Studies in Applied Mathematics, Vol. LII, No. 3, September 1973.

Contour Enhancement, Short Term Memory, and Constancies in Reverberating Neural Networks

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A model of the nonlinear dynamics of reverberating on-center off-surround networks of nerve cells, or of cell populations, is analysed. The on-center off-surround anatomy allows patterns to be processed across populations without saturating the populations' response to large inputs. The signals between populations are made sigmoid functions of population activity in order to quench network noise, and yet store sufficiently intense patterns in short term memory (STM). There exists a quenching threshold: a population's activity will be quenched along with network noise if it falls below the threshold; the pattern of suprathreshold population activities is contour enhanced and stored in STM. Varying arousal level can therefore influence which pattern features will be stored. The total suprathreshold activity of the network is carefully regulated. Applications to seizure and hallucinatory phenomena, to position codes for motor control, to pattern discrimination, to influences of novel events on storage of redundant relevant cues, and to the construction of a sensory-drive heterarchy are mentioned, along with possible anatomical substrates in neocortex, hypothalamus, and hippocampus.

1. Introduction

Recent experimental studies of the hippocampus (Anderson *et al*, 1969) have suggested that its cells are arranged in a recurrent on-center off-surround anatomy. The main cell type, the pyramidal cell, emits axon collaterals to interneurons. Some of these internueurons feed back excitatory signals to nearby pyramidal cells. Other interneurons scatter inhibitory feedback signals over a broad area. Recurrent on-center off-surround networks are found in a variety of neural structures other than hippocampus; for example, neocortex (Stefanis, 1969) and cerebellum (Eccles *et al*, 1967). What does this fundamental principle of neural design accomplish? What can a recurrent, or reverberating, network do that a non-recurrent, or feed-forward, network cannot? In the special case of the hippocampus, one can in particular ask: How does this anatomy contribute to seizure

* Supported in part by the Alfred P. Sloan Foundation and the Office of Naval Research (N00014-67-A-204-0051).

activity in response to topical application of either strychnine or penicillin crystals (Anderson *et al*, 1969)? Can one functionally interpret the suggestion that afferent fibers to the hippocampus excite the inhibitory interneurons directly (Anderson *et al*, 1969), thereby creating a feed-forward inhibitory action, in addition to the recurrent inhibition activated by pyramidal cell output?

This paper describes mathematical results that seem to be relevant to these issues. We study a model that emphasizes the properties of interacting populations of cell sites. These populations can be interpreted either as populations of small membrane patches on individual cells, or as populations of whole cells. The model is perhaps more general since it is defined by mass action laws involving excitatory and inhibitory processes. As in the paper of Wilson and Cowan (1972), we assume that the cell sites in a given population are distributed in such a fashion that their interactions are spatially random and densely distributed within each population and between population pairs. Our equations differ from those of Wilson and Cowan, however. Their excitatory and inhibitory interactions combine additively before they are further processed; our interactions are of shunting type (Hodgkin, 1964; Sperling, 1970; Sperling and Sondhi, 1968). Differences in the applicability of these equations are discussed in Section 5.

Denote the average excitation at time t of the ith population v_i by $x_i(t)$, $i = 1, 2, \ldots, n$. We will study how these averages are transformed through time by recurrent on-center off-surround interactions (Figure 1); that is, each population excites itself and inhibits other populations via the system of equations

$$\dot{x}_i = -Ax_i + (B - x_i)f(x_i) - x_i \sum_{k \neq i} f(x_k) + I_i,$$

where $i = 1, 2, \ldots, n$, and $x_i (\leq B)$ is the mean activity of the ith cell, or cell population, v_i of the network. Four effects determine this system: (1) exponential decay, via the term $-Ax_i$; (2) shunting self-excitation, via the term $(B - x_i)f(x_i)$: (3) shunting inhibition of other populations, via the term $-x_i \sum_{k \neq i} f(x_k)$; and (4) externally applied inputs, via the term I_i. The function $f(w)$ describes the mean output signal of a given population as a function of its activity w. In vivo, $f(w)$ is

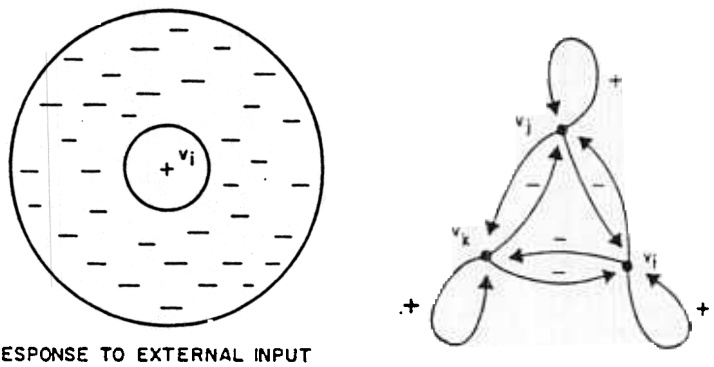

Figure 1. Recurrent on-center off-surround network

often a sigmoid function of w (Kernell, 1965a, b; Rall, 1955a–c). The mathematical results below will show that this is an important property of the above model for the effective processing of signals in noise.

First, why is an on-center off-surround anatomy needed at all? It has been noted that such an arrangement permits contour enhancement of sensory information (Ratcliff, 1965). We will show that a more basic property can be achieved as well. In many neural systems, noise cannot be avoided, if only because they operate near the quantum range, as in the case of sensory systems. Also cells, and therefore cell populations, have finite saturation levels in response to external inputs. Given these facts, consider the processing of a pattern of input signals delivered to an ensemble of noninteracting cell populations. If the signals are too small, they can be lost in the noise. If they are too large, they can saturate their respective populations, thereby creating a uniform pattern of excitation across populations and destroying all information about the input pattern. In short, noninteracting cell populations are caught between two unsatisfactory extremes. To avoid these extremes in the noninteracting case, input intensities must be restricted to a very narrow range, and one loses the ability to process arbitrary patterns with fluctuating input intensities. On-center off-surround interactions solve this problem: they permit effective processing of arbitrary input patterns across populations, without saturation, even if the inputs are large.

Recurrent on-center off-surround anatomies are capable of short term memory (STM); that is, they can reverberate a pattern of activity distributed over cell populations for an indefinite interval of time. This reverberation can also be switched off rapidly by inhibitory inputs if a new pattern is delivered by external sources; the decay rates of individual cells can be large after the excitatory reverberating loop is broken by inhibition, even if the reverberation through an active excitatory loop is long lived. See Figure 2. A single layer of nonrecurrent on-center off-surround network has limited STM capabilities. Such a network can store a pattern only if it has small decay rates. It will therefore also recover slowly

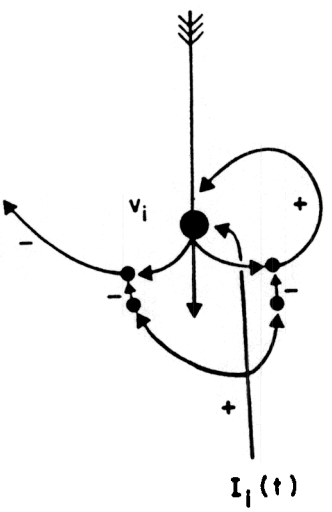

Figure 2. Input inhibits old reverberation as it imposes a new pattern to be reverberated.

from inhibition aimed at shutting the pattern off. Consequently, its response to new inputs will be biased by the lingering traces of old inputs. In a psychological context, the use of reverberation as a mechanism of STM has been suggested (Estes, 1972; Grossberg 1971a). For example, from operant conditioning experiments, one is led to seek reverberatory processes that can maintain in short term storage internal representations of sequences of external events until later rewards or punishments occur and transfer the memory of these sequences to long term storage (Grossberg, 1971a). The interplay of reverberatory and arousal processes on this transfer process has been discussed on various levels, for example neurophysiologically (John 1966) and psychologically (Grossberg, 1971a, 1972a, 1972b).

The STM capabilities of recurrent networks carry with them possible difficulties. If these networks can reverberate patterns imposed by external inputs, then why don't they also reverberate their own noise indefinitely, thereby flooding the network with its own noise? The answer is that they do, if the signal function $f(w)$ is improperly chosen. For example, if $f(w)$ is a linear function of w, or a function that grows slower than linearly, such as $f(w) = w(1 + w)^{-1}$, then noise will be amplified and reverberated. Note that if $f(w)$ is linear, then no contour enhancement will occur; the $f(w)$ that does provide contour enhancement is chosen, first and foremost, to prevent amplification and reverberation of noise. If $f(w)$ grows faster than linearly, such as $f(w) = w^2$, then this problem is avoided. Sufficiently small noise values will dissipate through time. If a brief, but sufficiently intense, input pattern is imposed on the noise, however, then two things happen. First, all populations which receive the largest input in the pattern will suppress the activity in all other populations, including the noise. Second, *normalization* occurs: the total activity $x(t) = \sum_{k=1}^{n} x_k(t)$ of all the populations approaches a fixed positive limit through time. The first property shows that an extreme form of contour enhancement occurs: only the peaks of the input pattern survive. If one population of the network receives more input than any other, then the network "chooses" this population and quenches all others. The second property shows that the system precisely regulates its total activity, and can store the activity of certain populations indefinitely in STM by reverberating their activity through excitatory recurrent interneuronal loops.

The first property is too strong: too much of the pattern is suppressed in the attempt to suppress the noise. How can this be avoided? The way is to choose $f(w)$ so that it grows faster than linearly for small values of w, and (approximately) linearly at larger values of w. Then noise dissipates, and there exists a *quenching threshold.* This means that, given a sufficiently energetic pattern of inputs, the activities of populations which fall below the threshold are quenched (including noise) and those which fall above the threshold are contour enhanced and stored in STM.

In the subsequent discussion, let the existence of a constant quenching threshold be assumed. Then the determination of which populations will be quenched, in the presence of sustained inputs, depends on the total strength $I = \sum_{k=1}^{n} I_k$ of the input to all populations. Consider Figure 3. In Figure 3, a nonspecific arousal input J_A combines with a specific input J_i at each population v_i. Two important cases arise. In Case 1, J_A and J_i combine multiplicatively to influence the activity level x_i. Input J_A is said to *shunt* the activity level (Grossberg, 1973). In Case 2,

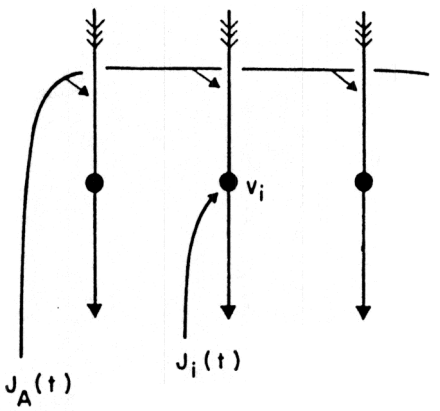

Figure 3. Interaction of arousal and specific inputs.

J_A and J_i combine additively to influence the activity level x_i. Consider Case 1 for definiteness. Then the input J_A does not change the *relative* input levels to the various populations. (In Case 2, a large J_A tends to uniformize any pattern of J_i's.) Let J_A be parametrically increased to ever higher levels. One hereby increases the number of populations that receive enough input to exceed the quenching threshold and are stored in STM. Conversely, reducing J_A decreases the number of populations that will be stored. Thus, given an input pattern in which many inputs are close to each other in relative size, one way to "make a choice" between populations is to lower the arousal level of the input until only one population exceeds the quenching threshold; in common parlance, put the network in a quiet place. By contrast, one way to make as many cues as possible relevant to further network processing is to substantially increase the arousal level. Thus, suppose that a "novel" stimulus excites the network's nonspecific arousal source. Then all recently presented cues can have their network representations brought into STM to play a part in further network processing, including the sampling and subsequent learning of motor responses (Grossberg, 1973). In this way, novel or unpredictable events can bring all possible information about presently available cues into an active state, to enhance the network's ability to deal with the unexpected situation. Using this mechanism, one can approach the problem of how redundant relevant cues are learned (Trabasso and Bower, 1968).

A particularly interesting case arises when the input J_i, unbolstered by a sufficiently large value of J_A, is too small to drive x_i above the quenching threshold. Then any mechanism that inhibits the action of J_A at a given population can prevent this population from reverberating in STM. Figure 4 provides two examples that illustrate this concept. In Figure 4a, the inhibitory input prevents arousal from activating x_i, but x_i's excitatory recurrent collateral bypasses the inhibition. Thus, if population v_i is already reverberating, it continues to do so when the inhibitory input is activated. By contrast, suppose that a new input pulse to v_i occurs simultaneously with inhibition of arousal. Then the afferent inhibition controlled by the new input briefly inhibits the reverberation to allow the new input to begin reverberating without bias due to the previously reverberated input. The new input cannot reverberate, however, because inhibition of arousal prevents

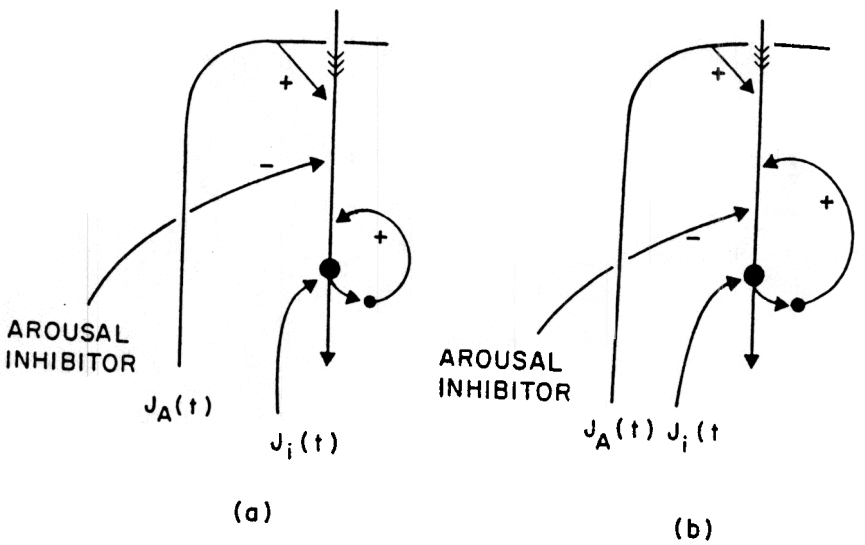

Figure 4. Arousal inhibitors can preserve old reverberations but prevent new reverberations.

it from exceeding the quenching threshold. In short, this type of arousal-inhibition can prevent transfer of new inputs into STM, but permits storage of old inputs in STM. By contrast, in Figure 4b, inhibition of arousal also inhibits STM of old and new inputs.

The above properties have many possible interpretations. For example, suppose that each population in the network responds to lines (Hubel and Wiesel, 1968), orientations (Blakemore and Campbell, 1969), or other geometrical features of external objects. Then varying the arousal level and/or arousal-inhibitors can determine whether a unique geometrical feature of the visual scene, or some particular combination of features, will control motor behavior.

In a similar fashion, particular features of a spatial pattern, such as its boundary, can be stored by the network, while other parts of the pattern are quenched. Suppose for example that the n interacting populations v_i form a rectangular grid in a plane. Choose n very large, and pack the populations closely together to achieve a good spatial resolution of external inputs. Let external inputs be delivered to the populations as follows. If an excitatory input is delivered to v_i, then inhibitory inputs are delivered to all v_k in a small circular region around v_i (non-recurrent on-center off-surround input field). Suppose that the strength of inhibition depends on the distance of v_k from v_i, and let the same be true for all $i = 1, 2, \ldots, n$. Let a filled triangle be presented to the field. One readily computes that the populations that are excited by the triangle's vertices receive the largest net excitatory input, the populations that are excited by the remainder of the triangle's boundary receive lesser excitatory inputs, and the populations excited by the deepest parts of the triangle's interior receive the smallest excitatory inputs. If the arousal level is sufficiently high, this pattern can be preserved as delivered to the network, apart from the occurrence of normalization. Smaller arousal levels can, however, either quench the interior of the triangle and contour enhance its boundary, or can quench all but the triangle's vertices.

We have delivered external inputs via a nonrecurrent on-center off-surround input field having a limited off-surround to suggest what might happen when the recurrent off-surround itself falls off with distance; namely, we suggest that if the triangle excites a recurrent field of this type, then the field can contour enhance the triangle boundary, especially its vertices, and can then preserve either vertices, boundary, or the entire contour enhanced pattern. The contour enhancement and quenching of significant features in other geometrical figures can be similarly analysed.

Whereas variations in arousal level can yield useful changes in network processing in the present context, overarousal can create inefficient network processing in certain anatomies. For example, it can create massive response interference and an inability to "pay attention" in networks capable of learning long lists (Grossberg and Pepe, 1971). It can produce "emotional depression" in networks which describe aspects of the interaction between drives and rewards (Grossberg, 1972b); the depressed state corresponds to a reduction in the network's incentive motivational response to emotionally charged cues.

