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Decisions, Patterns, and Oscillations in Nonlinear Competitive Systems with Applications to Volterra-Lotka Systems

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This paper describes new properties of competitive systems which arise in population biology, ecology, psychophysiology, and developmental biology. These properties yield a global method for analyzing the geometric design and qualitative behavior, e.g. limits or oscillations, of competitive systems. The method explicates a main theme about competitive systems: who is winning the competition? The systems can undergo a complicated series of discrete decisions, or jumps, whose structure can, for example, yield global pattern formation or sustained oscillations, as in the voting paradox. The method illustrates how a parallel continuous system can be analyzed in terms of discrete serial operations, but notes that the next operation can be predicted only from the parallel interactions. It is shown that binary approximations to sigmoid signals in nonlinear networks are not valid in general, It is also shown how a temporal series of nested dynamic boundaries can be induced by purely nonlinear interactive effects. These boundaries restrict the fluctuations of population sizes or activities to ever finer intervals. The method can be used where Lyapunov methods fail and often obviates the need for local stability analysis. The paper also strengthens and corrects some previous results on the voting paradox.

1. Introduction

Competitive systems arise in many areas of biology, such as population biology and ecology (May, 1973; May & Leonard, 1975), psychophysiology (Grossberg, 1973, 1977, 1978*a*, *d*; Ellias & Grossberg, 1975; Grossberg & Levine, 1975; Levine & Grossberg, 1976), and developmental biology (Grossberg, 1976*a*, *b*, *c*, 1978*c*, *d*). A system $\dot{x} = f(x)$, or

$$\dot{x}_i = f_i(x), \qquad x = (x_1, x_2, \ldots, x_n), \qquad i = 1, 2, \ldots, n, \tag{1}$$

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is said to be *competitive* if its solutions $x(t)$, $t \geq 0$, remain in a bounded region R and

$$\frac{\partial f_i}{\partial x_j}(x) \leq 0 \text{ if } i \neq j \text{ and } x \varepsilon R. \tag{2}$$

This paper describes a method for globally analyzing the limiting and oscillatory behavior of n-dimensional nonlinear competitive systems. The method explicates a main theme about competitive systems; namely, who is winning the competition? This analysis reveals several new physical concepts that are implied by the idea of competition. The first idea is *ignition;* namely, once a competitive system starts to enhance some population, thereafter some population will always be enhanced, albeit possibly different populations at different times. The second idea is *jumps*, or *local decisions;* namely, one keeps track of which population is being *maximally* enhanced at any given time. Otherwise expressed, one analyzes who is winning the competition at any given time. When a different population starts to be maximally enhanced, the system "decides" to enhance the new population, or "jumps" between populations. The method classifies the possible jumps in a given competitive system. This classification defines a discrete *jump diagram* that is induced by the continuous competitive system. The jump diagram explicates the idea that the system is making a series of decisions as time goes on. Thus the continuous parallel interactions of the system are analyzed in terms of discrete serial operations. The interrelations between these serial vs. parallel concepts shed some light on how a parallel system can sometimes seem serial, even though one cannot predict its temporal evolution without studying its parallel structure.

By studying the jump diagram, one can conclude whether the system approaches a limit as $t \to \infty$. If this occurs, one can speak of "pattern formation" or "global consensus" arising asymptotically from the system's series of decisions. Alternatively, the system can oscillate persistently as $t \to \infty$. In the particular case of three populations interacting according to the Volterra–Lotka system

$$\dot{x}_1 = x_1(1 - x_1 - \alpha x_2 - \beta x_3) \tag{3a}$$

$$\dot{x}_2 = x_2(1 - \beta x_1 - x_2 - \alpha x_3) \tag{3b}$$

$$\dot{x}_3 = x_3(1 - \alpha x_1 - \beta x_2 - x_3), \tag{3c}$$

where $\beta > 1 > \alpha$ and $\alpha + \beta \geq 2$, both periodic ($\alpha + \beta = 2$) and non-periodic ($\alpha + \beta > 2$) oscillations of bounded amplitude have been found and illustrate the "voting paradox" (May & Leonard, 1975). This paradox describes a global "contradiction" due to the fact that in purely pairwise competition, population v_1 beats v_2, v_2 beats v_3, and v_3 beats v_1. The jumps that take place in a competitive system are a source of oscillations, and whether global limits, persistent oscillations, or even chaos result will depend on details of system design. In particular, a series of very complicated decisions, or oscillations, can occur even if the system eventually undergoes pattern formation (Grossberg, 1978*a*). The existence of chaos is not necessary to explain certain aspects of biological complexity: cf. Li & Yorke (1975).

Another new idea is that of *dynamic boundary*. This is a purely nonlinear concept that arises from the interaction of nonlinear signals and nonlinear mass action laws in a competitive geometry. As the competition proceeds, the dynamic variables, e.g. population sizes, activity levels, etc. get trapped in a nested sequence of ever finer intervals. The dynamic boundaries are the endpoints of the intervals that have already appeared up to a given time. The decision process is essentially complete after all dynamical boundaries have been switched on.

The above concepts compare and contrast interestingly with previous concepts in the literature. Below some of these are briefly reviewed in order to make intuitive connections and to emphasize what is new in the present method.

(A) LOCAL ANALYSIS OF CRITICAL POINTS AND LYAPUNOV METHODS

Two classical approaches have been used to analyze the Volterra–Lotka system

$$\dot{x}_i = x_i\left(A_i - \sum_{k=1}^{n} B_{ik}x_k\right), \qquad i = 1, 2, \ldots, n. \tag{4}$$

Lyapunov methods provide global information about the system if symmetry assumptions are made about the competition coefficients B_{ij}. For example, if $B_{ij} = B_{ji}$ for all $i, j = 1, 2, \ldots, n$, then the quadratic form:

$$V = \sum_{i,j=1}^{n} (x - \bar{x}_i)B_{ij}(x_j - \bar{x}_j), \tag{5}$$

where the $\bar{x}_i$ are equilibrium population sizes, is a Lyapunov function; that is, the time derivative of V, evaluated along system trajectories, satisfies $\dot{V} \leq 0$ (MacArthur, 1970). Consequently the system tends to minimize V as $t \to \infty$. The method often fails in the absence of this physically unlikely assumption* (May, 1973, p. 54). The present global method does not require symmetry assumptions, but rather uses special properties of competitive systems to derive detailed dynamical information.

