



Joining distributed pattern processing and homeostatic plasticity in recurrent on-center off-surround shunting networks: Noise, saturation, short-term memory, synaptic scaling, and BDNF

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ABSTRACT

The activities of neurons vary within small intervals that are bounded both above and below, yet the inputs to these neurons may vary many-fold. How do networks of neurons process distributed input patterns effectively under these conditions? If a large number of input sources intermittently converge on a cell through time, then a serious design problem arises: if cell activities are sensitive to large inputs, then why do not small inputs get lost in internal system noise? If cell activities are sensitive to small inputs, then why do they not all saturate at their maximum values in response to large inputs and thereby become incapable of processing analog differences in inputs across an entire network? Grossberg (1973) solved this *noise-saturation dilemma* using neurons that obey the membrane, or shunting, equations of neurophysiology interacting in recurrent and non-recurrent on-center off-surround networks, and showed how different signal functions can influence the activity patterns that the network stores in short-term memory. These results demonstrated that maintaining a balance between excitation and inhibition in a neural network is essential to process distributed patterns of inputs and signals without experiencing the catastrophes of noise or saturation. However, shunting on-center off-surround networks only guarantee that cell activities remain sensitive to the relative sizes of inputs and recurrent signals, but not that they will use the full dynamic range that each cell can support. Additional homeostatic plasticity mechanisms are needed to anchor the activities of networks to exploit their full dynamic range. This article shows how mechanisms of synaptic scaling can be incorporated within recurrent on-center off-surround networks in such a way that their pattern processing capabilities, including the ability to make winner-take-all decisions, is preserved. This model generalizes the synaptic scaling model of van Rossum, Bi, & Turrigiano (2000) for a single cell to a pattern-processing network of shunting cells that is capable of short-term memory storage, including a representation of how BDNF may homeostatically scale the strengths of excitatory and inhibitory synapses in opposite directions.

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1. Introduction: Balancing excitation and inhibition to process patterns in neural networks

The activities of neurons vary within small intervals that are bounded both above and below, yet the inputs to these neurons may vary many-fold. How do networks of neurons process distributed input patterns effectively under these conditions? A classical example of this situation occurs during the visual perception of brightness. The retina receives luminance signals, which are a product of reflectances and illumination levels (Hurlbert, 1986; Lambert, 1760; Wyszecki & Stiles, 1982), from objects in the world. Surface reflectances, or the percentages of light reflected by

a surface in each wavelength, provide information about the material properties of objects. The spatiotemporal patterning of these reflectances across a network of neurons represents objects in a scene. From these patterns of luminance signals, the visual system is able to estimate object reflectances across a scene by compensating for an immense dynamic range of mean illuminations throughout each day and night, and for a wide dynamic range of luminances across each scene.

This process of “discounting the illuminant” is not sufficient, however, to efficiently see the world, because illuminant-discounted signals may represent only the *relative* amounts of light that each object surface reflects to the eyes. For effective perception, the brain also needs to compute an absolute lightness scale, by a process called “anchoring”, that can represent the full-range of experience from dim moonlight to dazzling sunlight (Gilchrist, 1977, 1980; Gilchrist & Bonato, 1995; Wallach, 1948, 1976). Grossberg and Hong (2006) and Hong and Grossberg (2004) have developed a neural model of anchoring to explain and quantitatively

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simulate a variety of perceptual and brain data about perceived lightness.

The lightness anchoring problem is a special case of a much more general problem that all neurons must face throughout life. Indeed, at every stage of neural processing, neuronal networks receive patterned inputs that represent many types of information. Moreover, many different input pathways may converge on a single target cell. Suppose that activities, or short-term memory (STM) traces, of cells in a network are defined by x_1, x_2, \dots, x_n . Each of the activities x_i may fluctuate within fixed finite limits. Such a bounded operating range for each x_i has the advantage that fixed decision criteria, such as output thresholds, can be defined. On the other hand, if a large number of input sources intermittently converge on a cell through time, or if an individual input can vary greatly in its intensity through time, then a serious design problem arises: If the activities x_i are sensitive to large inputs, then why do not small inputs get lost in internal cellular noise? If the activities x_i are sensitive to small inputs, then why do they not all saturate at their maximum values in response to large inputs and thereby become incapable of processing analog differences in inputs across an entire network?

Grossberg (1973) has called this problem the *noise-saturation dilemma*. Grossberg (1973) proved mathematically that neurons which obey the membrane, or shunting, equations of neurophysiology (Hodgkin, 1964) can solve the noise-saturation dilemma if their bottom-up inputs and recurrent interactions are organized in on-center off-surround networks. Such a network is also called a *recurrent competitive field*, or RCF. In other words, RCFs keep their stored activities large enough to avoid being distorted by internal cellular noise, yet not so large as to activate cells maximally, saturate their responses, and destroy a record of analog input differences. A shunting on-center off-surround network can thus contrast-normalize and preserve the analog sensitivity of its cell activities in response to an input pattern, no matter how large the inputs to the network may be chosen.