The flattening of a sigmoid $f(w)$ at large values of w (beyond the approximately linear range) can, in principle, cause amplification of noise, if the network is overaroused. Such a flattening cannot be avoided *in vivo* because cells have finite maximal firing rates and other bounded constraints on their operating characteristics. It is proved below, however, that robust choices of parameters exist for which the flattening of the sigmoid does not deleteriously affect network processing. The function $f(w)$ is determined by such parameters as the distribution of signal (or spiking) thresholds and of afferent synapses per cell within each population (Wilson and Cowan, 1972). The above results show that varying the function $f(w)$ can dramatically change the pattern features that are stored by the network in STM. Thus, by changing the relative number of cells having a given threshold *within* each population, one can change the pattern features that will be stored by interactions *between* populations.

A variant of the overarousal theme is embodied by the question: how can such a network go into seizure? *Any* operation that creates enough activity in a population to exceed its quenching threshold will cause the population activity to be amplified and maintained in STM. This can be done by creating a sufficiently large excitatory signal (or other perturbation of the population), or by reducing spiking thresholds thereby indirectly increasing noise levels), or by removing inhibitory feedback. If, for example, such cell populations subserve particular sensory impressions, such as in the visual cortices, then these impressions can be created in the absence of external sensory cues if the quenching threshold is exceeded by any other mechanism. If such cell populations control the elicitation of sensory memories, such as in the temporal cortices (Penfield, 1958), then such memories, or memory fragments, can be elicited in the absence of external sensory cues whenever the quenching threshold is exceeded. These "hallucinatory" effects (West, 1962) can be created (say) if sensory deprivation or drugs create a reduction in inhibitory controls, an increase in arousal level, or a decrease in cell spiking thresholds.

The property of normalization creates stable overall activity levels at which the network normally operates in its suprathreshold range. This property can be used to accomplish a variety of tasks by hooking up the network as a component in different overall input processing schemes. For example, it can establish position

codes for motor control. This use addresses the question: how does one prevent overshoots and undershoots of orienting responses to localized lights and sounds using our eyes, head, and neck, when these cues have fixed positions but variable intensities? An idealized example is sketched below to convey the basic idea without a pretense of physiological completeness. Consider a network of n populations whose inputs differentially excite a given subset of populations in response to a particular pattern of sensory excitation. For example, suppose that a spot of light in a given retinal position excites a particular population preferentially. Let each population send axonal connections to the various eye muscles, and let the strength of each connection depend on the retinal position represented by the population. The problem is to construct connections which will guarantee that the eye moves towards an arbitrary, but fixed, peripheral spot and fixates on the spot. In this context, normalization prevents undershoots or overshoots in response to a spot of fixed position but variable suprathreshold luminance by factoring out fluctuations in total input intensity. The position code for eye movements is then established by differential *relative* excitation of populations and by the strength of their axonal connections to the eye muscles.

In a similar fashion, such a mechanism can, in principle, maintain a fixed posture in agonist and antagonist muscle pairs. See Figure 5 for an idealized example. In Figure 5, v_i sends a fixed input to the (abstract) muscle M_i, $i = 1, 2$. The relative sizes of the inputs can be changed by descending inputs I_i that move the muscles. In the absence of such descending inputs, the pattern of $v_i \rightarrow M_i$ signals is fixed. In the absence of descending inputs, the fixed total output from v_1 and v_2 can maintain a fixed total muscle length in agonist plus antagonist during maintained postures. The muscle spindles can prevent external forces from altering the muscular position imposed by the signals from v_i (Matthews, 1971).

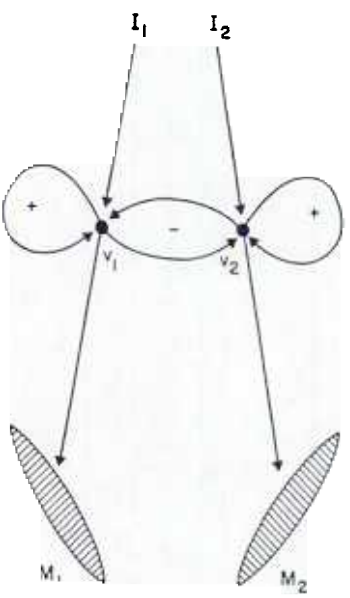

Figure 5. An idealized mechanism for maintaining a posture in the absence of continual inputs I_i

Normalization has other uses as well. An analysis of instrumental conditioning (Grossberg, 1971a; 1972a, 1972b) shows that the total input from sensory processing areas $\mathcal{S}$ (such as neocortex) to internal drive processing areas $\mathcal{D}$ (such as hypothalamus) should have an upper bound independent of the number of sensory channels which are active at any time. This upper bound is needed to prevent the firing of cells from $\mathcal{D}$ to $\mathcal{S}$ except when they receive a suitable combination of inputs. See Figure 6. In Figure 6, a sufficiently large input from internal homeostats designating that a particular drive needs satisfaction *and* an input from a conditioned reinforcer in $\mathcal{S}$ that is compatible with this drive must combine at cells such as v_3 in $\mathcal{D}$ before these cells can fire. If inputs from $\mathcal{S}$ alone could fire v_3, then the network would seek to persistently satisfy an already satiated drive; hence the bound on total $\mathcal{S} \rightarrow \mathcal{D}$ input.

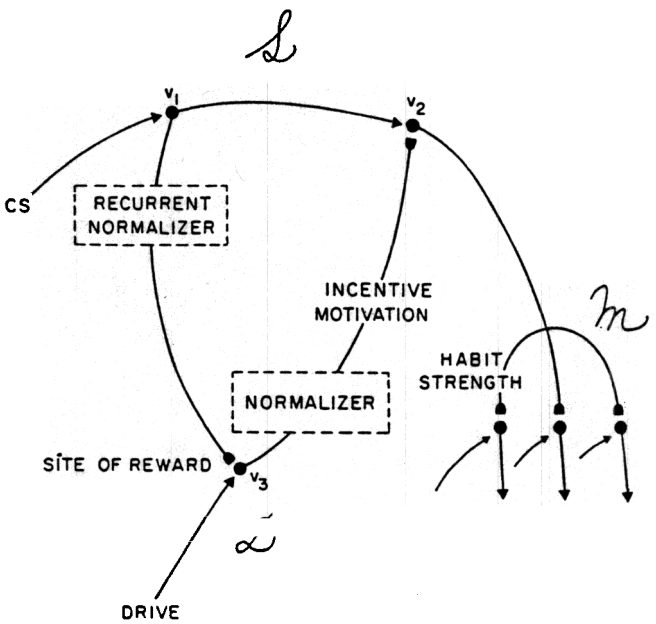

Figure 6. Two normalizers are needed to regulate total input.

The output from $\mathcal{D}$ to $\mathcal{S}$ supplies "incentive motivation", or a "Go" mechanism (Grossberg, 1971a; Logan, 1969; N. Miller, 1963), for activating the motor output at $\mathcal{M}$ controlled by the conditioned reinforcer in $\mathcal{S}$. An upper bound on total $\mathcal{D} \rightarrow \mathcal{S}$ output must also exist to prevent cells, such as v_2, in $\mathcal{S}$ from firing at unappropriate times and learning irrelevant sensory discriminations or motor acts at $\mathcal{M}$. These two upper bounds can be achieved by recurrent on-center off-surround networks.

These on-center off-surround networks can perform other important tasks in addition to guaranteeing the upper bounds. As noted above, the network that bounds $\mathcal{S} \rightarrow \mathcal{D}$ output can also influence which of the cues represented by $\mathcal{S}$ will reverberate in STM. The network that bounds $\mathcal{D} \rightarrow \mathcal{S}$ output can also prevent learning except in response to sensory cues which are compatible with the network's drive needs at any given time; cf., hippocampus (Olds, 1969). Such a network can

create a sensory-drive heterarchy (Grossberg, 1972b). Consider the situation in which a student regularly eats meals in spite of the prolonged absence of a sexual partner. A positive, but nonprepotent drive can control motor behavior in the presence of compatible sensory cues (e.g., eating food if hungry), if cues compatible with the prepotent drive are unavailable (e.g., absence of sexual partner). The combination of sensory cues and drive level which controls behavior at a given time can be normalized and stored in STM by the recurrent network. A steady baseline of incentive motivation to activate compatible motor output can hereby be achieved. Interruption of $\mathscr{D} \to \mathscr{S}$ feedback by ablation or other means can prevent transfer from STM to LTM by preventing the sampling by cells in $\mathscr{S}$ of the patterns to be learned at $\mathscr{M}$ (Milner, 1958).

Normalization can also be used as one stage in the construction of anatomies whose terminal cells respond only to prescribed features of a sensory pattern (Hubel and Wiesel, 1968; Grossberg, 1970, 1972c). It does so by averaging away fluctuations in total network activity and allowing the network to process a pattern's relative weights. In special cases, this construction yields cells whose responses exhibit color or brightness constancies (Grossberg, 1972c), sensitivity to particular velocities (Grossberg, 1970), etc. These examples illustrate that an on-center off-surround anatomy has properties which take on significant, and sometimes surprising, meanings when the network is hooked up at different locations in the overall processing of neural information.

We note in passing that the systems herein are examples of "dissipative structures" (Nichols, 1971), and contribute to the discussion of how patterns of activity can develop and be self-sustained within an interactive system.

In Section 2, the equations that define our networks are presented. Section 3 qualitatively outlines the main phenomena to be reported. Section 4 states the theorems that justify the comments in Section 3. These theorems are proved in the Appendix. Section 5 compares the equations of Section 2 with those of Wilson and Cowan.

2. Network equations

In general, each population v_i contains both excitatory (v_i^+) and inhibitory (v_i^-) subpopulations of cells. See Figure 7. Consider the excitatory cells v_i^+ for definiteness. Suppose on the average that the cell sites in v_i^+ receive randomly distributed afferent pathways from within each subpopulation of the network. Let there be b_i excitable sites in v_i^+, and let $x_i(t)$ be the number of active sites at time t. Three effects determine our equations:

(1) *Spontaneous decay of activity:* Active sites become inactive at a fixed rate. Hence $x_i(t)$ decreases at a rate proportional to $x_i(t)$, say $a_i x_i(t)$.

(2) *Shunting inhibition:* Active sites are inhibited at a rate jointly proportional to the number of active sites and to the total (randomly distributed!) inhibitory input $I_i^-(t)$. This rate is proportional to $x_i(t)I_i^-(t)$.

(3) *Shunting excitation:* Inactive sites are excited at a rate jointly proportional to the number of inactive sites and to the total (randomly distributed!) excitatory input $I_i^+(t)$. This rate is proportional to $(b_i - x_i(t))I_i^+(t)$. In all,

$$\dot{x}_i = -(a_i + I_i^-)x_i + (b_i - x_i)I_i^+, \tag{1}$$

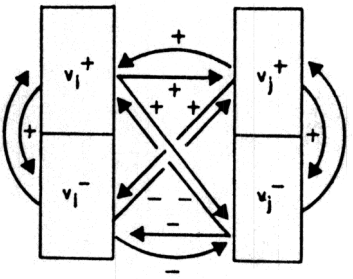

Figure 7. Interactions between excitatory and inhibitory subpopulations.

$i = 1, 2, \ldots, n$. The initial data satisfy the inequalities

$$0 \leq x_i \leq b_i, \qquad i = 1, 2, \ldots, n. \tag{2}$$

Inspection of (1) shows that the inequalities (2) then hold for all $t \geq 0$.

A similar analysis applies to inhibitory cells. Let $y_i(t)$ be the number of active sites in the inhibitory subpopulation v_i^- at time t. Let the total excitatory (inhibitory) input to v_i^- at time t be $J_i^+(t)(J_i^-(t))$. Then y_i is governed by an equation of the form

$$\dot{y}_i = -(A_i + J_i^-)y_i + (B_i - y_i)J_i^+, \tag{3}$$

$i = 1, 2, \ldots, n$, subject to the constraints

$$0 \leq y_i \leq B_i, \qquad i = 1, 2, \ldots, n. \tag{4}$$

The above equations have the same form as passive membrane equations (Hodgkin, 1964; Sperling, 1970; Sperling and Sondhi, 1968); in this context, the inputs I_i^+, I_i^-, J_i^+ and J_i^- represent (average) conductance changes. Thus our analysis formally applies to suitable interactions either between individual cells or between cell populations.

Total inputs are often sums of inputs from other cells (or cell populations) and external influences. For example, let

$$I_i^+ = \sum_{k=1}^{n} F_{ki}^+(x_k) + K_i^+(t), \tag{5}$$

$$I_i^- = \sum_{k=1}^{n} F_{ki}^-(y_k) + K_i^-(t), \tag{6}$$

$$J_i^+ = \sum_{k=1}^{n} G_{ki}^+(x_k) + L_i^+(t) \tag{7}$$

and

$$J_i^- = \sum_{k=1}^{n} G_{ki}^-(y_k) + L_i^-(t). \tag{8}$$

The functions $K_i^+(t)$, $K_i^-(t)$, $L_i^+(t)$ and $L_i^-(t)$ are external inputs. The signal strength

functionals F_{ki}^+, F_{ki}^-, G_{ki}^+, and G_{ki}^- determine how mean activities within the excitatory and inhibitory subpopulations of v_k are converted into mean excitatory and inhibitory signals to the excitatory and inhibitory subpopulations of v_i. For example, one can choose

$$[F_{ki}^+(x_k)](t) = \int_0^t x_k(v) \exp\left[-\int_v^t u_k(\xi)\, d\xi \right] dv,$$

or

$$[F_{ki}^-(y_k)](t) = \frac{v_{ki} y_k(t - \tau_{ki})}{w_{ki} + y_k(t - \tau_{ki})},$$

etc.

This paper studies influences of varying signal strength functionals in a setting that minimizes other effects. Hence we consider the special case in which the excitatory and inhibitory subpopulations of each population have the same parameters and receive the same inputs. That is, the excitatory and inhibitory subpopulations of a given population are indistinguishable with respect to every input source, and contain the same number of membrane sites constructed from similar materials. Then $a_i = A_i$, $b_i = B_i$,

$$F_{ki}^+(w) = G_{ki}^+(w),\ F_{ki}^-(w) = G_{ki}^-(w),\ K_i^+ = L_i^+, \text{ and } K_i^- = L_i^-.$$

In this situation one readily proves that the differences $(x_i - y_i)(t)$ converge exponentially to zero as $t \to \infty$, given otherwise arbitrary inputs. Hence the excitatory and inhibitory subpopulations can be lumped together.

We furthermore impose a recurrent on-center off-surround anatomy on the lumped model. See Figure 1. This anatomy is made as homogeneous and simple as possible by imposing the following assumptions:

(1) all numerical parameters are independent of population;

(2) all signals are transmitted instantly; the signal strength functionals are functions.

These constraints lead to the system

$$\dot{x}_i = -(A + I_i^-)x_i + (B - x_i)I_i^+, \tag{9}$$

$i = 1, 2, \quad , n$, where

$$I_i^+ = f(x_i) + K_i^+(t) \tag{10}$$

and

$$I_i^- = \sum_{k \neq i} f(x_k) + K_i^-(t). \tag{11}$$

To study reverberations of system (9)–(11), we always set the external inputs K_i^+ and K_i^- equal to zero, yielding the nonlinear system

$$\dot{x}_i = -\left[A + \sum_{k \neq i} f(x_k)\right] x_i + (B - x_i) f(x_i), \tag{12}$$

$i = 1, 2, \ldots, n$. Once reverberations are understood, the inputs K_i^+ and K_i^- can be switched on during a finite time interval $[-T, 0]$. Given prescribed initial data at $t = -T$, these inputs will determine a particular distribution of terminal

values $x_i(0)$, $i = 1, 2, \ldots, n$. The results on reverberations can then predict how the values $x_i(0)$ will be transformed as $t \to \infty$.