In the absence of Lyapunov methods, one typically makes a local stability

* Also see Siljak, D. D. (1976). *IEEE Trans. on Auto Control*, Vol. AC-21, 2, 149, and Goh, B. S. and Agnew, T. T. (1977). *J. Math. Biol.* 4, 275.

analysis of all equilibrium points, or local estimates of asymptotic solutions, and supplements these by computer simulations. May & Leonard (1975), for example, hereby study three competing populations in system (3). Their method makes use of a special choice of competition coefficients in which only three parameters (α, β, 1) rather than nine parameters appear. If $\beta > 1 > \alpha$ and $\alpha+\beta > 2$, these authors find non-periodic bounded oscillations of ever increasing cycle time. The non-periodic nature of the oscillations is justified using local approximations based on the assumption that the oscillating solution approaches the set of straight lines between the points (1, 0, 0), (0, 1, 0), and (0, 0, 1). This assertion is almost correct. Between each pair of these points, there exists a heteroclinic solution of system (3); namely, a solution that approaches one point as $t \to -\infty$ and the other point as $t \to +\infty$. These heteroclinic solutions are not, however, straight lines. The oscillating solution approaches the set of these three heteroclinic solutions, and this explains the existence of slower oscillations as $t \to +\infty$.

The present method permits a global analysis of systems that significantly generalize (3); for example,

$$\dot{x}_i = a_i(x)\left[1 - \sum_{k=1}^{n} N_{ik} f_k(x_k)\right], \tag{6}$$

where $x = (x_1, x_2, \ldots, x_n)$ and $i = 1, 2, \ldots, n$. In equation (6), the amplification $a_i(x)$ can be a nonlinear function of the system's state x; the signal functions $f_i(x_i)$ can be monotone-increasing nonlinear functions of x_i that satisfy mild positivity and smoothness conditions; and the competition coefficients N_{ik} are related by inequalities rather than equalities. Moreover this analysis identifies a large set of initial values $x(0)$ that generate limits or oscillations.

A further benefit of the present method is that it sometimes obviates the need to study equilibrium points at all. Instead one studies the geometry of the jump sets and of the ignition surfaces where competition sets in. When the number of populations is large, stability analyses of equilibrium points become tedious at best, and even where they are successful, they often do not provide an adequate insight into system design and dynamics. For example, the method explicates why system (3) cannot decide who should win, by generating jump sets which force cyclic decisions to continue unabated in the order $v_1 \to v_2 \to v_3 \to v_1$ as $t \to \infty$.

(B) BINARY APPROXIMATIONS OF CONTINUOUS SYSTEMS

Glass & Kauffman (1973) describe interesting results on some continuous biochemical networks with sigmoid (S-shaped) signal functions. They note that the sigmoid continuous networks can be approximated by discrete logical networks in which the sigmoid signals are replaced by 0's (where the sigmoid is small) and 1's (where the sigmoid is large). The present method also assigns a discrete system to a continuous system, but the two methods are otherwise quite different. The Glass–Kauffman method *approximates* a continuous system with a discrete one. The present method identifies a discrete system that is exactly generated by its continuous system. In particular, the Glass–Kauffman approximation is not generally valid in competitive systems. For example, in system (6) suppose that each $f_i(x_i)$ is a sigmoid function of x_i. The Glass–Kauffman approximation would replace this signal by a 0 when x_i is small and by 1 when x_i is large. By contrast, the change of variable $y_i = f_i(x_i)$ transforms equation (6) into:

$$\dot{y}_i = b_i(y)\left[1 - \sum_{k=1}^{n} N_{ik}y_k\right] \tag{7}$$

$y = (y_1, y_2, \ldots, y_n)$, where $b_i(y)$ is again an admissible amplification function. The dynamics of equation (7) are controlled by the signs of:

$$\sum_{k=1}^{n} (N_{ik} - N_{jk})b_k(y)$$

on the sets where:

$$\sum_{k=1}^{n} (N_{ik} - N_{jk})y_k = 0, i \neq j.$$

Thus combinations of decay rates and signals on sets governed by linear relations control equation (7), not an approximation by 0's and 1's.The system in the next section also cannot be approximated by binary signals. I suggest that the G–L method works only in certain cases where a serial mechanism operates, but not in cases where parallel dynamics exist. Moreover, even in serial cases, replacing a sigmoid by a 0–1 law is a singular limiting operation that will change the dynamics unless decay rates and other parameters are properly scaled; cf. Hsü (1977).

(C) SEQUENCES OF COMPARTMENTAL BOUNDARIES

Kauffman, Shymko & Trabert, e.g., Kauffman (1977), model the successive emergence of compartmental boundary lines during the development of imaginal discs. The boundary lines cannot be crossed by cells after they form. These authors model the phenomenon using a linear reaction–diffusion system. Since the disc is elliptic in shape, they impose elliptic boundary conditions on the system and find that the eigenfunctions of the system are switched on with a timing and a shape that agrees surprisingly well with the data. The remarkable implication of the model is that the boundary shape of the developing tissue might substantially control the switching-in of cell migration boundaries that are interior to the disc. Because the phenomenon described is a threshold phenomena, the linear model can be thought of as an approximation at threshold levels to whatever suprathreshold nonlinear interactions are taking place *in vivo*. The model's strong point (its general description of elliptical boundary influences at threshold) is also its main drawback, since not every elliptical region develops into the same adult tissue. Apart from describing how different cells can interpret the same linear threshold pattern, one must also ask how nonlinear systems generate different patterns at suprathreshold activity levels, even if they behave similarly at threshold levels.

