \quad (A17)$$

which generalizes  $CB^{-1} = (n - 1)^{-1}$  in A15. If a rectangular pattern perturbs such a network, 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, only activities near the edge of the rectangle will be enhanced. 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 nonuniform. In recurrent networks, this property is supplemented by active contrast-enhancing, disinhibitory, and STM processes that can join together cells with similar interaction gradients into a dynamically coherent subfield that is sensitive

to a band of spatial frequencies in the input patterns. (A15),

$$x_i = \frac{(B + C)(1 + \alpha)\bar{K}}{A + (1 + \alpha)\bar{K}} \left[ \theta_i - \frac{C}{B + C} \right], \quad (\text{A18})$$

Pattern matching is illustrated as follows. Suppose in A14 that each input  $I_i$  is a sum of two inputs  $J_i$  and  $K_i$  whose patterns  $J = (J_1, J_2, \dots, J_n)$  and  $K = (K_1, K_2, \dots, K_n)$  are to be matched. If  $J$  and  $K$  mismatch each other's peaks and troughs to form an almost uniform total pattern  $I = (I_1, I_2, \dots, I_n)$ , then by A15 all  $x_i$  will be inhibited if  $CB^{-1} \geq (n - 1)^{-1}$ . By contrast, if the two patterns reinforce each other, say  $J_i = \alpha K_i$ , then by

where

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

and  $\theta_i = K_i(\bar{K})^{-1}$ . In other words, matching  $J$  and  $K$  amplifies each  $x_i$  without changing the pattern  $\theta_i$ .

#### Appendix D

This section summarizes some properties of recurrent on-center off-surround networks, including normalization, contrast enhancement, quenching threshold, and STM properties.

To see how recurrent networks normalize their STM activity, we first note by Appendix C that these networks need competitive interactions to solve the noise-saturation dilemma. The simplest recurrent on-center off-surround network is defined by

$$\frac{d}{dt}x_i = -Ax_i + (B - x_i)[f(x_i) + I_i] - x_i \left[ \sum_{k \neq i} f(x_k) + J_i \right], \quad (\text{A18})$$

$i = 1, 2, \dots, n$ . As usual,  $x_i$  is the STM activity of  $v_i$ , term  $(B - x_i)f(x_i)$  describes the self-excitation of  $v_i$  via a positive feedback signal  $f(x_i)$ —the recurrent on-center—and term

$$-x_i \sum_{k \neq i} f(x_k)$$

describes the inhibition of  $v_i$  via negative feedback signals  $f(x_k)$ ,  $k \neq i$ —the recurrent off-surround. Term  $I_i$  is the  $i$ th excitatory input, and term  $J_i$  is the  $i$ th inhibitory input, for example,

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

in A12.

#### *Contrast Enhancement, Normalization, and Quenching Threshold*

An important problem in system A18 is to choose the feedback signal function  $f(w)$  as a function of activity level  $w$  in such a way as to suppress noise but contrast enhance and store in STM behaviorally important patterns. This problem was solved in Grossberg (1973).

The solution is reviewed in Grossberg (1978e, Sections 14 and 15).

To understand the simplest STM properties, A18 is transformed into pattern variables  $X_i = x_i x^{-1}$  and total activity variables

$$x = \sum_{k=1}^n x_k$$

using the notation  $g(w) = w^{-1}f(w)$  and supposing that all  $I_i = J_i = 0$ . Then

$$\frac{d}{dt}X_i = BX_i \sum_{k=1}^n X_k [g(X_i x) - g(X_k x)] \quad (\text{A19})$$

and

$$\frac{d}{dt}x = -Ax + (B - x) \sum_{k=1}^n f(X_k x). \quad (\text{A20})$$

For example, if  $f(w)$  is linear, namely,  $f(w) = Cw$ , then  $g(w) = C$  and all  $(d/dt)X_i = 0$  in A19. In other words, A19 can perfectly remember *any* initial pattern of reflectances. However, by A20 if  $A \geq B$ , then  $x(t)$  approaches zero as  $t \rightarrow \infty$ , whereas if  $B > A$ , then  $x(t)$  approaches  $B - A$  as  $t \rightarrow \infty$ , whether or not a prior input pattern occurs. Thus if STM storage is ever possible, then  $B > A$ , and consequently noise will be amplified as vigorously as inputs. A linear signal amplifies noise, and is therefore inadequate despite its perfect memory of reflectances.

A slower-than-linear signal  $f(w)$ , for example,  $f(w) = Cw(D + w)^{-1}$  or more generally, any  $f(w)$  such that  $g(w)$  is monotone decreasing, is even worse. By A19, if  $X_i > X_k$ ,  $k \neq i$ , then  $(d/dt)X_i < 0$  and if  $X_i < X_k$ ,  $k \neq i$ , then  $(d/dt)X_i > 0$ . All differences in reflectances are hereby erased by the reverberation, and noise amplification also occurs. The whole network experiences a type of seizure.