System (12) says that each state v_i excites itself and inhibits all other states with equal weight. This situation can arise even if the inhibitory fields of all populations do not coincide. For example, consider Figure 8. In Figure 8, only the populations

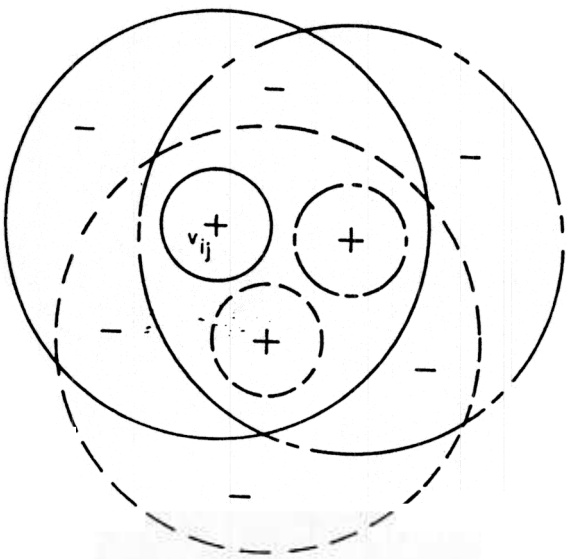

Figure 8. Overlapping inhibitory surrounds

v_{i_j}, $j = 1, 2, \ldots, m$, receive excitatory inputs $I_{i_j}^+$ at times $[-T, 0]$. Before time $t = -T$, all populations in the network have returned to their zero equilibrium values. The inhibitory fields of each excited population v_{i_j} inhibit all other excited populations v_{i_k}. Inhibited populations which do not receive excitatory inputs can be deleted from the network, since they start out with essentially zero activity and are inhibited thereafter. Thus system (12) includes anatomies in which inhibitory fields of different populations are not the same, but those populations which are excited by external inputs in a given time interval all inhibit each other. System (12) also includes cases in which the strength of inhibitory interactions decreases as a function of distance, if we assume that the excited populations are sufficiently close to each other that their mutual inhibitory interactions are approximately equally strong. Effects of inhomogeneous anatomies on widely separated populations will be considered in another place.

The results derived for system (12) carry over, with small modifications, to the more general system

$$\dot{z}_i = -A(z_i - U) + (V - z_i)I_i^+ - (z_i - W)I_i^- \tag{13}$$

where $W \leq U < V$, $I_i^+ = F(z_i)$, and $I_i^- = \sum_{k \neq i} F(z_k)$. Passive membrane equations generally contain the extra parameters U and W. Defining $x_i = z_i - W$, $B = V - W$, $C = A(U - W)$, and $f(x_i) = F(W + x_i)$, (13) becomes

$$\dot{x}_i = -\left[A + \sum_{k \neq i} f(x_k)\right] x_i + (B - x_i) f(x_i) + C. \tag{14}$$

System (14) differs from (12) only in the terms $C \geq 0$, which act like a uniformly distributed tonic input. These tonic terms tend to uniformize the distribution of random noise across populations (compare Theorem 8). The uniformizing effect can be overcome by sufficiently large external inputs (compare Theorem 9). The size of external inputs needed to drive the total activity $x(t) = \sum_{i=1}^{n} x_i(t)$ above the uniformizing range depends on the size of C, and in turn on the size of $U - W$. The term $U - W$ is generally much smaller than $B = V - W$, which is the maximum possible value of $x(t)$.

3. Summary of results

We will study how the choice of $f(w)$ influences the answers to two main questions:

(i) Under what circumstances is the reverberation persistent? transient?

(ii) How is the initial pattern of activity, that was laid down by previous external inputs, transformed as time goes on? Is there a limiting pattern of activity, or does the pattern oscillate indefinitely?

These concepts are made precise by the following definitions:

DEFINITION 1. The *total activity* is the function $x = \sum_{i=1}^{n} x_i$.

DEFINITION 2. The ith *pattern variable* is the function

$$X_i = x_i x^{-1}.$$

DEFINITION 3. The reverberation is *persistent* if there exists an $\varepsilon > 0$ such that $x(t) \geq \varepsilon$ for all $t \geq 0$.

DEFINITION 4. The reverberation is *transient* if $\lim_{t \to \infty} x(t) = 0$.

If the limit $\lim_{t \to \infty} X_i(t)$ exists, it will be denoted by Q_i. If the limit $\lim_{t \to \infty} x(t)$ exists, it will be denoted by E. Below we define the major limiting distributions and tendencies that will arise in our discussion, and thereby set the stage for this discussion.

DEFINITION 5. The limiting distribution is *fair* if

$$Q_i = X_i(0), \qquad i = 1, 2, \ldots, n.$$

DEFINITION 6. The limiting distribution is *uniform* if

$$Q_i = \frac{1}{n}, \qquad i = 1, 2, \ldots, n.$$

DEFINITION 7. The limiting distribution is *locally uniform* if $P_{i_j} = 1/m$, $j = 1, 2, \ldots, m$, where $1 < m < n$.

DEFINITION 8. The limiting distribution is *0 − 1* if $Q_i = 1$ for some i.

DEFINITION 9. The limiting distribution is *trivalent* if each Q_i assumes one of three values.

DEFINITION 10. The limiting distribution exhibits *quenching* if $Q_{i_j} = 0$ for $j = 1, 2, \ldots, m$.

DEFINITION 11. Let $M(t) = \max\{X_i(t) : i = 1, 2, \ldots, n\}$ and $m(t) = \min\{X_i(t) : i = 1, 2, \ldots, n\}$. The limiting distribution exhibits *contour enhancement* if $\dot{M}(t) \geq 0$ and $\dot{m}(t) \leq 0$, and neither of these derivatives is identically zero.

DEFINITION 12. The limiting distribution is *uniformized* if $\dot{M}(t) \leq 0$ and $\dot{m}(t) \geq 0$, and neither of these derivatives is identically zero.

DEFINITION 13. The reverberation is normalized if there exists a unique positive E_1 such that $E = E_1$.

The following paragraphs illustrate these definitions.

(*A*) *Fair Distribution.* Suppose that $f(w)$ is a linear function of w, as in Figure 9. Then $X_i(t)$ is constant, $i = 1, 2, \ldots, n$. Moreover, the reverberation is either transient or normalized. The conditions under which the reverberation is persistent are independent of the initial data $x_i(0)$. In other words, given persistence, the network can preserve an *arbitrary* pattern indefinitely. Moreover, if $x(0)$ is too small, the network will amplify the total activity until E_1 is reached, whereas if $x(0)$ is too large, activity will dissipate until E_1 is reached.

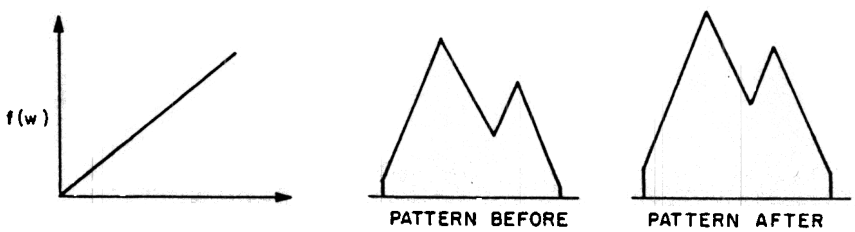

Figure 9. Fair distribution.

The fair signal function unfortunately amplifies noise in the absence of signals as vigorously as it amplifies signals.

The existence of normalization in recurrent networks constrains the possible sensory codes that these networks can sustain. Measurement of the absolute sizes of spiking frequencies given off by a cell, or cell population, in a recurrent network can be misleading. A code based on relative sizes of spiking frequencies across populations focuses on pattern transformations. To determine such a code, an experimentalist must simultaneously measure from a sample of populations. Fluctuations in signals from a single population need not be due to changes in $X_i(t)$, as this example shows; only $x(t)$ need be changing. In some of the examples below, both $x(t)$ and $X_i(t)$ can change through time, although the limits E and Q_i are ultimately approached, with E determined independently of the pattern Q_i. Thus, later readings of the relative spiking frequencies are often functionally more revealing than readings which are taken immediately after the offset of external input pulses. Macrides and Chorover (1972) describe results in the olfactory bulb which are in the spirit of this approach. The olfactory system is known to contain recurrent interactions (Freeman, 1969).

Previous papers (Grossberg, 1971b, 1972a) show that the learning capabilities of various networks are compatible with such a relative code. These networks can learn the pattern of relative excitation across an ensemble of cells, or cell populations, by classical or instrumental conditioning. They can reliably reproduce the learned pattern with an absolute intensity that depends on a complex interplay of various factors.

Deviations from a fair limiting distribution are due to whether $f(w)$ grows more slowly or more rapidly than linearly for various values of w; that is, whether the function $g(w) = w^{-1}f(w)$ is monotone decreasing or increasing.

(*B*) *0–1 or locally uniform distribution.* Suppose that $f(w)$ grows faster than a linear function, as in Figure 10. Again the reverberation is either transient or persistent. It is not necessarily normalized, however, unless $g(w)$ is convex. If the reverberation is persistent, then the limiting distribution exhibits an extreme form of contour enhancement and quenching whenever the initial pattern $X_i(0)$ is nonuniform: All pattern variables such that $X_i(0) < M(0)$ satisfy $Q_i = 0$, while the maximal pattern weights ($X_i(0) = M(0)$) receive all the weight asymptotically.

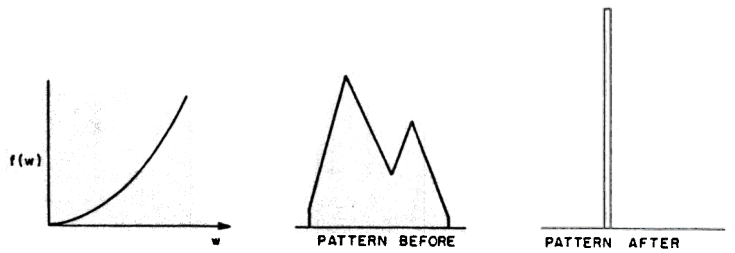

Figure 10. 0–1 Distribution.

In this example, when noise alone is present in the network, it continually dissipates (the reverberation is transient). If a sufficiently energetic pattern is imposed upon the noise, then the highest peaks of the pattern actively suppress both the noise and lesser pattern weights. Simultaneously, these peaks are accentuated, and the total energy of the pattern approaches a positive limit, which is unique if $g(w)$ is convex.

(*C*) *Uniform distribution.* Let $f(w)$ grow slower than linearly, as in Figure 11. Then pattern uniformization occurs. The reverberation is either transient or normalized. In the latter case, the limiting distribution is uniform.

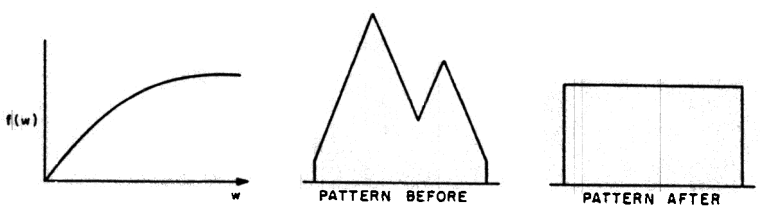

Figure 11. Uniform distribution.

Pattern uniformization can have unfortunate consequences in the presence of noise. Then all states which receive either external inputs or random noise will asymptotically have equal importance.

Functions $f(w)$ exist which combine all the three tendencies listed above; for example, the sigmoid function in Figure 12. Such a function $f(w)$ gives rise to a quenching threshold. Uniformly distributed tonic signals produce yet another uniformizing region. This region tends to uniformize the distribution of noise across populations, and thus to reduce the probability that noise can accumulate in a given population, and thereby create a persistent reverberation in the absence of signals. See Figure 13. Section 4 provides a rigorous discussion of how these regions interact to determine limiting distributions that are combinations of 0–1, fair. and uniform tendencies.

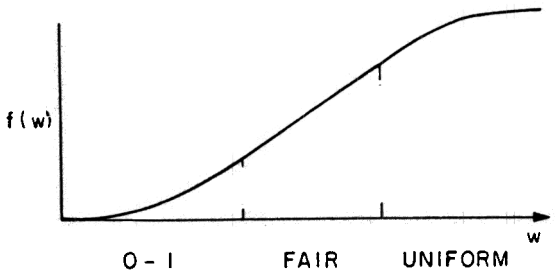

Figure 12. Sigmoid signal function.

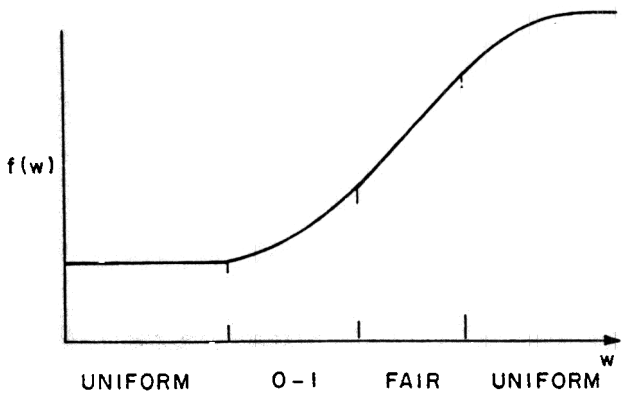

Figure 13. Tonically based Sigmoid signal function.

4. Mathematical results

This section lists results whose proofs are given in the Appendix. First the system

$$\dot{x}_i = -\left[A + \sum_{k \neq i} f(x_k)\right] x_i + (B - x_i) f(x_i), \tag{12}$$

$i = 1, 2, \ldots, n$, with $f(w)$ continuous and nonnegative, is transformed to show how the total activity $x = \sum_{i=1}^{n} x_i$ and the pattern variables $X_i = x_i x^{-1}$ interact. Below we assume that $x(0)$ and all $X_i(0)$ are positive to avoid trivialities. These assumptions imply that $x(t)$ and all $X_i(t)$ are positive for $t \geq 0$. If some $X_i(0) = 0$, then $X_i(t) = 0$ for $t \geq 0$, since v_i receives only inhibition in this case. Such a v_i can be deleted from the network without loss of generality. The notations $g(w) = w^{-1} f(w)$, $g_k = g(x_k)$, and $G = \sum_{k=1}^{n} X_k g_k$ will be used below.

PROPOSITION 1. (*Pattern Variables*). The following equations hold.

$$\dot{X}_i = B X_i \sum_{k=1}^{n} X_k (g_i - g_k), \tag{15}$$

$= 1, 2, \ldots, n$, and

$$\dot{x} = x(B - x)\left(G - \frac{A}{B - x}\right), \tag{16a}$$

or alternatively

$$\dot{x} = xG(B - AG^{-1} - x). \tag{16b}$$

Alternatively, (15) can be written as

$$\dot{X}_i = BX_i(g_i - G) \tag{17}$$

or as

$$\dot{X}_i = BX_i \sum_{k=1}^{n} X_k[g(X_i x) - g(X_k x)]. \tag{18}$$

Remarks: (1) By (15), the influence of v_k on v_i, namely $X_i X_k(g_i - g_k)$ is the negative of the influence of v_i on v_k, namely $X_k X_i(g_k - g_i)$. Thus the interactions between pattern variables are antisymmetric.

(2) By (17) and (16a), the direction of change of each X_i and x depends on the size of g_i and $A/(B - x)$, respectively, compared to $G = \sum_{k=1}^{n} X_k g(X_k x)$, which is a weighted average of all pattern variables and x. For example, suppose that $g(w)$ has the graph in Figure 14. If $g_i \geq G$, then by (17), $\dot{X}_i \geq 0$. This is depicted in Figure 14 by the arrows facing right. If $g_i < G$, then $\dot{X}_i < 0$, which yields arrows

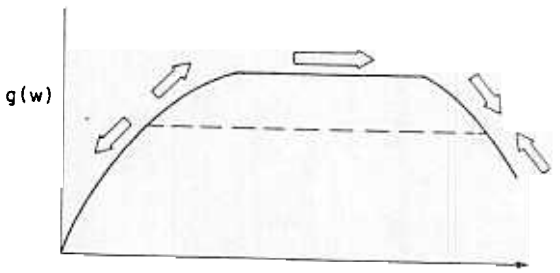

Figure 14. Convex $g(w)$ with fair intermediate range.

facing left. The collision of arrows to the right tends to produce a uniform distribution at large values of X_i. The parting of arrows to the left tends to produce contour enhancement of intermediate X_i values and quenching of small (for example, noisy) X_i values. The mathematics is complicated by the fact that an increase in X_i does not necessarily imply an increase in x_i, since x can be decreasing rapidly. In particular, even if X_i is increasing rapidly, x can be decreasing so rapidly that x_i is dragged down into a region where X_i begins to decrease. Thus the interaction between total activity and pattern variables can produce oscillations, as Proposition 4 illustrates. The results below study how these oscillations can be controlled.

PROPOSITION 2. (*Preservation of Order*). Suppose the states v_i are labelled in such a way that $X_1(0) \leq X_2(0) \leq \cdots \leq X_{n-1}(0) \leq X_n(0)$. Then $X_1(t) \leq X_2(t) \leq \cdots \leq X_{n-1}(t) \leq X_n(t)$ for all $t \geq 0$.

Remark: Consider the pattern depicted in Figure 15a. Proposition 2 says that no matter how the relative sizes of pattern weights are transformed, say as in Figure 15b, their ordering is preserved. This property does not hold in arbitrary anatomies. Henceforth, states will be labelled so that the inequalities $X_1 \leq X_2 \leq X_{n-1} \leq X_n$ hold.