Below an example is briefly sketched in which purely nonlinear interactions, uninfluenced by boundary biases, can induce a temporal sequence of nested dynamic boundaries (Grossberg, 1977, 1978*a*). The papers Ellias & Grossberg (1975), Grossberg & Levine (1975), and Levine & Grossberg (1976) describe some influences of boundary biases on suprathreshold nonlinear network dynamics. An open problem of considerable importance is to classify how different physical boundaries and suprathreshold nonlinear interactions work together to induce hybrid sequences of nested dynamic boundaries.

Systems of the form:

$$\dot{x}_i = -A_i x_i + (B_i - x_i)[f_i(x_i) + I_i] - x_i\Big[\sum_{k \neq 1} f_k(x_k) + J_i\Big], \tag{8}$$

describe mass action competition among n populations v_i, $i = 1, 2, \ldots, n$. Each v_i has B_i excitable (or occupiable) sites, of which x_i are excited (occupied), and $B_i - x_i$ are unexcited (unoccupied) at any given time. The feedback signals $f_i(x_i)$ are triggered by cellular activity. Term $(B_i - x_i)$ $[f_i(x_i) + I_i]$ describes the switching on of unexcited sites $B_i - x_i$ by a positive feedback signal $f_i(x_i)$ from v_i to itself, or by an excitatory input I_i. Term

$$-x_i\Big[\sum_{k \neq 1} f_k(x_k) + J_i\Big]$$

describes switching-off of excited sites x_i by negative (or competitive) feedback signals $f_k(x_k)$ from other populations v_k, $k \neq i$, or by an inhibitory input J_i. System (8) is the special case of system:

$$\dot{x}_i = a_i(x)[b_i(x_i) - c(x)], \tag{9}$$

wherein

$$a_i(x) = x_i,\ b_i(x_i) = B_i x_i^{-1}[f_i(x_i) + I_i] - A_i - I_i - J_i,$$

and

$$c(x) = \sum_{k=1}^{n} f_k(x_k).$$

Using the present method, essentially any competitive system of the form equation (9) can be proved to undergo global pattern formation (given any $x(0)$, the limit $x(\infty)$ exists) if it satisfies mild smoothness and positivity assumptions (Grossberg, 1977, 1978*a*). In other words, global pattern formation occurs given any number of competing populations, essentially any state-dependent amplifications $a_i(x)$, essentially any signal functions $b_i(x_i)$, and essentially any mean competition function, or adaptation level, $c(x)$. No boundary effects occur in system (9) because each v_i experiences the same competition function, or adaptation level, $c(x)$. This theorem implies that a tremendous liberty in choosing signals and amplifications is compatible with global consensus, even under parametric excitations, if there exists a common, albeit fluctuating baseline of competitive activity, namely $c(x)$, against which to evaluate these signals. Speaking heuristically, one can say that arbitrary "individual differences" (such as signals and amplifications) in arbitrarily many "individuals" ($n \geq 2$) can be harmonized to yield a global consensus if there exist shared "communal understandings" (mean competition function, adaptation level).

The proof is established by showing that the signal functions $b_i(x_i)$ induce a nested sequence of dynamic boundaries as the system evolves. For example, in Fig. 1, activity level is denoted by w and all $b_i(w)$ are set equal to the same function $b(w)$ for simplicity. In system (8), for example, if all $f_i(w) \equiv f(w)$, all $B_i = B$, all $A_i = A$, all $I_i = J_i = 0$, and $f(w)$ is linear ($f(w) = dw$), then $b(w)$ is constant. Hence fluctuations in $b(w)$ describe

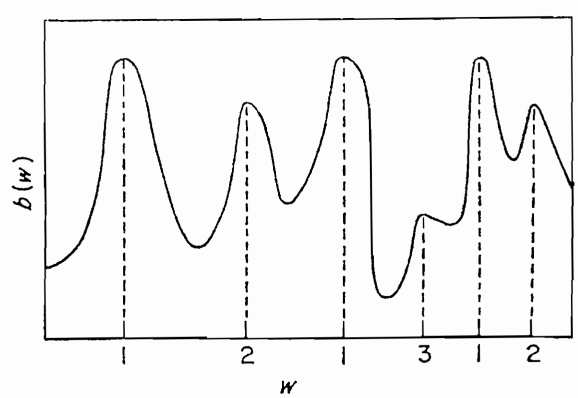

FIG. 1. Dynamic boundaries set in at a sequence of times $T_1 < T_2 < T_3 < \ldots$ with boundary values labelled 1, then 1 or 2, then 1 or 2 or 3, and so on.

nonlinearities of the signal function $f(w)$. Each "hill" in the graph of $b(w)$ is due to a random factor in its population; e.g. a subpopulation whose signal thresholds are Gaussianly distributed about a mean threshold value. It can be proved that, after a finite time T_1 goes by, no x_i can cross any of the abscissa values labelled 1. These values have as their ordinate the highest height of any "hill" in the graph of $b(w)$. Then after a finite time $T_2 > T_1$ goes by, no x_i can cross any of the abscissa values labelled 1 or 2, where the 2 values have as their ordinate the second highest height of any "hill" in the graph of $b(w)$. This process of switching-in uncrossable dynamic boundaries continues until each x_i is trapped in a "bowl" between two consecutive peaks in the graph of $b(w)$. After this occurs, the decision process is essentially complete, and a series of minor decisions can occur that lead ultimately to global pattern formation. A visual metaphor of this process is a lava field in which the height of the lava at each point v_i is $x_i(t)$. Initially there can be wild flowing and bubbling of lava across the field, but eventually the lava cools enough to simmer for awhile before hardening into a definite asymptotic pattern.

Equation (9) also includes a class of generalized Volterra–Lotka systems as a special case; namely, the systems

$$\dot{x}_i = A_i(x)[1 - \sum_{k=1}^{n} N_{ik}(x) f_k(x_k)], \tag{6b}$$

whose state-dependent coefficients satisfy $N_{ik}(x) = g_i(x_i)h_k(x_k)$. In these systems, the populations v_i and v_k influence $N_{ik}(x)$ via statistically independent factors $g_i(x_i)$ and $h_k(x_k)$, respectively. System (6b) can be written in the form equation (9) by letting

$$a_i(x) = A_i(x)g_i(x_i),\ b_i(x_i) = g_i^{-1}(x_i),$$

and

$$c(x) = \sum_{k=1}^{n} f_k(x_k)h_k(x_k).$$

Consequently, Volterra–Lotka systems with statistically independent interactions, that are essentially arbitrary, undergo global pattern formation. Otherwise expressed, the vector function $G(x) = (g_1(x_1), g_2(x_2), \ldots, g_n(x_n))$ describes a state-dependent preference order that leads to global consensus. Theorem 3 below shows that when no adaptation level exists in Volterra–Lotka systems, global pattern formation need not occur. There seems to be a trade-off, or complementarity, between how global the adaptation level ("communal understanding") is and how freely local signals ("individual differences") can be generated without destroying global consensus.