After this initial discovery, theorems and computer simulations were provided for increasingly complicated non-recurrent and recurrent shunting on-center off-surround networks to demonstrate how they respond when their interaction strengths, feedback signal functions, and other network parameters are varied. The earliest analyses of this kind include those of Ellias and Grossberg (1975) and Grossberg and Levine (1975, 1976). Specialized shunting networks have hereby been classified in terms of their specific pattern processing and memory storage properties, thereby providing a storehouse of networks to serve as a resource for explaining and predicting a wide range of behavioral and brain data. Such networks have also helped to solve technological problems wherein stable content-addressable memories are needed. Increasingly general theorems have been proved, using both Lyapunov functions and functionals, about how recurrent cooperative-competitive networks can be designed so that they always converge to stable limiting patterns (e.g., Cohen & Grossberg, 1983 (Cohen-Grossberg theorem and Lyapunov function); Grossberg, 1978a, 1978b, 1980). These theorems clarify what design features are essential for effective pattern processing across many specialized networks. The results include the Lyapunov function that was popularized by Hopfield (1984).

All of these results demonstrated that maintaining a *balance* between excitation and inhibition in a neural network is essential for the network to be able to process distributed patterns of inputs and signals without experiencing the catastrophes of noise or saturation. The results also show that the simplest properties of shunting on-center off-surround networks can only ensure that cell activities remain sensitive to the *relative* sizes of inputs and recurrent signals, but not that they will use the full dynamic range that each cell can support. In other words,

additional mechanisms are needed to “anchor” the activities of networks to exploit their full dynamic range. This article shows how such anchoring can be achieved by incorporating synaptic scaling mechanisms of homeostatic plasticity within recurrent on-center off-surround networks in such a way that their pattern processing capabilities, including the ability to make winner-take-all decisions, is preserved. These results suggest how BDNF may homeostatically scale the strengths of excitatory and inhibitory synapses in opposite directions (Rutherford, Nelson, & Turrigiano, 1998).

2. How stored patterns depend on feedback signal functions in a recurrent competitive field

The theorems of Grossberg (1973) analyzed how the feedback signal functions in recurrent on-center off-surround networks whose cells obey membrane, or shunting, equations (Fig. 1(a)) transform input patterns before they are stored in short term memory as equilibrium activity patterns. In these simplest networks, the on-center of self-excitatory feedback is narrow, and the off-surround of recurrent lateral inhibition reaches all other cells. Such a network is defined by

$$\dot{x}_i = -Ax_i + (B - x_i)(I_i + f(x_i)) - x_i \left[J_i + \sum_{k \neq i} f(x_k) \right]. \quad (1)$$

In (1), x_i is the activity of the i th cell, or cell population; A is the passive decay rate; B is the excitatory saturation point of cell activity; I_i is the excitatory input to the i th cell; $f(x_i)$ is the on-center positive feedback signal; J_i is the inhibitory input to the i th cell; and $\sum_{k \neq i} f(x_k)$ is the negative feedback from the off-surround. Eq. (1) may be derived from the following equation for cell activity, or voltage $V(t)$:

$$C \frac{d}{dt} V = (V^p - V)g^p + (V^+ - V)g^+ + (V^- - V)g^-, \quad (2)$$

where C is capacitance; the constants V^+ , V^- , and V^p are excitatory, inhibitory, and passive saturation points of V , respectively, and g^+ , g^- , and g^p are conductances that can be changed by inputs (Hodgkin, 1964). In (1), $x_i = V$, $A = g^+$, $V^- = V^+ = 0$, $B = V^+$, and g^+ and g^- are the total on-center and off-surround inputs, respectively. The choice of the feedback signal function f determines how an input pattern is transformed before it is stored in short-term memory (i.e., before the network reverberates the stored pattern for all time), and indeed whether it will be stored in short-term memory at all.

The theorems in Grossberg (1973) assumed that inputs were on until time $t = 0$, when they were shut off to allow the network to transform and store the input pattern in short-term memory using its recurrent interactions. The theorems included all possible initial values $x_i(0)$ of the activities, corresponding to the effect of all possible input patterns. As shown in Fig. 1(b), if the signal function is linear (e.g., $f(w) = Aw$), then the initial input pattern is preserved. If the signal function is slower-than-linear (e.g., $f(w) = Aw/(B + w)$), then all differences in the input are eliminated as time goes on, and a uniform pattern of activities is stored. In both of these cases, noise is amplified. If a signal function is faster-than-linear (e.g., $f(w) = Aw^2$), then noise is suppressed. In fact, noise is suppressed so vigorously that only the cell, or cell population, with the largest input survives the competition, and its activity is stored in short term memory. This is thus a winner-take-all (WTA) network.

In order to enable cells with activities less than the maximum to be stored in short-term memory, a sigmoid cell function suffices (e.g., $f(w) = Aw^2/(B^2 + w^2)$), because it is a hybrid of the

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