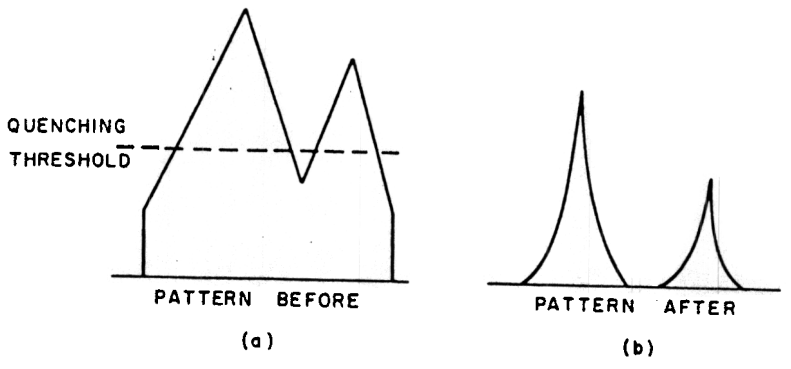

Figure 15. Preservation of order.

The next proposition describes an important condition under which limits of pattern and total activity variables always exist.

PROPOSITION 3. (*Pattern Limits and Energy Normalization*). Let all x_i, $i = 1, 2, \ldots, n$, vary in a region where $g(w)$ is monotonic. Then all the limits $Q_i = \lim_{t\to\infty} X_i(t)$ and $E = \lim_{t\to\infty} x(t)$ exist. Suppose $g(w)$ is monotone decreasing or constant. If $g(0) \leq A/B$, then $E = 0$. If $g(0) > A/B$, then E equals the unique positive solution of the equation

$$\sum_{k=1}^{n} Q_k g(Q_k x) = \frac{A}{B - x} \tag{19}$$

Suppose $g(w)$ is monotone increasing. E can equal zero only if $g(0) < A/B$. If $E \neq 0$, then E is a positive solution of (19). For general monotone increasing $g(w)$, (19) can have any number of solutions. If however, $g(w)$ is convex (as in Figure 9) then (19) has a unique positive solution if $g(0) \geq A/B$ and two positive solutions if $g(0) < A/B$. The smaller solution is unstable; the larger solution is stable.

Remarks: (1) If $g(w)$ is increasing, then (19) can have any number of solutions unless $g(w)$ is convex. In physical situations, convexity (or near convexity) is a likely property, since $f(w)$ is often sigmoid (Kernell, 1965a, b; Rall, 1955a, b, c; Wilson and Cowan, (1972) and the simplest $g(w)$ that can achieve this shape is convex, as in Figure 14. (2) The case $g(0) \geq A/B$ is undesirable, since even small noise values can be amplified and preserved indefinitely by the network. The inequality $g(0) < A/B$ allows noise to dissipate, but sufficiently large signals in the noise can persist. Theorems 2 and 4 describe systems in which signals can quench noise, and can use the noise to accentuate the contours of the pattern that is imposed on the noise. This contour enhanced pattern can then be preserved indefinitely by the network.

The following results show how particular choices of $f(w)$ determine the limiting distribution Q_i. The crucial fact is whether $f(w)$ grows faster or slower than linearly, or linearly, for particular values of w; that is whether $g(w)$ is increasing, decreasing, or constant. There exist $f(w)$'s with the following property: given a fixed initial pattern $X_i(0)$ and fixed $f(w)$, more than one limiting pattern Q_i can occur. The particular pattern Q_i that occurs depends on $x(0)$, or the initial "arousal" level: varying the arousal level can change the type of information processing

that occurs. For example, one can either preserve a given pattern or induce contour enhancement and quenching of this pattern, simply by varying $x(0)$:

THEOREM 1. (*Fair Distribution*). Let $f(w) = Cw$ for some $C > 0$. Then $Q_i = X_i(t) = X_i(0)$ for all $t \geq 0$. Let $D = BC - A$. If $D > 0$, the reverberation is persistent. If $D \leq 0$, the reverberation is transient. In fact, if $D \neq 0$,

$$x_i(t) = \frac{x_i(0)\exp(Dt)}{1 + x(0)CD^{-1}[\exp(Dt) - 1]},$$

whereas if $D = 0$,

$$x_i(t) = \frac{x_i(0)}{1 + x(0)Ct}. \tag{21}$$

In particular, if $D > 0$, then $\lim_{t\to\infty} x_i(t) = X_i(0)(B - AC^{-1})$, and thus energy normalization occurs as $t \to \infty$.

Remark: Given a linear $f(w)$, if any pattern can reverberate persistently, then even small values of noise will reverberate albeit with small relative weight in the presence of large signals. This can be a liability in such systems, since in the absence of signals, noise will be amplified, and will receive a large relative weight.

The next theorem shows that if $f(w)$ grows faster than linearly, then noise can dissipate, and large values can quench small values before they are amplified and maintained. To discuss this situation, we again use the notation $M(t) = \max\{X_i(t): i = 1, 2, \ldots, n\}$ and $m(t) = \min\{X_i(t): i = 1, 2, \ldots, n\}$. By Proposition 2, if $X_i(t_0) = M(t_0)$, then $X_i(t) = M(t)$ for all $t \geq t_0$. Similarly for $m(t)$.

THEOREM 2. (*0–1 Distribution*). Let $f(w) = wg(w)$, where $g(w)$ is continuous, nonnegative, and strictly monotone increasing. If $M(0) = m(0) = 1/n$, then $M(t) = m(t) = 1/n$ for all $t \geq 0$. Otherwise, $M(t)$ is monotone increasing faster than any function $X_i < M$, and $m(t)$ is monotone decreasing. Suppose moreover that the reverberation is persistent. (It is if $g(0) \geq A/B$, or if $g(0) < A/B$ and $x(0) \geq \hat{x}$, where $\hat{x}$ is the smaller root of

$$(n - K)M(0)g(M(0)x) = \frac{A}{B - x} \tag{22}$$

(g convex) and $X_K(0) < M(0) = X_{K+1}(0)$.) Then the limiting distribution is 0–1 or locally uniform, and satisfies $Q_1 = Q_2 = \cdots = Q_K = 0$ and $Q_{K+1} = \cdots = Q_n = (n - K)^{-1}$.

A wide variety of functions are special cases of Theorem 2; for example,

$$f(w) = \sum_{k=1}^{\infty} a_k w^k$$

with all $a_k \geq 0$ and $0 < \sum_{k=2}^{\infty} a_k B^k < \infty$;

$$f(w) = \frac{Cw}{D + \exp(-Ew)}, \tag{23}$$

with $C, D, E > 0$; and

$$f(w) = \frac{w(A + Bw + Cw^2)}{D + Bw + Cw^2} \tag{24}$$

with $A, B, C, D > 0$ and $D > A$.

If $f(w)$ increases slower than linearly, then the opposite tendency occurs; the initial distribution is uniformized.

THEOREM 3. (*Uniform Distribution*). Let $f(w) = wg(w)$, where $g(w)$ is continuous, nonnegative, and strictly monotone decreasing. Then the function $M(t)$ is monotone decreasing and $m(t)$ is monotone increasing. Suppose moreover that the reverberation is persistent (that is, $g(0) > A/B$). Then all $Q_i = 1/n$, and E equals the unique positive solution of

$$g\left(\frac{x}{n}\right) = \frac{A}{B - x}. \tag{25}$$

Some special $f(w)$'s are listed below, for definiteness. An important class of functions is defined by

$$f(w) = \frac{w}{\sum_{k=0}^{\infty} b_k w^k}$$

where $b_0 > 0$, $b_k \geq 0$ and $0 < \sum_{k=1}^{\infty} b_k B^k < \infty$.
For example,

$$\frac{Cw}{D + w}$$

with $C, D > 0$; or

$$f(w) = \frac{Cw}{D + \exp(Ew)}, \tag{26}$$

with $C, D, E > 0$ (contrast (23)); or

$$f(w) = \frac{Cw \exp(-Dw^m)}{\quad}$$

with $C, D, E, F > 0$ and $m,n \geq 1$.

Remark: Not all of the above $f(w)$'s are monotonic; nonetheless Theorem 3 holds. For example, $f(w)$ in (26) increases at small values of w and decreases to zero at large values of w.

Theorems 1–3 suggest how to construct functions $f(w)$ that will combine 0–1, fair, and uniform tendencies. For example, define a continuous, positive $g(w)$ that is strictly increasing at small values of w and is strictly decreasing at large values of w. Theorems 2 and 3 suggest that 0–1 and uniform tendencies will be included in this way. A "fair" intermediate region can be constructed by choosing $g(w)$ constant (or, for all practical purposes, approximately so) between its increasing and decreasing values, since then $f(w)$ is linear in this range. See Figure 14. More complex combinations of these three tendencies can be included by defining a $g(w)$ that oscillates finitely many times. This procedure can also be reversed. *Given* a function $f(w)$, define $g(w) = w^{-1}f(w)$ and test where $g(w)$ increases, decreases, and is constant to get an idea of $f(w)$'s 0–1, uniform, and fair tendencies. The next theorems discuss various combinations of these possibilities. First we consider an $f(w)$ that combines 0–1 and fair tendencies. In this situation, three possibilities occur. The reverberation can be transient or persistent. If the reverberation is persistent, the limiting distribution can be fair; in both cases the limiting

distribution can combine contour enhancement and quenching tendencies. The choice between fair or contour enhancing and quenching tendencies can be controlled by $x(0)$.

THEOREM 4. (*Fair, or Contour Enhancing and Quenching*). Let $f(w) = wg(w)$, where $g(w)$ is continuous, non-negative, and strictly monotone increasing for $0 \leq w \leq x^{(1)}$, and $g(w) = C$ for $w \geq x^{(1)}$. (See Figure 16). Then all limits Q_i and E exist. The function $M(t)$ increases monotonically and no slower than any $X_i < M$, and the function $m(t)$ is monotone decreasing. If $x_1(t) \geq x^{(1)}$, then all $\dot{X}_i(t) = 0$. If $g_i(t) = g_j(t) = C$, then $(d/dt)(X_i X_j^{-1})(t) = 0$.

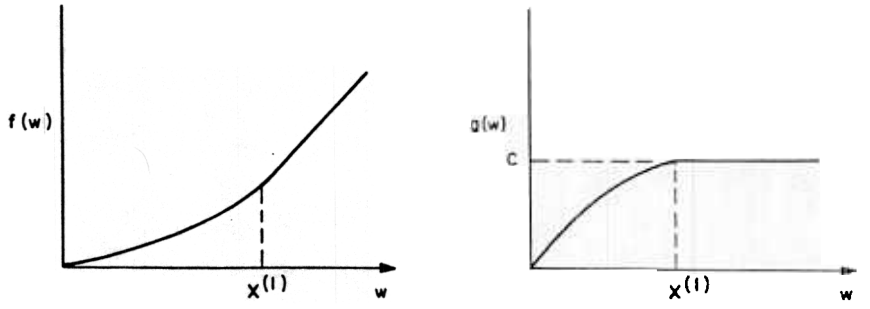

Figure 16. Fair, or contour enhancing and quenching.

Suppose moreover that the reverberation is persistent. (It is under the conditions given in Theorem 2.) Define K by $X_K(0) < M(0) = X_{K+1}(0)$. Then either $Q_i = 0$ or $g(Q_i E) = C, i = 1, 2, \ldots, K$, and $Q_i = 1/(n - K)$ or $g(Q_i E) = C, i = K + 1, \ldots, n$. In particular, if

$$X_L(0) \min\left(B - \frac{A}{\sum_{i=L}^{n} X_i(0)C}, x(0)\right) \geq x^{(1)},$$

then $\dot{X}_i \geq 0$ and $(X_i X_j^{-1})^{\bullet} = 0$ for $t \geq 0$ and $i, j \geq L$. If

$$X_1(0) \min(B - AC^{-1}, x(0)) \geq x^{(1)},$$

then $Q_i = X_i(t) = X_i(0)$ for $t \geq 0$ and $i = 1, 2, \ldots, n$. If however

$$X_1(0)(B - AC^{-1}) < x^{(1)},$$

then $Q_1 = 0$. If

$$X_i(t_i)(B - AC^{-1}) < x^{(1)}$$

for some sufficiently large time $t = t_i$, then $Q_i = 0$. Moreover if

$$B - AC^{-1} < Nx^{(1)} \tag{31}$$

with $1 < N \leq n$, then $Q_1 = Q_2 = \cdots = Q_{n-N+1} = 0$.

If the limiting distribution is 0–1 or locally uniform, then E satisfies the equation

$$g(Q_n x) = \frac{A}{r} \tag{32}$$

If not, then $E = B - AC^{-1}$

Remarks:

(1) Condition (27) provides a condition under which contour enhancement occurs without quenching all but the highest pattern weight.

(2) Condition (28) shows that all patterns whose weights satisfy $X_i(0) \geq \theta_1$ can be preserved by choosing the initial arousal level $x(0)$ sufficiently high if $\theta_1 = x^{(1)}(B - AC^{-1})^{-1}$. Condition (29) shows that θ_1 is a threshold value for preserving patterns, since if (29) holds, then some pattern quenching and contour enhancement occurs. If the inequality $X_i < \theta_1$ persists, then by (30), X_i is treated as noise and is quenched.

(3) Condition (31) shows that the amount of pattern quenching can be regulated by a judicious choice of numerical parameters. For example, if $N = 2$, then the network "chooses" the dominant state and quenches all others.

(4) Energy normalization occurs if the reverberation is persistent, and yields the same value $B - AC^{-1}$ whenever some nonmaximal states are not totally quenched. Thus, if an initial pattern contains enough energy to guarantee persistence, then the pattern will be contour enhanced, and the contour enhanced pattern will be normalized and preserved in short term memory as long as it is needed.

(5) The fact that $(d/dt)(X_iX_j^{-1})(t) = 0$ if $g_i(t) = g_j(t) = C$ has an important effect on the asymptotic slope of patterns as they are distributed in space. Whenever $g_i = g_j = C$, the *relative* growth rates of X_i and X_j remain fixed. If this happens, then the slope of a pattern in space is steepened as more pattern quenching occurs, but pattern shape of unquenched states is otherwise unchanged. Not all indices i are equally likely to satisfy the equation $g_i = C$, however. Since $X_1 \leq X_2 \leq \cdots \leq X_{n-1} \leq X_n$, the identity $g_n = C$ holds most often, $g_{n-1} = C$ holds next most often (and only if $g_n = C$), and so on. If $g_i < C$ while $g_{i+1} = C$, then $(d/dt) \cdot (X_iX_{i+1}^{-1}) < 0$. The *relative* growth rate of X_{i+1} as compared to that of X_i is increasing. This creates effects such as those in Figure 15. Note that straight lines in Figure 15a become curved inwards in Figure 15b due to the greater relative growth rates of larger pattern values.

The next theorem describes the possibility of mixing fair and uniform tendencies.

THEOREM 5. (*Fair or Uniformizing*). Let $f(w) = wg(w)$, where $g(w)$ is continuous, nonnegative, and $g(w) = C$ for $0 \leq w \leq x^{(2)}$ whereas $g(w)$ is strictly decreasing for $w > x^{(2)}$. (See Figure 17). Then all limits Q_i and E exist.

The function $M(t)$ is monotone decreasing, and $m(t)$ is monotone increasing. If $x_n(t) \leq x^{(2)}$, then all $\dot{X}_i(t) = 0$. If $g_i(t) = g_j(t) = C$, then $(d/dt)(X_iX_j^{-1})(t) = 0$.

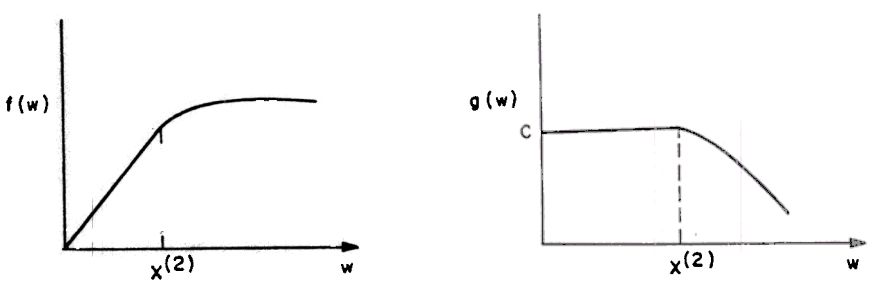

Figure 17. Fair or uniformizing.