2. Competitive Systems

It is often convenient to write a competitive system in the form

$$\dot{x}_i = a_i(x)M_i(x), \tag{10}$$

$x = (x_1, x_2, \ldots, x_n)$, $i = 1, 2, \ldots, n$, where the continuous function $a_i(x)$ represents the state-dependent amplification, and the differentiable function $M_i(x)$ describes the state-dependent competitive balance at population v_i; e.g. in equation (6):

$$M_i(x) = 1 - \sum_{k=1}^{n} N_{ik}f_k(x_k),$$

and in equation (9):

$$M_i(x) = b_i(x_i) - c(x).$$

In addition to amplifying the competitive balance, $a_i(x)$ keeps x_i positive; that is, keeps

$$x \,\varepsilon\, \mathbb{R}^n_+ = \{y \,\varepsilon\, \mathbb{R}^n : y_i > 0, i = 1, 2, \ldots, n\}.$$

Populations v_i with $x_i(0) = 0$ are deleted from the network without loss of generality. Throughout the discussion below, we therefore restrict attention to systems whose variables remain in a bounded region R with positive co-ordinates. The intuition that $a_i(x)$ is an amplification becomes

$$a_i(x) > 0 \text{ if } x \,\varepsilon\, R \text{ and } x_i > 0, x_j \geq 0. j \neq i. \tag{11a}$$

That $a_i(x)$ keeps x_i positive becomes: There exists a continuous function $\bar{a}_i(x)$ such that

$$\bar{a}_i(x_i) \geq a_i(x) \text{ if } x \,\varepsilon\, R \tag{11b}$$

and

$$\int_0^\lambda \frac{\mathrm{d}w}{\bar{a}_i(w)} = \infty \text{ if } \lambda > 0, \tag{11c}$$

(cf. Grossberg, 1977*c*). Finally that $M_i(x)$ represents a competitive balance becomes

$$\frac{\partial M_i}{\partial x_j}(x) \leq 0 \text{ if } i \neq j \text{ and } x \,\varepsilon\, R, \tag{12a}$$

and keeping positive x_i values from becoming unbounded is achieved by supposing that there exists a constant $C > 0$ such that each

$$M_i(x) < 0 \text{ if } |x| \geq C \tag{12b}$$

where

$$|x| = \left(\sum_{k=1}^{n} x_k^2\right)^{1/2}.$$

3. Ignition and Jumps

Every competitive system has the properties of *positive ignition* and *negative ignition*. Positive ignition means that, after any population starts to be enhanced, some population will be enhanced at all future times. Negative ignition means that, after any population starts to be suppressed, some population will be suppressed at all future times. These properties are made precise in terms of the *maximal* and *minimal balance functions*.

$$M^+(x) = \max_k M_k(x) \tag{13a}$$

and

$$M^-(x) = \min_k M_k(x), \tag{13b}$$

respectively.

Definition 1 (*Ignition*)

A system has the property of *positive ignition* if $M^+(x(T)) = 0$ for some T implies $M^+(x(t)) \geq 0$ for all $t \geqslant T$. It has the property of *negative ignition* if $M^-(x(T)) = 0$ for some T implies $M^+(x(t)) \leq 0$ for all $t \geq T$.
These ignition properties hold in a more general class of systems than competitive systems. It is sufficient for the system to possess *positive* and *negative ignition surfaces*.

Definition 2 (*Ignition Surfaces*)

System (10) has a *positive ignition surface*

$$S^+ = \{x \varepsilon R : M^+(x) = 0\} \tag{14a}$$

if

$$\frac{\partial M_i}{\partial x_j}(x) \leq 0 \text{ if } i \neq j \text{ and } x \varepsilon S^+. \tag{15a}$$

ALSO NEED (39).

System (10) has a *negative ignition surface*

$$S^- = \{x \varepsilon R : M^-(x) = 0\} \tag{14b}$$

if

$$\frac{\partial M_i}{\partial x_j}(x) \leq 0 \text{ if } i \neq j \text{ and } x \varepsilon S^-. \tag{15b}$$

Lemma 1 (*Ignition*)

System (10) has the properties of positive and negative ignition if it satisfies (11) and possesses positive and negative ignition surfaces.

The simple proof, along with all other proofs, is in the Appendix. An immediate consequence of Lemma 1 is the basic fact that every competitive system possesses the properties of positive and negative ignition.

How are the ignition properties used? Suppose for example that the system never positively ignites. Then $M^+(x(t)) < 0$ for $t \geq 0$, so by system (10) and (11), $\dot{x}_i(t) \leq 0$ for $t \geq 0$ and all $i = 1, 2, \ldots, n$. Since each x_i is bounded, it monotonically decreases to a limit $x_i(\infty)$. Speaking intuitively, the competition never gets started. The positive ignition surface S^+ represents a type of competition threshold. It remains only to consider what happens if positive ignition does occur. Below we often let $M^+(x(0)) \geq 0$ without loss of generality. By system (10) and (11), this means that at every time $t \geq 0$, there exists some i such that $\dot{x}_i(t) \geq 0$. We will keep track of which i satisfies $M^+(x(t)) = M_i(x(t))$ at prescribed values of t. In other words, we define the integer-valued function $I(t)$ such that at every time $t \geq 0$,

$$M^+(x(t)) = M_{I(t)}(x(t)). \tag{16}$$

The variable that is maximally enhanced is thus the variable

$$y(t) = x_{I(t)}(t). \qquad t \geq 0. \tag{17}$$

Where can the trajectory $x(t)$, $t \geq 0$, be found after positive or negative ignition takes place? The answer uses the notion of *positive* and *negative ignition regions*.