Suppose moreover that the reverberation is persistent (that is, $g(0) > A/B$). Then either all $Q_i = 1/n$ or all $g(Q_i E) = C$. In the former case, E equals the unique root of

$$g\left(\frac{x}{n}\right) = \frac{A}{B - x}.$$

In the latter case, $E = B - AC^{-1}$. In particular, if

$$X_n(0) \max(B - AC^{-1}, x(0)) \leq x^{(2)},$$

then $Q_i = X_i(t) = X_i(0)$ for $t \geq 0$ and $i = 1, 2, \ldots, n$. If however

$$X_1(0)\hat{E} > x^{(2)},$$

where $\hat{E}$ is the unique root of (25) and g is convex, then all $Q_i = 1/n$. Indeed if

$$\hat{E} > nx^{(2)}$$

and g is convex, then all $Q_i = 1/n$.

Remarks: As in Theorem 4, there is a condition, namely (33) guaranteeing that all patterns that satisfy a given constraint will be preserved. In this case, if all $X_i(0) \leq \theta_2 \equiv x^{(2)}(B - AC^{-1})^{-1}$, and the initial arousal level is sufficiently small, then the patterns will be preserved. Energy normalization also occurs. By contrast, a proper choice of numerical parameters can guarantee a uniform limiting distribution.

Now we consider functions $f(w)$ that combine 0–1, fair, and uniform tendencies; for example, sigmoid functions. See Figure 18. The influence of these $f(w)$'s on the limiting distribution depends on particular choices of the parameters $x^{(0)}$ defined by $g(x_0) = g(B)$, $x^{(1)} = \min\{w : g(w) = C\}$, and $x^{(2)} = \max\{w : g(w) = C\}$. Before making such choices, we note the following proposition.

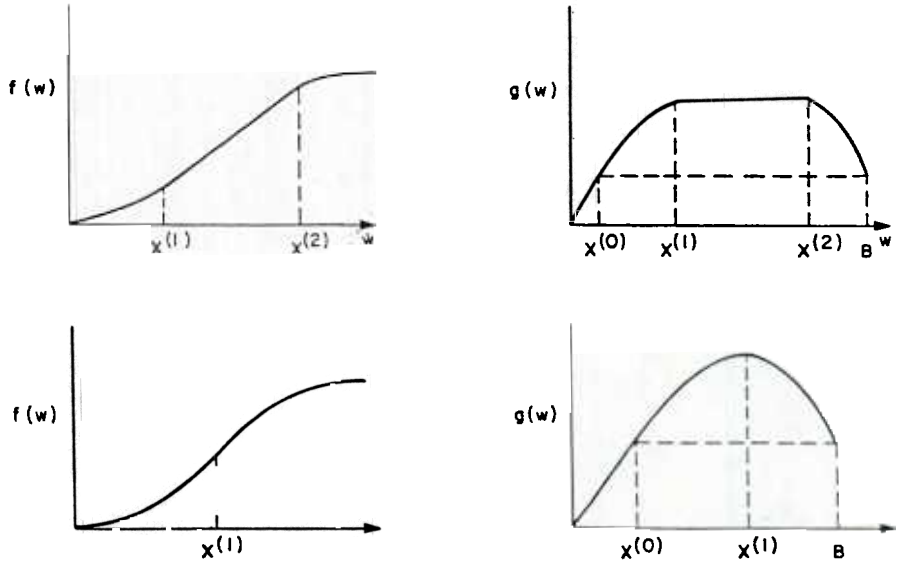

Figure 18. Important numerical parameters in $g(w)$.

PROPOSITION 4. Let $f(w) = wg(w)$, where $g(w)$ is continuous, nonnegative, strictly monotone increasing for $0 \le w \le x^{(1)}$, equal to C for $x^{(1)} \le w \le x^{(2)}$, and strictly monotone decreasing for $x^{(2)} \le w \le B$. If all limits $Q_i E$ exist, then the limit E also exists. Moreover there exists a $K \ge 0$ such that $Q_i E = Q_j E$, $i, j = 1, 2, \ldots, K$, and $g(Q_i E) = g(Q_j E)$ if $i, j > K$. If $g(0) \ge A/B$ and g is convex, then E is the unique solution of

$$g(Q_n x) = \frac{A}{B - x}. \tag{32}$$

If $g(0) < A/B$ and g is convex, then E equals 0 or one of the two solutions of (32). The smaller solution is unstable; the larger solution is stable.

In particular, if $x^{(1)} = x^{(2)}$ in Figure 13, then there exist integers L and M, $L \ge 0, M \ge 0, L + M \le n$, such that

$$Q_i = \begin{cases} 0 & \text{if } i \le L \\ \dfrac{\xi}{M\xi + (n - L - M)\eta} & \text{if } L + 1 \le i \le L + M \\ \dfrac{\eta}{M\xi + (n - L - M)\eta} & \text{if } L + M < i \le n \end{cases} \tag{36}$$

where ξ and η satisfy $g(\xi) = g(\eta)$. Moreover $E = 0$ or $[M\xi + (n - L - M)\eta]$.

Remark: The proposition shows that, if a limiting distribution exists, then, supposing that $x^{(1)} < x^{(2)}$, it is either fair ($g_i = C$ for $i = 1, 2, \ldots, n$ and $t \ge 0$), or uniform ($Q_i = Q_j$, $i, j = 1, 2, \ldots, n$), or $0 - 1 (K = n - 1)$, or contour enhancing and quenching ($0 < K < n - 1$ and $g(Q_i E) = C$, $i > K$), or trivalent (as in (36)). If $x^{(1)} = x^{(2)}$, then only trivalence is possible, including the uniform, $0 - 1$, or locally uniform cases. The existence of values w for which $f(w)$ is linear substantially enriches the limiting possibilities.

Below we constrain $x^{(0)}$, $x^{(1)}$, and $x^{(2)}$ to guarantee suitable subclasses of limiting possibilities. These constraints will be relevant to the following observations. The slope of many realistic signal functions $f(w)$, such as sigmoid functions, eventually becomes horizontal, if only because the cells in a population have maximum response rates and other finite properties. The above results show that the flattening of $f(w)$ can yield a uniform distribution. In the presence of noise, a uniformizing $f(w)$ imparts equal weight to essentially all states v_i, whether they are excited by signals or not, after sufficient reverberation has taken place. The flattening of $f(w)$ can thus be disadvantageous to effective signal processing. We will show that suitable choices of $x^{(0)}$, $x^{(1)}$, and $x^{(2)}$ can prevent uniformization even if the maximum value B of $x(t)$ exceeds $x^{(2)}$ and therefore lies in the uniformizing range.

THEOREM 6. Let $g(w)$ be continuous, nonnegative, strictly monotone increasing for $0 \le w \le x^{(1)}$, equal to C for $x^{(1)} \le w \le x^{(2)}$, and strictly monotone decreasing for $x^{(2)} \le w \le B$.

(I) *Fair:* If

$$X_1(0) \min(B - AC^{-1}, x(0)) \ge x^{(1)} \tag{37}$$

and

$$X_n(0) \max(B - AC^{-1}, x(0)) \le x^{(2)}, \tag{38}$$

then $Q_i = X_i(t) = X_i(0)$, $i = 1, 2, \ldots, n$, and $x(t)$ approaches $E = B - AC^{-1}$ monotonically.

(II) *Fair, or Contour Enhancing and Quenching:* Let

$$x^{(0)} + x^{(2)} \geq \max(B - AC^{-1}, x(0)), \tag{39}$$

hold throughout this section. Then all Q_i exist, $M(t)$ is monotone increasing faster than all $X_i < M$, and $m(t)$ is monotone decreasing. The limiting distribution is either fair, 0–1, locally uniform (only if several $X_i(0) = M(0)$), or contour enhancing and quenching; no uniformization occurs. If moreover, for some $L < n$,

$$X_L(0) \min\left(B - \frac{A}{\sum_{i=L}^{n} X_i(0)C}, x(0)\right) \geq x^{(1)}, \tag{27}$$

then $\dot{X}_i \geq 0$ and $(X_i X_j^{-1})^{\cdot} = 0$ for $t \geq 0$ and $i, j \geq L$, so that contour enhancement occurs. If

$$X_1(0) \min(B - AC^{-1}, x(0)) \geq x^{(1)},$$

then $Q_i = X_i(t) = X_i(0)$, for $t \geq 0$ and $i = 1, 2, \ldots, n$. If, however, the reverberation is persistent, and

$$B - AC^{-1} < Nx^{(1)}$$

with $1 < N \leq n$ and $X_{n-N+1}(0) < X_n(0)$, then $Q_1 = Q_2 = \quad = Q_{n-N+1} = 0$, so that quenching occurs. If

$$X_1(0)(B - AC^{-1}) \leq x^{(0)}, \tag{40}$$

the reverberation is persistent, and $X_1(0) < X_n(0)$, then $Q_1 = 0$. If

$$X_i(t_i)(B - AC^{-1}) \leq x^{(0)} \tag{41}$$

for a sufficiently large $t = t_i$, then $Q_i = 0$ if $X_i(t_i) < X_n(t_i)$ and the reverberation is persistent. If $x^{(1)} = x^{(2)}$ and the reverberation is persistent, then the limiting distribution is 0–1 if $X_n(0) > X_{n-1}(0)$ and locally uniform otherwise.

(III) *Quenching:* If

$$X_1(0) \max(B - AC^{-1}, x(0)) \leq x^{(0)}, \tag{42}$$

then $\dot{X}_1 \leq 0$ for $t \geq 0$. If moreover $X_1(0) < X_n(0)$ and the reverberation is persistent, then $Q_1 = 0$. If (41) holds for t_i sufficiently large and $i < n$, then $\dot{X}_i \leq 0$ for $t \geq t_i$, and $Q_i = 0$ if the reverberation is persistent and $X_i(t_i) < X_n(t_i)$.

(IV) *Quenching:* If

$$(n-1)x^{(0)} + x^{(2)} > \max(B - AC^{-1}, x(0)), \tag{43}$$

then $\dot{X}_i \leq 0$ for $t \geq 0$. If moreover $X_1(0) < X_n(0)$ and the reverberation is persistent, then $Q_1 = 0$.

(V) *Uniformizing:* If for some K, $0 < K < n$,

$$(n - K + 1)x^{(2)} \geq \max(B - AC^{-1}, x(0)) \tag{44}$$

and

$$X_1(0)\min\left(B - \frac{A}{\sum_{i=1}^{K} X_i(0)C}, x(0)\right) \geq x^{(1)}, \tag{45}$$

then all Q_i exist with $Q_1 < 1/n < Q_n$, even though $\dot{X}_i \geq 0$ and $\dot{X}_n \leq 0$ for $t \geq 0$.

Remarks: (1) Theorem 6 provides readily computable conditions under which a given $f(w)$ will not uniformize or contour enhance. For example, consider the sigmoid function

$$f(w) = \frac{Dw^2}{E + w^2}.$$

By (39), if

$$E + B\sqrt{E} > B\max(x(0), B - 2AE^{1/2}D^{-1}),$$

then uniformization is prevented.

(2) The results in (II) hold for large t, rather than all $t \geq 0$, if $x^{(0)}$ is replaced by $x^{(3)}$, which is defined by $g(x^{(3)}) = g(B - AC^{-1})$. In making this definition, we assume that $x^{(2)} < B - AC^{-1}$. Otherwise all x_i will fall into the monotone nondecreasing range of $g(w)$ for large t, and Theorem 4 holds for large t.

Although Theorem 6 provides practical constraints on $x^{(0)}, x^{(1)}, x^{(2)}$ that guarantee functionally useful behavior, it has not yet been proved in general that all Q_i exist in the absence of constraints. Such a theorem would be of particular interest in pathological conditions where $x^{(0)}$, $x^{(1)}$, and $x^{(2)}$ might deviate from normal values. Can sustained oscillations occur in pathological cases? Interaction between x and $(X_1, X_2, \ldots, X_n)$ can produce oscillations, but whether these oscillations always dissipate remains to be proved. Such an oscillation is described in the following proposition.

PROPOSITION 5. (*Oscillation*). Let

$$x_1(0) > x^{(2)} > B - AC^{-1} > 0 \tag{46}$$

and suppose that $X_1(0) < X_n(0)$. Then $\dot{X}_1(0) > 0$ and $\dot{X}_n(0) < 0$, but asymptotically $\dot{X}_1 \leq 0$ and $\dot{X}_n \geq 0$ with $\dot{X}_1 < 0$ and $\dot{X}_n > 0$ unless all $g_i = C$.

An important class of functions $f(w)$ such that $f(0) = 0$ are those that can be written as ratios of absolutely convergent power series. Given such an $f(w)$, it is instructive to expand (15) in the form

$$\dot{X}_i = \sum_{k=1}^{n} L_{ik}(X_i - X_k), \tag{47}$$

and to note the influence of the coefficients L_{ik} on the limiting distribution in special cases. Thus we introduce the class $\mathcal{R} = \{f\}$ of functions defined by $f(w) = N(w)D^{-1}(w)$, such that

$$N(w) = \sum_{m=1}^{\infty} a_m w^m \geq 0, \qquad D(w) = \sum_{m=0}^{\infty} b_m w^m > 0,$$

$$\sum_{m=1}^{\infty} |a_m| B^m < \infty, \quad \text{and} \quad \sum_{m=0}^{\infty} |b_m| B^m < \infty.$$

Introducing the notation $N_i = N(x_i)$ and $D_i = D(x_i)$, we find the following theorem.

THEOREM 7. If $f(w)$ is in $\mathscr{R}$, then

$$\dot{X}_i = \sum^{n} L_{ik}(X_i - X_k) \tag{47}$$

with $L_{ik} = U_{ik}V_{ik}$, where

$$\begin{aligned} U_{ik} &= BxX_iX_k(D_iD_k)^{-1}, \\ V_{ik} &= \sum_{m=1}^{\infty} a_m W_m(x_i, x_k), \\ W_m(y, z) &= \sum_{r=0}^{m-2} b_r(yz)^r S_{m-r-1}(y, z) \\ &\quad - \sum_{r=m}^{\infty} b_r(yz)^{m-1} S_{r-m+1}(y, z), \end{aligned} \tag{50}$$

and

$$S_p(y, z) = \begin{cases} 0 & \text{if } p = 0 \\ 1 & \text{if } p = 1 \\ y^{p-1} + y^{p-2}z + \cdots + yz^{p-2} + z^{p-1} & \text{if } p > 1. \end{cases}$$

Thus if $L_{ik} \leq -\varepsilon$, $k \neq i$, for some $\varepsilon > 0$, then the limiting distribution is uniform. Suppose that

$$L_{ij}X_j^{-r} \geq \varepsilon \tag{51}$$

for some $\varepsilon > 0$, $r \geq 1$, and all i and j such that $X_i(0) = M(0) > X_j(0)$. If $M(0) > \frac{1}{2}$, then the limiting distribution is $0 - 1$. If $L_{ik} \geq L_{jk}$ whenever $X_i = M > X_j$ and $k \neq i, j$, then the limiting distribution is $0 - 1$ or locally uniform even if $M(0) < \frac{1}{2}$.

Remark: Theorem 7 shows that the limiting distribution is determined essentially by the sign of each L_{ik}, and thus by the signs of the summands $W_m(x_i, x_k)$. In (50), the summands $W_m(x_i, x_k)$ can be composed of positive and negative terms. Herein lies the main sources of mathematical difficulty in studying arbitrary functions in $\mathscr{R}$.

Uniformly distributed tonic signals (as well as uniformly distributed excitatory tonic inputs) tend to create a uniform limiting distribution. For example, we have

THEOREM 8. (*Tonic Signals Uniformize*). Let

$$f(w) = K + wg(w), \qquad K > 0 \tag{52}$$

where $g(w)$ is a continuous, nonnegative, monotone nonincreasing (not necessarily decreasing) function. Then the limiting distribution is uniform and energy normalization occurs, such that E is the unique positive solution of

$$A + nK = \frac{nBK}{x} + (B - x)g\left(\frac{x}{n}\right). \tag{53}$$

Remarks: (1) Uniformly distributed tonic signals can uniformize the distribution of random noise, and thereby prevent fluctuations in noise from unduly favoring any given population of cells. A price is paid for this additional stability,

however: the tonic level of activity never dissipates. This activity can be prevented from sending signals to cells further downstream by interpolating a nonrecurrent on-center off-surround field between the recurrently interacting populations and the cells downstream (Grossberg, 1970).

(2) Functions $f(w)$ exist that are not manifestly of type (52); for example, the linear fractional transformations

$$f(w) = \frac{A + Bw}{C + Dw}$$

with $A, B, C, D > 0$ and $BC \geq AD$ are of type (52).

(3) If in (52), $g(w)$ is strictly monotone increasing, then the tonic signal K and the phasic signal $wg(w)$ create opposing limiting tendencies. Given small values of w (or of $x(t)$), uniformization is favored, whereas for large values of w, contour enhancement is favored.

The following theorem illustrates this competition between uniformizing and contour enhancing tendencies in a special case.

THEOREM 9. (*Tonic vs. Phasic Signals*). Let $n = 3$ and

$$f(w) = a_0 + a_1 w + a_2 w^2 \tag{55}$$

with $a_i > 0, i = 0, 1, 2$. Choose $x_i(0) = x_j(0)$ and let Y be the common value of X_i and X_j at every time t. Then

$$\operatorname{sign} \dot{Y} = \operatorname{sign}(\tfrac{1}{3} - Y)(Y - U)(Y - V), \tag{56}$$

where

$$U = \tfrac{1}{4}[1 + \sqrt{1 - 8a_0 a_2^{-1} x^{-2}}] \tag{57}$$

and

$$V = \tfrac{1}{4}[1 - \sqrt{1 - 8a_0 a_2^{-1} x^{-2}}]. \tag{58}$$

Thus if $x \leq \sqrt{8a_0 a_2^{-1}}$, the system tends towards a uniform distribution. In the limiting case $x = \infty$, the system tends towards a $0 - 1$ distribution with $Q_3 = 1$ if $Y < \frac{1}{3}$, and towards a locally uniform distribution with $Q_1 = Q_2 = \frac{1}{2}$ if $Y > \frac{1}{3}$. If $\sqrt{8a_0 a_2^{-1}} < x \leq B$, the system exhibits mixed $0 - 1$ and uniform tendencies.

Figure 19 illustrates the flow patterns that can be achieved given various values of $x(t)$. A point on the triangle codes particular values of the three functions X_1, X_2, X_3. The system is at the ith vertex V_i of the triangle at time t if $X_i(t) = 1$. The system is at the midpoint of the edge L_i opposite V_i at time t if $\frac{1}{2} = X_j(t) = X_k(t)$, where $\{i, j, k\} = \{1, 2, 3\}$. Note that $X_j(t_0) = X_k(t_0)$ implies $X_j(t) = X_k(t)$ for $t \geq t_0$. Thus if the system starts out on the line through V_i and the midpoint of L_i, then it remains on this line. The distance from V_i on this line increases as X_i decreases. All three bisecting lines interact at the point where $X_1 = X_2 = X_3 = \frac{1}{3}$. Arrows along these lines denote the direction in which the system flows given various values of x. Closed circles denote stationary points of the system (that is, points where all $\dot{X}_i = 0$).

Consider Figure 19a for definiteness. Note that distributions close to the uniform distribution are attracted towards the uniform distribution; distributions a little further away are attracted towards the 0–1 distribution but never reach it; and distributions close to the 0–1 distribution tend to be uniformized somewhat.

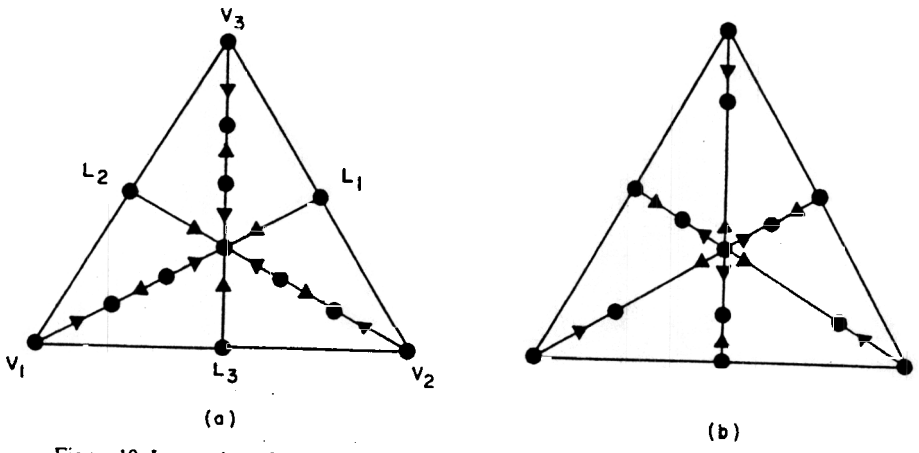

Figure 19. Interaction of uniformizing tonic signal and contour enhancing quadratic signal

Thus there are two uniformizing regions separated by a contour enhancing region. In Figure 19b, this situation is reversed: patterns close to the uniform distribution are contour enhanced, whereas those close to the 0–1 distribution are uniformized.

The structure of these regions becomes correspondingly more complex as the degree of the polynomial

$$f(w) = \sum_{k=0}^{m} a_k w^k$$

is increased beyond the value $m = 2$ of (55). For example, if $m = 3$, (56) is replaced by a polynomial of degree 4, with a corresponding more complicated diagram replacing Figure 19.

5. Comparison with the Wilson–Cowan equations

The Wilson–Cowan equations have the form

$$\dot{x}_i = -a_i x_i + (b_i - x_i) F\Big(\sum_k x_k c_{ki} - \sum_k y_k d_{ki} + e_i\Big) \tag{59}$$

and

$$\dot{y}_i = -A_i y_i + (B_i - y_i) G\Big(\sum_k x_k C_{ki} - \sum_k y_k D_{ki} + E_i\Big). \tag{60}$$

The function $x_i(y_i)$ describes the activity of the ith excitatory (inhibitory) subpopulation. Consider the right-hand side of (59) for definiteness. The activity x_i decays at a spontaneous rate $a_i x_i$. The term

$$(b_i - x_i) F\Big(\sum_k x_k c_{ki} - \sum_k y_k d_{ki} + e_i\Big)$$

has the following interpretation. $F(w)$ is a sigmoid signal function. It sums up excitatory inputs $(\sum_k x_k c_{ki})$, inhibitory inputs $(-\sum_k y_k d_{ki})$, and the external input (e_i) before computing the signal $F(w)$ as a function of the resultant

$$w = \sum_k x_k c_{ki} - \sum_k y_k d_{ki} + e_i. \tag{61}$$

Thus all input contributions combine independently before they generate the population signal. No shunting inhibition occurs, and shunting excitation, via the term $(b_i - x_i)F(w)$, occurs only after excitatory and inhibitory inputs combine independently. How can such a system be physically realized?

An approximate way is pictured in Figure 20. The inputs (61) to v_i are delivered to independent branches of the dendritic tree(s) of cell(s) v_i; then they send signals, perhaps electrotonically, to the cell body (or bodies) v_i with a net strength determined by $F(w)$. At v_i, there exist b_i excitable sites. At any time t, v_i is excited at a rate proportional to the number $[b_i - x_i(t)]$ of unexcited sites. Activity $x_i(t)$ also spontaneously decays at rate $a_i x_i(t)$. Linear output signals from v_i feed back to the dendritic trees of the cells v_k.

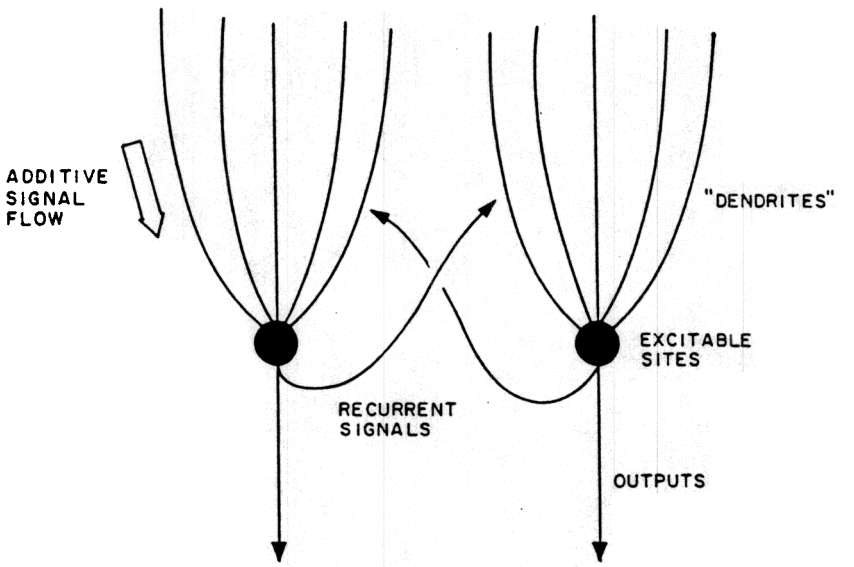

Figure 20. Graphical interpretation of Wilson–Cowan equations.

The mixture of independently combining inputs and shunting excitation seems to require a formal diagram such as that in Figure 20, whether or not we interpret the input receiving stations as dendrites. This diagram means that the interactions between excitatory and inhibitory inputs are so "weak" that they can be approximated by independent increments, without mutual shunting terms. Correspondingly, individual inputs will have a small effect on the cell body. Also, since the summands in (61) are linear functions of population activity, the outputs from each population are linear functions of population activity. Only after these outputs combine independently is a sigmoid function of their resultant computed in (59) and (60). This fact does not seem to be compatible with the interpretation that the output from each population is a sigmoid function of that population's activity.

The systems studied herein contain both shunting excitation and inhibition, such that the output of each population can be a sigmoid function of its activity. These systems thus permit "strong interactions" between excitatory and inhibitory

inputs, whether at the cell body, or between cell body and dendrites. A marriage between two experimentally verified phenomena—passive membrane equations and recurrent on-center off-surround anatomies—is hereby demonstrated. Whereas the present systems are, in a naive sense, "more nonlinear" than those of Wilson and Cowan, their particular nonlinearities blend harmoniously with an on-center off-surround anatomy, thereby making possible the rigorous mathematical theory presented herein.

Appendix: Proofs of results

The notation $f_i = f(x_i)$, $F = \sum_{k=1}^{n} f_k$, and $F_i = f_i F^{-1}$ will be used below.

Proof of Proposition 1: First we show that

$$\dot{X}_i = P(F_i - X_i), \tag{62}$$

where $P = BFx^{-1}$. By (12),

$$\dot{x}_i = -(A + F)x_i + Bf_i,$$

which when summed over i shows that

$$\dot{x} = -(A + F)x + BF. \tag{64}$$

Apply the identity

$$(UV^{-1})^{\cdot} = V^{-1}(\dot{U} - U\dot{V}V^{-1})$$

to $U = x_i$ and $V = x$ and find

$$\dot{X}_i = x^{-1}(\dot{x}_i - X_i\dot{x}). \tag{65}$$

Substituting (63) and (64) into (65) yields (62) after cancellation and rearrangement of terms. Now $F_i - X_i$ is computed as follows:

$$\begin{aligned} F_i - X_i &= x_i g_i(\sum_k x_k g_k)^{-1} - x_i(\sum_k x_k)^{-1} \\ &= x_i(Fx)^{-1} \sum_k x_k(g_i - g_k). \end{aligned}$$

Substituting this result into (62) yields (15). Equation (17) follows from (15) and the fact that $\sum_k X_k = 1$. Equation (18) is obvious.

To derive (16), write (64) as

$$\dot{x} = -Ax + (B - x)F$$

and note that $F = xG$. QED.

Proof of Proposition 2: Suppose for definiteness that $X_i(0) < X_{i+1}(0)$. By the continuity of the functions X_i and X_{i+1}, the inequality $X_i(t) > X_{i+1}(t)$ cannot hold at any time t unless $X_i(t_0) = X_{i+1}(t_0)$ at some time $t_0 < t$. By (15), the identity $X_i(t_0) = X_{i+1}(t_0)$ implies $X_i(t) = X_{i+1}(t)$ for $t \geq t_0$. Hence ordering is preserved. QED.

Proof of Proposition 3: First we prove the existence of all limits Q_i. Recall the definitions $M(t) = \max\{X_i(t): i = 1, 2, \ldots, n\}$ and $m(t) = \min\{X_i(t): i = 1, 2, \ldots,$

$n\}$. Suppose that $g(w)$ is monotone increasing. Then by (15), $\dot{M}(t) \geq 0$ and $\dot{m}(t) \leq 0$ for $t \geq 0$. If $g(w)$ is monotone decreasing, then (15) implies $\dot{M}(t) \leq 0$ and $\dot{m}(t) \geq 0$ for $t \geq 0$. In both cases, the limits Q_1 and Q_n exist, and $Q_1 + Q_n > 0$. If $g(w)$ is monotone increasing, then $Q_n > 0$. If $g(w)$ is monotone decreasing, then $Q_1 > 0$. Consider the former case for definiteness.

Using the fact that Q_n exists, we will prove that Q_{n-1} exists. Using the existence of Q_n and Q_{n-1}, we will prove that Q_{n-2} exists, and so on.

Integrate (15) from $t = S$ to $t = T$. Then

$$X_n(T) - X_n(S) = B \int_S^T X_n \sum_{k=1}^{n} X_k |g_n - g_k| \, dt \tag{66}$$

Let $T \to \infty$ and note that for all $t \geq 0$, $X_n(t) \geq X_n(0)$. Then (66) implies

$$Q_n - X_n(S) \geq X_n(0) \sum_{k=1}^{n} h_{n,k}(S), \tag{67}$$

where

$$h_{m,k}(S) = B \int_S^{\infty} X_k |g_m - g_k| \, dt$$

Letting $S \to \infty$ in (67) shows that

$$\lim_{S \to \infty} h_{n,k}(S) = 0, \qquad k = 1, 2, \quad ., n. \tag{69}$$

Now consider X_{n-1}. By (15), for any $T \geq S \geq 0$,

$$|X_{n-1}(T) - X_{n-1}(S)| \leq B \int_S^T \left(\sum_{k=1}^{n-1} X_k |g_{n-1} - g_k| + X_{n-1} |g_n - g_{n-1}| \right) dv.$$

By (68) and Proposition 2,

$$h_{n,k}(S) \geq h_{n-1,k}(S) \geq 0, \qquad k = 1, 2, \quad , n -$$

Thus (69) implies that

$$\lim_{S \to \infty} h_{n-1,k}(S) = 0, \qquad k = 1, 2, \ldots, n-1,$$

which by (69) and (70) implies the existence of Q_{n-1}.

Use the existence of Q_n and Q_{n-1} to prove the existence of Q_{n-2} by showing that

$$\lim_{S \to \infty} h_{m,k}(S) = 0, \qquad m = n, n-1 \quad \text{and} \quad k = 1, 2, \ldots, n$$

implies that

$$\lim_{S \to \infty} h_{n-2,k}(S) = 0, \qquad k \neq n-2.$$

Iterate the argument until the existence of all Q_i is proved.

Now the existence of E is proved. Consider the function $H(x) = \sum_{k=1}^{n} Q_k g(Q_k x)$. $H(x)$ is monotonic since $g(w)$ is monotonic. Since $G = \sum_{k=1}^{n} X_k g(X_k x)$, $\lim_{t \to \infty} (G - H) = 0$. Thus (16) can be written in the form

$$\dot{x} = x(B - x)\left(H(x) - \frac{A}{B - x} \right) + \varepsilon(t)$$

where $\lim_{t \to \infty} \varepsilon(t) = 0$. As $t \to \infty$, the sign of $\dot{x}$ becomes essentially equal to that of $H(x) - A/(B - x)$. This situation is graphed in Figure 21 for various choices of $g(w)$. The arrows indicate the direction in which x moves at various of its values. Clearly E equals zero or is a solution of the equation $H(x) = A(B - x)^{-1}$, which is (19). The distribution of E's values, given specific choices of $g(w)$, can be read off from graphs such as those in Figure 21. Figure 16c uses the fact that if $g(w)$ is increasing and convex, then $H(x)$ is also increasing and convex. QED.

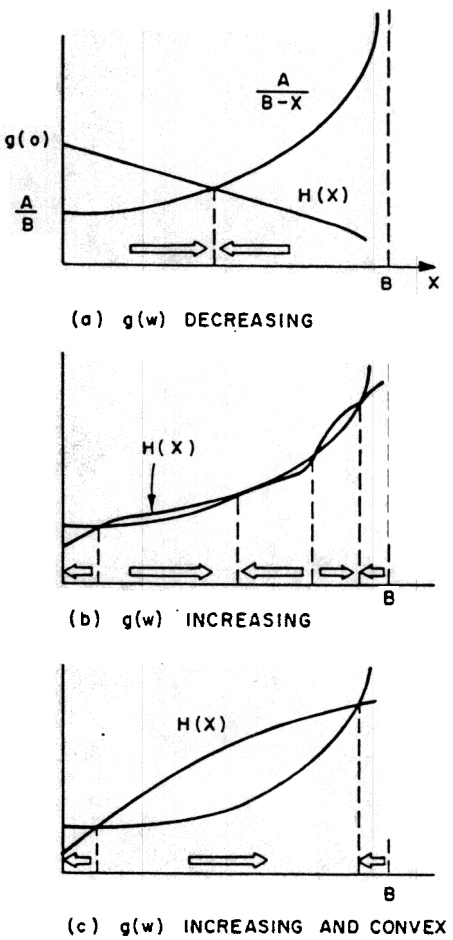

Figure 21. Equilibrium points of $x(t)$ as $t \to \infty$.