Definition 3 (*Ignition Regions*)

The *positive ignition region* is

$$R^+ = \{x \varepsilon R : M^+(x) \geq 0\}. \tag{18a}$$

The *negative ignition region* is

$$R^- = \{x \varepsilon R : M^-(x) \leq 0\}. \tag{18b}$$

After positive ignition occurs, $x(t) \in R^+$; after negative ignition occurs, $x(t) \in R^-$. It suffices to restrict attention to system dynamics within these regions.

To analyze system behavior more finely after positive ignition occurs, we will study the function $I(t)$. To do this, we need the concept of *jumps*, or parallel choices.

Definition 4 (*Jumps*)

The system *jumps* from i to j at time $t = T$ if there exist constants S and U with $S < T < U$ such that $I(t) = i$ for $S \leq t < T$ and $I(t) = j$ for $T \leq t < U$.

4. Global Limits in a Generalized Pecking Order

The importance of the maximal balance function M^+ and the jump concept will now be illustrated by statements that imply the existence of a limit $x(\infty)$ given any $x(0) \in R$, or that global pattern formation occurs.

Theorem 1

Given an $x(0) \in R$, suppose that

$$\int_0^\infty M^+(x(t))\,\mathrm{d}t < \infty. \tag{19}$$

Then the limit $x(\infty)$ exists.

Using Theorem 1, one can prove that if only finitely many jumps occur in response to initial data $x(0)$, then $x(\infty)$ exists. Intuitively, this means that after all local decisions have been made, the system can form a well-defined pattern.

Corollary 1

If in response to initial data $x(0)$, all jumps cease after some time $T < \infty$, then $x(\infty)$ exists.

How can we decide in a particular system whether there are only finitely many jumps? To do this, we must study geometrical relationships that exist between the sets where jumps can occur between any pair (v_i, v_j) of populations. Of particular interest are cases wherein, given any pair (v_i, v_j) of populations, if a jump can go from i to j at some $x \in R$, then no jump can go from j to i at any $x \in R$. Intuitively, this concept establishes a local ordering of decisions between populations that is the same no matter what dynamical state the system attains.

Definition 5 (*Jump Sets*)

Given any pair (v_i, v_j) of distinct populations, and any set $\hat{R} \subset R$, the set

$$J_{ij}^+(\hat{R}) = \{x \varepsilon \hat{R} : M^+(x) = M_i(x) = M_j(x) \geq 0\} \tag{20a}$$

is called the *positive jump set* between v_i and v_j in $\hat{R}$. If a positive jump can go from i to j at some $x \in \hat{R}$, but no jump can go from j to i at any value of $x \in \hat{R}$, then the jump set is said to be *directed* from i to j, and is denoted by $J_{ij}^+(\hat{R})$ but not $J_{ji}^+(\hat{R})$. The (*directed*) *negative jump set* from v_i to v_j in $\hat{R}$, namely

$$J_{ij}^-(\hat{R}) = \{x \varepsilon \hat{R} : M^-(x) = M_i(x) = M_j(x) \leq 0\}. \tag{20b}$$

is similarly defined.

Typically, we will choose $\hat{R} = R^+$, or R^-, or $R^* = R^+ \cap R^-$, since we are interested in jumps only after positive and/or negative ignition occurs.

One important case in which global limits exist arises because there exists a "generalized pecking order" among all populations. This concept can be described using the idea of a *directed jump cycle*.

Definition 6 (*Directed Jump Cycle*)

Suppose that all jump sets in $\hat{R}$ are directed. A *directed jump cycle* is said to exist among the ordered and distinct populations $v_{i_1}, v_{i_2}, \ldots, v_{i_r}$ if the jump sets

$$J^+_{i_1 i_2}(\hat{R}), J^+_{i_2 i_3}(\hat{R}), \ldots, J^+_{i_{r-1} i_r}(\hat{R}), J^+_{i_r i_1}(\hat{R})$$

are non-empty.

Theorem 2 (*Global Pattern Formation*)

Consider any competitive system whose jump sets in R^+ are directed and contain no directed jump cycle. Then given any $x(0) \in R$, the limit $x(\infty) \in R$ exists.

Using Theorem 2, one can prove the existence of global pattern formation in a class of generalized n-dimensional Volterra–Lotka systems. Consider the systems

$$\dot{y}_i = A_i(y)\left[1 - \sum_{k=1}^{n} N_{ik} f_k(y_k)\right], \tag{21}$$

where $y = (y_1, y_2, \ldots, y_n)$ and $i = 1, 2, \ldots, n$. System (21) contains general state-dependent amplifications $A_i(y)$, nonlinear signal functions $f_k(y_k)$, and competition coefficients N_{ik}. Our first task is to reduce system (21) to a system of the form

$$\dot{x}_i = a_i(x)\left[1 - \sum_{k=1}^{n} N_{ik} x_k\right], \tag{22}$$

using the substitution $x_i = f_i(y_i)$. System (22) possesses linear interpopulation signals. A formal comparison of systems (21) and (22) shows that

$$a_i(x) = f_i'(f_i^{-1}(x_i)) A_i(f^{-1}(x_1), \ldots, f^{-1}(x_n)). \tag{23}$$

One set of assumptions will be imposed to guarantee that $a_i(x)$ in equation (23) satisfies conditions (11). The other set of assumptions concerns the jump sets $J^+_{ij}(R^+)$. In equation (22),

$$M_i(x) = 1 - \sum_{k=1}^{n} N_{ik} x_k,$$

so that $M_i(x) = M_j(x)$ only if

$$\sum_{k=1}^{n} (N_{ik} - N_{jk})\, x_k = 0. \tag{24}$$

Equation (24) defines a hyperplane H_{ij} through the origin in $\mathbb{R}^n$. Since

$$R^+ = \left\{x \in \mathbb{R}^n_+ : 1 \geq \min_i \sum_{k=1}^{n} N_{ik} x_k\right\}, \tag{25}$$

the (i, j)th jump set is contained in $H_{ij} \cap R^+$, which is a polyhedral section of a hyperplane. We will impose conditions on the coefficients N_{vu} which imply the existence of directed jump sets $J_{ij}^+(R^+)$ that contain no directed jump cycle. In particular, the jumps define a unidirectional drift, or pecking order, among the populations (Fig. 2).