Proof of Theorem 1: Since $f(w) = Cw$, $g(w) = C$, and (15) implies that $\dot{X}_i \equiv 0$, and that every $X_i(t)$ is constant for $t \geq 0$. Thus $x_i(t) = X_i(0)x(t)$, and it suffices to study $x(t)$. By (16),

$$\dot{x} = x(D - Cx) \tag{71}$$

where $D = BC - A$. Equation (71) is of Riccati type. It can be routinely solved using the change of variables $x = \dot{y}(Cy)^{-1}$, yielding (20) and (21) (Bellman, 1967).

The proofs of Theorem 2 and 3 make use of the following Lemma.

LEMMA 1. The following equations hold.

$$(X_i - X_j)^{\cdot} = R_i(X_i - X_j) + S_j(g_i - g_j) \tag{72}$$

$$R_i = B \sum_{k=1}^{n} X_k(g_i - g_k) \tag{73}$$

$$S_j = BX_j. \tag{74}$$

Proof: By (17),

$$\dot{X}_i = BX_i(g_i - G)$$

$$\dot{X}_j = BX_j(g_j - G).$$

Subtract these two equations and use the identity

$$X_ig_i - X_jg_j = (X_i - X_j)g_i + X_j(g_i - g_j).$$

A rearrangement of terms yields (72). QED.

Proof of Theorem 2: If $M(t_0) = m(t_0) = 1/n$, then (15) implies $\dot{X}_i(t_0) = 0$. Hence $M(0) = m(0) = 1/n$ implies $M(t) = m(t) = 1/n$ for $t \geq 0$.

Suppose $M(0) > m(0)$. If $X_j(t_0) = M(t_0) > X_i(t_0)$, then also $g_j(t_0) > g_i(t_0)$, and by (15), $\dot{X}_j(t_0) > \dot{X}_i(t_0)$. Hence $M(t)$ is monotone increasing faster than any $X_i < M$. By (15) and Proposition 2, $m(t)$ is monotone decreasing.

We will show that the limiting distribution is 0–1, given a persistent reverberation, in the special case that $X_n(0) > X_{n-1}(0)$; that is, $Q_n = 1$. The general proof is essentially the same. By (73), $R_n \geq 0$. Since also $X_n > X_j$, $j \neq n$, (72) and (74) imply that

$$(X_n - X_j)^{\cdot} \geq BX_j(g_n - g_j), \qquad j \neq n. \tag{75}$$

Consider $g_n - g_j$ in the light of three facts:

(i) $g(w)$ is *strictly* monotone increasing;

(ii) $X_n - X_j \geq X_n(0) - X_j(0) > 0, j \neq n$;

and

(iii) $x(t)$ varies in a positive closed interval.

Thus there exists a $\delta > 0$ such that for any $j \neq n$,

$$g_n - g_j = g(X_nx) - g(X_jx) \geq \delta.$$

By (75),

$$(X_n - X_j)^{\cdot} \geq \delta BX_j, \qquad j \neq n.$$

Integrating this inequality from $t = 0$ to ∞, and using the fact that all X_i satisfy $0 \leq X_i \leq 1$, yields the inequalities

$$\infty > (\delta B)^{-1} \geq \int_0^\infty X_j dt, \qquad j \neq n.$$

The function X_j is also a nonnegative function which, by (15), has a bounded first derivative. Hence $Q_j = 0$ for every $j \neq n$, and thus $Q_n = 1$.

We now prove that the reverberation is persistent if $g(0) < A/B$ and $x(0) \geq \hat{x}$ where $\hat{x}$ is the smaller root of (22). If $X_K(0) < M(0) = X_{K+1}(0)$, then $X_n(t) = X_{n-1}(t) = \cdots = X_{K+1}(t) = M(t) > X_K(t)$, and $\dot{M}(t) > 0$. In particular,

$$G \geq \sum_{i=K+1}^{n} X_i g(X_i x) = (n - K)Mg(Mx) \geq (n - K)M(0)g(M(0)x).$$

Thus if $\hat{x}$ is a root of (22), then by (16), $\dot{x} > 0$ if $x = \hat{x}$. Hence if $x(0) \geq \hat{x}$, then $x(t) \geq \hat{x} > 0$ for $t \geq 0$, which proves persistence. QED.

The function in (24) can be written as $f(w) = wg(w)$ with $g(w)$ strictly increasing by defining

$$g(w) = \frac{}{1 + (D - A)(A + Bw + Cw^2)^{-1}}$$

Proof of Theorem 3: By (15) and Proposition 2, $M(t)$ is monotone decreasing and $m(t)$ is monotone increasing. Thus the limits $M(\infty)$ and $m(\infty)$ exist. We now show that $M(\infty) = m(\infty)$, and thus that all $Q_i = 1/n$, if the reverberation is persistent. By Proposition 2, $M \equiv X_n$ and $m \equiv X_1$. If $X_1(0) = X_n(0)$, we are done. Suppose that $X_n(0) > X_1(0)$. By (73), $R_n \leq 0$. Thus by (72),

$$(X_n - X_1)^{\cdot} \leq S_1(g_n - g_1).$$

By (74),

$$S_1 = BX_1 \geq BX_1(0) = \varepsilon > 0$$

Thus

$$(X_n - X_1)^{\cdot} \leq -\varepsilon(g_1 - g_n).$$

By the monotone decrease (increase) of $X_n(X_1)$,

$$(X_n - X_1)^{\cdot} \leq -\varepsilon[g(m(\infty)x) - g(M(\infty)x)].$$

Suppose $M(\infty) > m(\infty)$. Then since $g(w)$ is strictly monotone decreasing, and x varies in a positive closed interval, there exists a $\delta > 0$ such that

$$(X_n - X_1)^{\cdot} \leq -\delta < 0.$$

This implies the contradiction $1 \geq Q_1 = \infty$. Hence $M(\infty) = m(\infty)$.

To prove that E satisfies (25) if $g(0) > A/B$, it suffices to note by Proposition 3 that the reverberation is persistent if $g(0) > A/B$, and thus that all $Q_k = 1/n$. Hence

$$\sum_{k=1}^{n} Q_k g(Q_k x) = g\left(\frac{x}{n}\right).$$

Substitution of this expression into (19) yields the desired result. QED.

Proof of Theorem 4: The statements about monotone increase of $M(t)$ and decrease of $m(t)$ follow as in the proof of Theorem 2.

If $x_1(t) \geq x^{(1)}$, then all $g_i = C$, and by (15), all $\dot{X}_i(t) = 0$. If $g_i(t) = g_j(t) = C$, then by (17),

$$(\dot{X}_i X_i^{-1})(t) = C - G(t) = (\dot{X}_j X_j^{-1})(t).$$

Since

$$(X_i X_j^{-1})^{\cdot} = X_i X_j^{-1}(\dot{X}_i X_i^{-1} - \dot{X}_j X_j^{-1}),$$

it follows that $(d/dt)(X_i X_j^{-1})(t) = 0$.

Suppose that the reverberation is persistent. By (18), if $X_n(0) > 1/n$, then

$$\dot{X}_n \geq BX_n(0) \sum_{i=1}^{n} X_i[g(X_n x) - g(X_i x)] > 0.$$

Integrate this inequality and use the inequalities $0 \leq X_n \leq 1$ to conclude that

$$\int_0^\infty H_i \, dt < \infty \tag{76}$$

1, 2, , n, where

$$H_i = X_i[g(X_n x) - g(X_i x)] \geq 0.$$

Inequality (76) implies that H_i approaches zero arbitrarily closely at arbitrarily large times. Since all Q_i and E exist,

$$Q_i[g(Q_n E) - g(Q_i E)] = 0.$$

Either $Q_i = 0$ or $g(Q_i E) = g(Q_n E)$. Suppose that $i \leq K$. Then $Q_i < Q_n$. Since $g(w)$ is strictly monotone increasing until $w = x^{(1)}$, the identity $g(Q_i E) = g(Q_n E)$ implies that $g(Q_i E) = C$. Suppose that $i > K + 1$. Then $g(Q_i E) = g(Q_n E)$ because $Q_i = Q_n$. If moreover $Q_i \neq 1/(n - K)$ then $Q_K > 0$. Thus $g(Q_K E) = g(Q_n E)$, which implies that $g(Q_K E) = C$. Since $Q_i \geq Q_K$ for $i \geq K$, also $g(Q_i E) = C$ for $i \geq K$.

Suppose that (27) holds. By (17), to show that $\dot{X}_i \geq 0$ for $t \geq 0$ it suffices to show that $x_i \geq x^{(1)}$ and thus that $g_i = C \geq G$ for $t \geq 0$. Suppose that $i \geq L$, where L is defined by (27). At any fixed time $t = T$, the inequalities

$$G \geq \sum_{i=L}^{n} X_i g(X_i x)$$

$$\geq \sum_{i=L}^{n} X_i(0) C$$

hold if $x_L(t) \geq x^{(1)}$ for $t \leq T$. Let $t = T$ be the first time that

$$x(t) = B - \frac{A}{\sum_{i=L}^{n} X_i(0) C}. \tag{77}$$

By (27), then

$$x_L(t) = X_L(t) x(t) \geq X_L(0) x(t) \geq x^{(1)} \tag{78}$$

for $t \leq T$. Consequently

$$G \geq \sum_{i=L}^{n} X_i(0)C \geq \frac{A}{B - x}$$

at this time, and by (16), $\dot{x}(T) \geq 0$. The same argument is valid at every time t such that (77) holds, and thus $x(t)$ is increasing whenever (77) holds. This shows that

$$x(t) \geq \min\left(B - \frac{A}{\sum_{i=L}^{n} X_i(0)C}, x(0)\right) \tag{79}$$

for $t \geq 0$. Inequality (77) implies that (78) is true for $t \geq 0$. Since $x_i \geq x_L \geq x^{(1)}$ for all $i \geq L$, also $\dot{X}_i \geq 0$ for $t \geq 0$ and $i \geq L$.

A similar argument shows that if (28) holds, then $x_1 \geq x^{(1)}$ for $t \geq 0$: thus all $g_i = C$ for $t \geq 0$, and by (15), all X_i are constant for $t \geq 0$.

Suppose that (29) holds. Since $G \geq C$, (16) shows that for every $\varepsilon > 0$, there exists a T_ε such that

$$x(t) \leq B - AC^{-1} + \varepsilon, \qquad t \geq T_\varepsilon. \tag{80}$$

By (15), $\dot{X}_1 \leq 0$ for $t \geq 0$. Thus for sufficiently large t, (80) implies that

$$x_1(t) = X_1(t)x(t) \leq X_1(0)(B - AC^{-1} + \varepsilon) < x^{(1)};$$

thus g is bounded away from C for $t \gg 0$; $g(Q_1E) < C$; and finally $Q_1 = 0$.

This argument can be successively applied to $X_1, X_2, \ldots, X_i$ to show that $Q_1 = Q_2 = \cdots = Q_i = 0$ if (30) holds. Suppose that we have already shown that $Q_1 = Q_2 = \cdots = Q_{i-1} = 0$. Then the terms $X_k(g_i - g_k)$, $k \leq i - 1$, in (15) approach zero as $t \to \infty$. The terms $X_k(g_i - g_k)$ with $k > i$ are nonpositive. The term $X_n(g_i - g_n)$ is moreover bounded away from zero at $t = t_i \gg 0$, since by (30) and (80),

$$x_i(t_1) \leq X_i(t_i)(B - AC^{-1} + \varepsilon) < x^{(1)}$$

for some $\varepsilon > 0$, and hence $C - g_i \geq \delta$ for some $\delta > 0$, while the gap between X_n and X_i increases as $t \to \infty$. Thus $\dot{X}_i(t_i) < 0$. This argument can be repeated at all times $t \geq t_i$ to show that $x_i(t) \leq X_i(t_i)(B - AC^{-1} + \varepsilon) < x^{(1)}$; thus $g(Q_iE) < C$; and finally $Q_i = 0$.

Suppose that (31) holds. If for arbitrarily large t, $x_{n-N+1}(t) \geq x^{(1)}$, then

$$x(t) > \sum_{i=n-N+1}^{n} x_i(t) \geq Nx^{(1)} > B - AC^{-1},$$

which contradicts (80). Hence for sufficiently large t, $x_i(t) \leq x^{(1)} + \delta$ for some $\delta > 0$ and all $i \leq n - N + 1$; thus $g(Q_iE) < C$; and finally $Q_i = 0, i \leq n - N + 1$.

If the limiting distribution is locally uniform, then E satisfies (32) because $\lim_{t\to\infty}[G - g(Q_n x)] = 0$. If the limiting distribution is not locally uniform, then some Q_K such that $X_K(0) < M(0)$ exceeds zero. Thus $g(Q_KE) = g(Q_{K+1}E) = \cdots = g(Q_nE) = C$. This is true for every such K. Hence $\lim_{t\to\infty} G = C$, and $E = B - AC^{-1}$. QED.

Proof of Theorem 5: The first few statements of the Theorem follow from Proposition 3 and arguments in the proof of Theorem 3. If $x_n(t) \leq x^{(2)}$, then all

$\dot{X}_i(t) = 0$ because all $g_i(t) = C$. If $g_i(t) = g_j(t) = C$, then $(d/dt)(X_i X_j^{-1})(t) = 0$ by the same reasoning that was used in Theorem 4.

We now show that, given a persistent reverberation, either all $Q_i = 1/n$ or all $g(Q_i E) = C$. We use the facts $\dot{X}_1 \geq 0$, $\dot{X}_n \leq 0$, and the existence of all limits Q_i and E. By (15),

$$\begin{aligned} B^{-1}\dot{X}_1 &= X_1 \sum_{k=1}^{n} X_k(g_1 - g_k) \\ &\geq X_1 X_n(g_1 - g_n) \\ &\geq X_1^2[g(X_1 x) - g(X_n x)] \\ &\geq X_1^2(0)[g(Q_1 x) - g(Q_n x)] \geq 0. \end{aligned} \tag{81}$$

If $Q_1 = Q_n$, then all $Q_i = 1/n$ and we are done. Suppose $Q_1 < Q_n$. Integrate inequality (81) from $t = 0$ to $t = \infty$. Since $0 \leq X_1 \leq 1$ and $X_1(0) > 0$,

$$\int_0^\infty [g(Q_1 x(t)) - g(Q_n x(t))]\, dt < \infty.$$

Thus the nonnegative function $[g(Q_1 x) - g(Q_n x)]$ approaches zero arbitrarily closely at arbitrarily large times. Since E exists, $g(Q_1 E) = g(Q_n E)$. Since $Q_1 \leq Q_i \leq Q_n$, $g(Q_i E) = g(Q_n E)$ for $i = 1, 2, \ldots, n$.

If all $Q_i = 1/n$, then $\lim_{t\to\infty}[G - g(x/n)] = 0$. Hence E satisfies (25). If all $g(Q_i E) = C$, then $\lim_{t\to\infty} G = C$, and $E = B - AC^{-1}$.

Suppose that (33) holds. Since $G \leq C$, (16) shows that

$$x(t) \leq \max(B - AC^{-1}, x(0)) \tag{82}$$

for $t \geq 0$. Since $\dot{X}_n(t) \leq 0$ for $t \geq 0$,

$$x_n(t) = X_n(t)x(t) \leq X_n(0)\max(B - AC^{-1}, x(0)) \leq x^{(2)};$$

thus all $x_i(t) \leq x^{(2)}$ for $t \geq 0$; all $g_i \equiv C$; and finally all X_i are constant.

Suppose that (34) holds. If g is convex, then

$$\frac{1}{n}\sum_{k=1}^{n} f(x_k) \geq f\left(\frac{\sum_{k=1}^{n} x_k}{n}\right),$$

$$\frac{1}{n}\sum_{k=1}^{n} x_k g(x_k) \geq \frac{x}{n} g\left(\frac{x}{n}\right),$$

and finally

$$G = \sum_k X_k g_k \geq g\left(\frac{x}{n}\right). \tag{83}$$

By (16) and (83), if the reverberation is persistent, then for every $\varepsilon > 0$, there exists a T_ε such that

$$x(t) \geq \hat{E} - \varepsilon \quad \text{for} \quad t \geq T_\varepsilon$$

Since $\dot{X}_1(t) \geq 0$ for $t \geq 0$,

$$x_1(t) \geq X_1(t)x(t) \geq X_1(0)(\hat{E} - \varepsilon) \tag{84}$$

for $t \geq T_\varepsilon$. By (34) and (84), there exists a $\delta > 0$ such that $x_1(t) \geq x^{(2)} + \delta > 0$ for all sufficiently large t. Thus $g(Q_1 E) < C$, and all $Q_i = 1/n$.