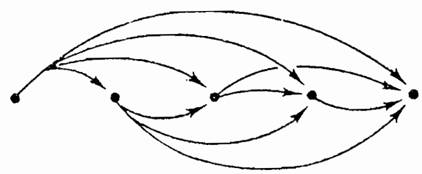

FIG. 2. A pecking order, or unidirectional drift, in the jumps between populations.

These conditions involve inequalities, rather than equalities, among the coefficients N_{vu}, and are therefore physically robust.

Corollary 2

In system (21), let each $f_i(w)$, $w \geq 0$, be a strictly monotone increasing differentiable function such that

(1) the system is positive; that is,

$$f_i(0) = 0 \tag{26}$$

and $a_i(x)$ in equation (23) satisfies (11);

(2) the system is bounded; that is,

$$1 < \sum_{k=1}^{n} N_{ik} f_k(\infty), \qquad i = 1, 2, \ldots, n; \tag{27}$$

and

(3) no directed jump cycle exists; that is, the populations $\{v_i\}$ can be relabelled such that for any $i < j$,

$$N_{ik} \leq N_{jk} \text{ if } k \neq i, j, \tag{28a}$$

and if

$$\sum_{k=1}^{n} (N_{ik} - N_{jk}) x_k = 0$$

then

$$\sum_{k=1}^{n} (N_{ik} - N_{jk}) a_k(x) \geq 0. \tag{28b}$$

Then given any positive initial data $x(0)$, at most $n-1$ jumps occur so that a finite non-negative limit $x(\infty)$ exists.

Note that these global results do not require any study of equilibrium points.

Corollary 2 shows that the Glass–Kauffman binary approximation of continuous networks is not justified in Volterra–Lotka systems, since sigmoid signals $f_i(y_i)$ can be chosen to satisfy its hypotheses. For example, one constraint on $f_i(t_i)$ is that $a_i(x)$ in equation (23) satisfies (11). Condition (11) constrains $\bar{a}_i(x_i)$ only near $x_i \cong 0$. For example, if

$$A_i(y) = \bar{A}_i(y_i) \cong y_i^{\alpha} \text{ for } y_i \cong 0, \tag{29}$$

and

$$f_i(y_i) \cong y_i^{\beta} \text{ for } y_i \cong 0, \tag{30}$$

then

$$a_i(x) = \bar{a}_i(x_i) \cong \beta x_i^{1+(\alpha-1)/\beta} \text{ for } x_i \cong 0, \tag{31}$$

and conditions (11) are satisfied for any $\beta > 0$ if $\alpha \geq 1$. In particular, sigmoid behavior near $y_i = 0$ (namely, $\beta > 1$) is a special case of Corollary 2. Constraint (28b) can also be satisfied by sigmoid signals. For example, if $A_i(y) = y_i$ and $f_i(y_i) = y_1^2(1+y_1^2)^{-1}$, then $a_i(x) = 2x_i(1-x_i)$. Condition (28b) then becomes
if

$$\sum_{k=1}^{n} (N_{ik} - N_{jk})x_k = 0$$

then

$$\sum_{k=1}^{n} (N_{ik} - N_{jk})x_k^2 \leq 0.$$

A special case of equation (22) is the Volterra–Lotka system

$$\dot{x}_i = x_i\left[1 - \sum_{k=1}^{3} N_{ik}x_k\right], \tag{32}$$

$i = 1, 2, 3$, in which three populations compete. Herein it is easily deduceif from the proof of Corollary 2 that all jump sets are directed, since d $M^+ = M_i = M_j \geq 0$ and $M^+ \geq M_k$, where $\{i, j, k\} = \{1, 2, 3\}$, then

$$\dot{M}_j - \dot{M}_i = (M^+ - M_k)x_k(N_{ik} - N_{jk}),$$

so that the sign of $N_{ik} - N_{jk}$ determines the direction of jumps between v_i and v_j. By Corollary, 2 if any pair (v_1, v_2), (v_2, v_3), or (v_3, v_1) of populations has an empty jump set, or if the jumps form a pecking order, then global pattern formation occurs. For example, if any two planar sets

$$P_i(1) = \left\{x \in \mathbb{R}_+^3 : \sum_{k=1}^{3} N_{ik}x_k = 1\right\}, \tag{33}$$

do not intersect, then the corresponding pairs of planar sets

$$P_i(\gamma) = \left\{x \in \mathbb{R}_+^3 : \sum_{k=1}^{3} N_{ik}x_k = \gamma\right\}, \tag{34}$$

do not intersect for any $\gamma \in (0, 1)$. Then at least one jump set in R^+ is empty, so that no directed jump cycle exists, and thus global pattern formation occurs. This condition generates easily drawn examples of nonlinear competition schemes among three populations in which global limits exist (Fig. 3).

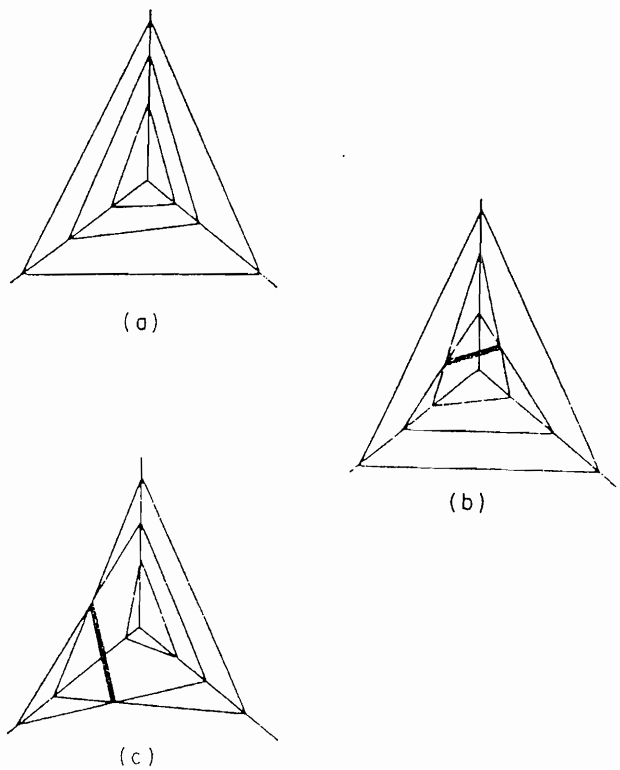

FIG. 3. Intersections of the sets $P_i(1)$ that produce global pattern formation.

5. Parametric Excitations Change the Decision Scheme

Figure 3 illustrates a physically interesting fact. Consider Fig. 3(c) for definiteness. In Fig. 3(c), only one jump can occur. Suppose that the planar surface closest to 0 is moved away from 0 without changing its direction. The surface will eventually intersect the other two surfaces. If it does so in a way that defines a pecking order, then global limits will again exist, but two jumps can occur. If, however, the surface creates a cycle of directed jump sets, then, as the next section will prove, sustained oscillations due to infinitely many cyclic jumps among the populations can be generated. If the surface is then moved further away from 0, it will again form no intersection with the other two surfaces; again only one jump can occur. Such motions of a surface can be effected by parametric excitation, via a parameter θ, of the form

$$\dot{x}_i = x_i \left[1 - \theta \sum_{k=1}^{3} N_{ik} x_k \right]. \tag{35}$$

To say that this parametric change does not alter the direction of the planar sets $P_i(\gamma)$ means that the *relative* strengths of the competition coefficients on v_i do not change in time. Parameter θ can thus describe changes in the sensitivity of v_i to competitive signals. For example, if θ increases slowly as a function of time, then it can switch the system from global pattern formation, to sustained oscillations, and finally back to global pattern formation. With these remarks as a point of departure, it is clear that parametric excitations that do change the direction of the planar sets $P_i(\gamma)$ can exert even more dramatic effects, such as switching a system in which two jumps generate pattern formation to a system in which infinitely many jumps occur, to a system in which a different pair of jumps generates pattern formation, and so on. These parametric changes can alter the system's geometry of interpopulation competition, rather than its intrapopulation sensitivities. Such geometrical changes can be caused, for example, by population migration if the competition coefficients are a function of interpopulation distance; cf. Grossberg (1978*c*, section 19) for a related discussion of cell aggregation in a nonlinear competitive system. Thus in systems where the competitive interactions cause changes in system parameters via feedback (say by creating gradients in which cells move), the jump structure can also change as new parametric configurations emerge. An important open problem (the "parametric feedback problem") is to characterize the types of feedback that generate a fixed asymptotic jump structure (including jump cycles) vs. types of feedback for which no asymptotic jump structure exists. In both types of system, the cells v_i generate a "field" via their competitive signals. This field, in turn, changes system parameters; for example, by causing cell motion and thereby changing the competition coefficients, or by altering cellular sensitivity by changing rate parameters. Given the new parameters, the intercellular signalling creates a new field, which changes system parameters once again. This feedback alternation between successive fields and parametric responses thereupon continues. If an asymptotic field exists, i.e. a field as $t \to \infty$ that is left invariant by its parametric feedback, an observer might conclude that the system is "developing" towards this asymptotic field. If no asymptotic field exists, an observer might conclude that the system is unpredictable, or physically "chaotic".

System parameters describe system structure, e.g. intercellular distances, in the parametric feedback problem. Structure becomes a dynamic property that is dependent on the nature of system feedback. For example, we might say that a system has a definite geometry if certain parameters change very slowly with respect to the time scale of jumps, yet could still understand how this geometry disintegrates rapidly when its maintaining feedback is disturbed.

Before leaving the subject of global limits, we note that Corollary 1 has a partial converse. Corollary 1 is proved by showing that the existence of finitely many jumps implies equation (19). Under what circumstances does equation (19) imply that only finitely many jumps occur? To make the main point, we restrict attention to Volterra–Lotka systems (32). The main idea is that if the jumps in any jump cycle are separated from each other, then equation (19) prevents the trajectory from travelling far enough to cross more than finitely many jumps sets. This fact is particularly easy to state when $n = 3$, since then all jumps are directed.

Definition 7 (*Separated jump sets*)

Two directed jump sets $J_{ij}(R^*)$ and $J_{jk}(R^*)$, where $R^* = R^+ \cap R^-$, are *separated* if the stable manifold $S(P)$ of every point P in their intersection lies outside R^*. (The stable manifold of P is the set of points, other than P, which lie on trajectories that approach P as $t \to \infty$.) In mathematical notation,

$$\text{if } P \varepsilon J_{ij}(R^*) \cap J_{jk}(R^*), \text{then } S(P) \cap R^* = \phi. \tag{36}$$

The definition assures that system trajectories are repelled away from points where directed jump sets of consecutive jumps intersect, so that there will exist a positive minimum distance traversed between successive jumps.

Corollary 3.

Suppose that a Volterra–Lotka system (32) with $n = 3$ has separated jump sets. Then the following statements are equivalent:

(1) global pattern formation occurs;
(2) given any $x(0) \in \mathbb{R}^3_+$, there exist finitely many jumps;
(3) given any $x(0) \in \mathbb{R}^3_+$,

$$\int_0^\infty M^+ \, (x(t)) \, dt < \infty. \tag{19}$$

6. Sustained Oscillations

Below some global results are proved concerning the existence of undamped oscillations in n-dimensional competitive systems. Several points of interest concerning these results will now be summarized. First, one can derive important information about oscillations by studying the positive ignition surface S^+. To carry out this study, it is unnecessary to consider equilibrium points that do not lie on S^+. In system (3), for example, if $(1-\alpha)(1-\beta) < 0$, there are five possible equilibrium points in $\mathbb{R}^3_+$, but only one of them lies on S^+. This result is of philosophical and biological interest. The existence of an ignition surface essentially characterizes the system as a competitive one. The result shows that system design at the extremal states where competition sets in (the competitive boundary) substantially constrains the competition after it gets under way (the competitive interior). In addition to designing S^+ properly, we need also to guarantee that the jump sets are sufficiently far apart from each other, as in equation (36).