Suppose that (35) holds. To prove that all $Q_i = 1/n$, we argue by contradiction. Let $Q_n > 1/n$. Then

$$x_n(\infty) = Q_n E > (1/n)\hat{E} > x^{(2)};$$

hence $g(Q_n E) < C$, and all $Q_i = 1/n$. QED.

Proof of Proposition 4: The proof imitates that of Proposition 3 as much as possible. The limit E exists because $\lim_{t \to \infty} (G - H) = 0$, where $H(x) = \sum_{k=1}^{n} Q_i \times g(Q_k x)$. Thus $E = 0$ or is a solution of (19).

By (15), for every $i = 1, 2, \ldots, n$,

$$\lim_{t \to \infty} \dot{X}_i(t) = BQ_i[g(Q_i E) - \sum_{k=1}^{n} Q_k g(Q_k E)].$$

These limits must all equal zero, since otherwise some $X_i(t)$ will be unbounded as $t \to \infty$. Either $Q_i = 0$ or

$$g(Q_i E) = \sum_{k=1}^{n} Q_k g(Q_k E).$$

In particular, if $Q_i Q_j > 0$, then $g(Q_i E) = g(Q_j E)$. Since $Q_i \leq Q_{i+1}$, then exists a K, possibly zero, such that $Q_1 = Q_2 = \cdots = Q_K = 0$ and $g(Q_i E) = g(Q_j E)$ if $i, j > K$. In particular $\lim_{t \to \infty} [G - g(Q_n x)] = 0$.

Suppose that $g(0) \geq A/B$ and let g be convex. Then $G(0) \geq A/B$, and since $\lim_{t \to \infty} [G - g(Q_n x)]$, E is a solution of (32). Since $g(Q_n x)$ is convex and $A/(B - x)$ is concave, (32) has a unique solution. If $g(0) < A/B$ and g is convex, then (32) has two solutions.

If $x^{(1)} = x^{(2)}$, then $g(w)$ has no constant interval. Hence the equality $g(Q_i E) = g(Q_j E)$ can occur only if $Q_i = Q_j$, or if $Q_i E = \xi$ and $Q_j E = \eta$, for some ξ and η such that $g(\xi) = g(\eta)$. This readily yields the trivalent distribution of (36). QED.

Proof of Theorem 6: This proof uses ideas similar to those used before; hence we merely sketch the main arguments below.

Impose (37) and (38). The main effect is that

$$\min(B - AC^{-1}, x(0)) \leq x(t) \leq \max(B - AC^{-1}, x(0)),$$

for $t \geq 0$. At time $t = 0$, $x^{(1)} \leq x_1(0) \leq x_n(0) \leq x^{(2)}$; thus all $g_i(0) = C$, and all $\dot{X}_i(0) = 0$. The bounds (85) on $x(t)$ cause these inequalities to propagate to all $t \geq 0$. Thus $G \equiv C$, and $E = B - AC^{-1} > 0$.

Consider (39). This condition implies that $g_i \leq g_n$ for $t \geq 0$ and $i = 1, 2, \ldots, n$. To see this, note by (39) and (82) that

$$x^{(0)} + x^{(2)} \geq x(t), \; t \geq 0. \tag{86}$$

If for any $T \geq 0$, $x_n(T) \geq x^{(2)}$, then all $x_i(T) \leq x^{(0)}$, $i = 1, 2, \ldots, n - 1$. Suppose not. Then some $x_i(T) > x^{(0)}$, and

$$x(T) \geq x_i(T) + x_n(T) > x^{(0)} + x^{(2)},$$

which contradicts (86). Consequently, by definition of $x^{(0)}$ and $x^{(2)}$, $g_i(T) \leq g_n(T)$ for $i = 1, 2, \ldots, n$. If for any $T \geq 0$, $x_n(T) \leq x^{(2)}$, then since $g(w)$ is monotone

increasing for $0 \le w \le x^{(2)}$, and since all $x_i(T) \le x_n(T)$, again $g_i(T) \le g_n(T)$ for $i = 1, 2, \ldots, n$. In all cases $g_i(T) \le g_n(T)$, whence by (15), $\dot{X}_n \ge 0$ and $\dot{X}_1 \le 0$ for $t \ge 0$. The arguments of Proposition 3 can therefore be used to show that all limits Q_i and E exist with $M(t)$ monotone increasing faster than all $X_i < M$, and $m(t)$ monotone decreasing.

Condition (27) is treated here much as it was in the proof of Theorem 4, but its use here is more subtle. By (27), $x_L(0) \ge x^{(1)} > x^{(0)}$. Thus by (39), $x_n(0) < x^{(2)}$. By interpolation, for every $i \ge L$, $x^{(2)} > x_i(0) \ge x^{(1)}$, and consequently $g_i(0) = C$. By the continuity of the functions x_i, there exists a time interval $[0, T]$ such that $g_i(t) = C$ if $0 \le t \le T$. For $0 \le t \le T$, therefore, $\dot{X}_i(t) \ge 0$ and $(d/dt)(X_i X_j^{-1})(t) = 0$. We now show that $T = \infty$.

For $0 \le t \le T$,

$$G \ge \sum_{i=L}^{n} X_i g_i \ge \sum_{i=L}^{n} X_i(0) C.$$

In particular, if for any t, $x(t)$ satisfies (77), then $\dot{x}(t) \ge 0$, so that, by (27), (79) holds.

Moreover, by (27) and (79), for every $i \ge L$,

$$x_i(t) = X_i(t)x(t) \ge X_i(0)x(t) \ge x^{(1)} > x^{(0)}. \tag{87}$$

Consequently, the inequality $x_n(t) > x^{(2)}$ is impossible, since when the function $R(t) = x_n(t) - x^{(2)}$ changes sign from negative to positive, all $x_i(t)$, $L \le i \le n-1$, would have to instantaneously jump from values $\ge x^{(1)}$ to values $\le x^{(0)}$ in order to satisfy (39). This they cannot do, since they are continuous. Thus the inequalities $\dot{X}_i(t) \ge 0$, $i \ge L$, (79), and (87) maintain each other for $t \ge 0$. A similar argument shows that all X_i are constant if (28) holds.

Suppose that (31) holds. To show that $Q_{n-N+1} = 0$, we argue by contradiction. If $Q_{n-N+1} > 0$, then by Proposition 4, $g(Q_{n-N+1}E) = g(Q_nE)$. By (39), $g(Q_{n-N+1}) = C$. Thus for $i \ge n - N + 1$,

$$x_i(\infty) \ge x_{n-N+1}(\infty) = Q_{n-N+1}E \ge x^{(1)},$$

and

$$E \ge \sum_{i=n-N+1}^{n} x_i(\infty) \ge Nx^{(1)} > (B - AC^{-1}).$$

This contradicts (80).

The statements involving (40) and (41) are proved as in Theorem 4.

Suppose that $x^{(1)} = x^{(2)}$ and that (39) holds. Then by Proposition 4, either $Q_i = 0$ or $g(Q_iE) = g(Q_nE)$. The latter can hold only if $Q_i = Q_n$. Hence the limiting distribution is 0–1 or locally uniform.

The assertions in (III) based on (41) and (42) are proved as in Theorem 4.

Condition (43) implies that $\dot{X}_1 \le 0$ for $t \ge 0$, since either all $x_i(t) \le x^{(2)}$, or $x_n(t) > x^{(2)}$, which implies that $x_1(t) \le x^{(0)}$ by (43). The other assertions of (IV) follow readily from this.

Condition (44) implies that $(n - K + 1)x^{(2)} > x(t)$, $t \ge 0$, and thus that at most $(n - K)x_i$'s can exceed $x^{(2)}$ at any time. In particular, if

$$x_{K+1}(t) > x_2(t) \ge x^{(2)} \tag{88}$$

then $x_i(t) \leq x^{(2)}$, $i = 1, 2, \ldots, K$. Condition (45) guarantees that X_1 will increase and X_n will decrease just so long as $x^{(1)} \leq x_i(t) \leq x^{(2)}$, and thus $g_i(t) = C$, for $i = 1, 2, \ldots, K$. By (88), these inequalities hold for $t \geq 0$. Using the monotone increase of X_1, the existence of all limits can be proved as in Proposition 3. The inequalities $Q_1 < 1/n < Q_n$ hold because $x_1(t)$ is bounded away from $x^{(2)}$ by (44). QED.

Proof of Proposition 5: By (46), $x_i(0) \geq x_1(0) > x^{(2)}$, $i = 1, 2, \ldots, n$: all x_i begin in the uniformizing region, so that $\dot{X}_1(0) > 0$ and $\dot{X}_n(0) < 0$. By (46) and (80), for t sufficiently large,

$$x_i(t) \leq x(t) < B - AC^{-1} < x^{(2)};$$

all x_i end up in the contour enhancing region, so that $\dot{X}_1 < 0$ and $\dot{X}_n > 0$ unless all $g_i = C$. QED.

Proof of Theorem 7: First we prove equations (47)–(50). By (62), we must compute $F_i - X_i$.

$$\begin{aligned} F_i - X_i &= \frac{N_i D_i^{-1}}{\sum_{k=1}^{n} N_k D_k^{-1}} - \frac{x_i}{\sum_{k=1}^{n} x_k} \\ &= \frac{1}{Fx} \cdot \sum_{m=1}^{\infty} a_m \sum_{k=1}^{n} (x_k x_i^m - x_i x_k^m D_i D_k^{-1}) \\ &= \frac{1}{FxD_i} \sum_{m=1}^{\infty} a_m \sum_{k=1}^{n} x_i x_k D_k^{-1} \left[x_i^{m-1} \sum_{r=0}^{\infty} b_r x_k^r - x_k^{m-1} \sum_{r=0}^{\infty} b_r x_i^r \right] \\ &= \frac{1}{FxD_i} \sum_{m=1}^{\infty} a_m \sum_{k=1}^{n} x_i x_k D_k^{-1} \left[\sum_{r=0}^{m-2} b_r (x_i x_k)^r (x_i^{m-r-1} - x_k^{m-r-1}) \right. \\ &\qquad \left. \sum_{r=m}^{\infty} b_r (x_i x_k)^{m-1} (x_i^{r-m+1} - x_k^{r-m+1}) \right]. \end{aligned}$$

The identity

$$y^p - z^p = (y - z) \sum_{q=0}^{p-1} y^q x^{p-1-q}$$

is now applied with $y = x_i$, $z = x_k$, and $p = \pm(m - r - 1)$. Then this expression is multiplied by $P = BFx^{-1}$, as required by (62), to yield (47).

The proofs yielding uniform, 0–1, and locally uniform distributions are much like those in Theorems 1–6. Consider the 0–1 case for definiteness; thus let $X_n(0) > X_{n-1}(0)$. By (47) and (51),

$$\dot{X}_n \geq \varepsilon \sum_{k=1}^{n-1} X_k^r (X_n - X_k). \tag{89}$$

Suppose that $X_n(0) > \frac{1}{2}$. Since $\dot{X}_n \geq 0$ and $\sum_{k=1}^{n} X_k = 1$, there exists a $\delta > 0$ such that

$$\dot{X}_n \geq \delta \sum_{k=1}^{n-1} X_k^r \geq \delta \left(\frac{1 - X^n}{n - 1} \right)^r, \tag{90}$$

which implies $Q_n = 1$.

Suppose that $L_{nj} \geq L_{kj}$ for all $j \neq k, n$. By (48)–(50), $L_{nk} = L_{kn}$. Thus by (47) applied successively with $i = n$ and $i = k$, we conclude that $\dot{X}_n \geq \dot{X}_k$, $k \neq n$. The positive functions $X_n - X_k$, $k \neq n$, are therefore monotone increasing. Define

$$\delta = \varepsilon^{-1} \min\{(X_n - X_k)(0) : k \neq n\} > 0.$$

Then (89) implies (90), which implies $Q_n = 1$. QED.

Proof of Theorem 8: The proof is essentially the same as that of Theorem 3. Equation (15) is modified by adding an extra term $D(1/n - X_i)$ to its right hand side, where $D = nBKx^{-1} > 0$. This term pulls X_i towards $1/n$ even if $g(w)$ is constant.

To prove (53), one computes

$$\dot{x} = x[-(A + nk) + (B - x)G + nBKx^{-1}],$$

notes that $\lim_{t \to \infty} [G - g(x/n)] = 0$, and checks that $\dot{x} = 0$ only if (53) holds. (53) has one solution because its right hand side is a monotone decreasing function of x. QED.

Equation (54) defines a function of type (52) if $K = AC^{-1}$ and

$$g(w) = (BC - AD)C^{-1}(C + Dw)^{-1}.$$

Proof of Theorem 9: By (62), we must compute $F_i - X_i$, premultiply by $P = BFx^{-1}$ and find an expression equal to $\dot{X}_i$. The result is, for any $n > 1$,

$$\dot{X}_i = U(1 - nX_i) + VX_i \sum_{k=1}^{n} X_k(X_i - X_k), \tag{91}$$

where $U = a_0 Bx^{-1}$ and $V = a_2 Bx$. Let $n = 3$. Suppose $X_i(0) = X_j(0)$ for some i and j, $i \neq j$. Then $X_i(t) = X_j(t)$, $t \geq 0$. Denote the common value of $X_i(t)$ and $X_j(t)$ by $Y(t)$. Then $X_k(t) = 1 - 2Y(t)$, where $k \neq i, j$. Letting $W = 6a_2 Bx$, equation (91) becomes

$$\begin{aligned} \dot{Y} &= U(1 - 3Y) + VY(1 - 2Y)(3Y - 1) \\ &= W(\tfrac{1}{3} - Y)[Y^2 - \tfrac{1}{2}Y + a_0(2a_2x^2)^{-1}] \end{aligned}$$

or

$$\dot{Y} = W(\tfrac{1}{3} - Y)(Y - U)(Y - V), \tag{92}$$

Since $W > 0$, (92) implies (56). Equations (56), (57), and (58) show that the value of x determines the limits to which Y converges. In particular, letting $L = (8a_0a_2^{-1})^{1/2}$, (56) implies that

$$\begin{aligned} &\text{sign } \dot{Y} = \text{sign}(\tfrac{1}{3} - Y) \quad \text{if } 0 \leq x < L, \\ &\text{sign } \dot{Y} = \text{sign}(\tfrac{1}{3} - Y)(Y - \tfrac{1}{4})^2 \quad \text{if } x = L, \\ &\text{sign } \dot{Y} = \text{sign}(\tfrac{1}{3} - Y)(Y - U)(Y - V) \end{aligned}$$

with

$$0 < V < \tfrac{1}{4} < U < \tfrac{1}{2} \quad \text{if } L < x \leq B,$$

and

$$\text{sign } \dot{Y} = \text{sign}(Y - \tfrac{1}{3}) \quad \text{if } x = \infty.$$

These changes due to progressive increase in x are pictured in Figure 22. If $x < L$, the limiting distribution is uniform. If $x = L$, $Y = \frac{1}{4}$ is an unstable critical point; hence $Y(\infty) = \frac{1}{3}$ or $\frac{1}{4}$. If $B \geq x > L$, this unstable critical point branches and creates two stable and one unstable critical points. Either U or $\frac{1}{3}$ is the unstable critical point, depending on which is smaller. As x increases, the limiting case of $x = \infty$ is approached. Here, if $Y > \frac{1}{3}$, then $Y(\infty) = \frac{1}{2}$, which defines the locally uniform distribution $P_i = P_j = \frac{1}{2}$, whereas if $Y < \frac{1}{3}$, then $Y(\infty) = 0$, which defines the 0–1 distribution $P_k = 1$. QED.

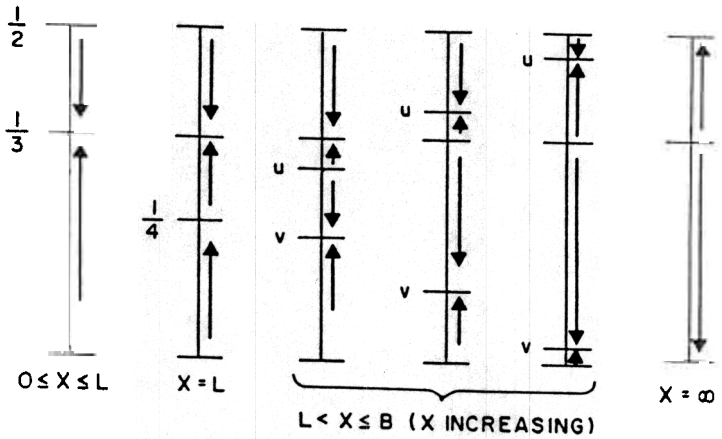

Figure 22. Influence of x on limiting distribution.

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(Received May 9, 1973)