The results will be built up as a series of lemmas. Theorem 1 and Corollary 1 imply the following lemma, which is our point of departure.

Lemma 1 (*Infinitely Many Jumps*)

If in response to initial data $x(0) \in \mathbb{R}^n_+$, the trajectory satisfies

$$\int_0^\infty M^+(x(t))\,\mathrm{d}t = \infty, \tag{37}$$

then infinitely many jumps occur.

Condition (37) has the following important consequence.

Lemma 2 (*Negative Ignition*)

If condition (37) holds, then negative ignition occurs.

Since obviously condition (37) implies that positive ignition occurs, condition (37) implies that the trajectory remains in the set $R^* = R^+ \cap R^-$ after some finite time, and jumps infinitely often within this set. Two tasks remain. The first task is to see how proper design of S^+ allows us to conclude that condition (37) holds in response to a well-defined class of initial data. The second task is to show how the existence of infinitely many jumps implies the existence of undamped oscillations in the x_i.

To guarantee condition (37), it is sufficient to repel a trajectory away from S^+ after positive ignition takes place. Since S^+ is characterized as the surface in $\mathbb{R}^n_+$ where $M^+ = 0$, by repelling $x(t)$ into the interior of R^+, one keeps $M^+(x(t)) \geq \theta > 0$ for $t \geq T_\theta$, and thus condition (37) holds. This observation leads to the next lemma, which we state using the notation $S(P)$ for the stable manifold of an equilibrium point P, with P deleted.

Lemma 3 (*Ignition Surface*)

Suppose that there are at most finitely many equilibrium points $P_1, P_2, \ldots, P_L$ in S^+. Let:

$$S(P_j) \cap R^* = \phi, \qquad j = 1, 2, \ldots, L. \tag{38}$$

Suppose that there exist positive constants δ and ε such that at every nonequilibrium point $y \in S^+$ that is outside the domain of repulsion of the equilibrium points $P_1, P_2, \ldots, P_L$, these exists an $i = i(y)$ such that

$$a_i(y)M_i(y) \leq -\delta \tag{39a}$$

and

$$\frac{\partial M^+}{\partial x_i}(y) \leq -\varepsilon. \tag{39b}$$

Then any trajectory that intersects S^+ at a nonequilibrium point satisfies condition (37).

Thus *any* trajectory that ignites without being trapped at an equilibrium point of S^+, is repelled into R^* thereafter if conditions (38) and (39) hold. In particular, if every trajectory eventually ignites, then condition (37) holds for all

$$x(0) \notin \bigcup_{j=1}^{L} S(P_j).$$

If condition (37) holds, how much can one conclude about the existence of oscillations?

Definition 8 (*Persistent and Undamped Oscillations*)

The function x_i undergoes *persistent oscillations* if it oscillates at arbitrarily large times. The function x_i undergoes *undamped oscillations* if it undergoes persistent oscillations and the limit $\lim_{t \to \infty} x_i(t)$ does not exist.

Lemma 4

If condition (37) holds, then some x_i undergoes persistent oscillations.

The proof notes that there must be some $x_i(t)$ such that $y(t) = x_i(t)$ in an infinite sequence of time intervals $T_{i1}, T_{i2}, \ldots$ whose union

$$T_i = \bigcup_{k=1}^{\infty} T_{ik}$$

satisfies:

$$\int_{Ti} M_i(x(t))\, dt = \infty. \tag{40}$$

If x_i were monotone increasing after some finite time, then equation (40) would imply the contradiction that $x_i(\infty) = \infty$. Consequently x_i undergoes persistent oscillations.

Equation (40) does not, however, imply that x_i undergoes undamped oscillations, since it is possible for x_i to approach zero in the intervals when $M_i < M^+$. Then equation (40) might produce progressively smaller oscillations as $t \to \infty$ since $a_i(x) = 0$ when $x_i = 0$. To derive undamped oscillations from persistent oscillations, we must study whether x_i is driven away from 0 while $M^+ = M_i$. In particular, we must study the geometry of the jump sets. The geometry of jump sets must also be studied to test whether more than one x_i oscillates persistently, in particular whether all x_i oscillate persistently.

Definition 9 (*Asymptotic Graph*)

The (*positive*) *asymptotic graph* A^+ is the directed network of all vertices v_i such that $y(t) = x_i(t)$ at arbitrarily large times, and of all directed edges e_{ij} such that a jump occurs from v_i to v_j at arbitrarily large times; i.e. $v_i \rightarrow v_j$ means that jumps occur from i to j at arbitrarily large times.

In this definition, we do not explicitly say which initial data $x(0)$ generates the asymptotic graph under consideration, but this will always be clear in a particular context. Because the asymptotic graph contains only vertices and edges that represent configurations that repeat themselves infinitely often, the following lemma holds.

Lemma 5 (*Asymptotic Cycles*)

The asymptotic graph A^+ consists of a union of directed cycles $v_{i_1} \rightarrow v_{i_2} \rightarrow \ldots \rightarrow v_{i_k} \rightarrow v_{i_1}$ such that any two vertices are connected by a directed chain of edges; i.e., it is a Eulerian graph (Fig. 4).

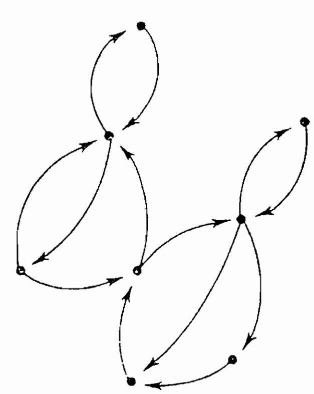

FIG. 4. The asymptotic graph A^+ is composed of cycles in which any population is connected to any other population by a directed chain of asymptotic jumps.

It suffices to consider the jump sets of vertices in A^+. We now study the geometry of jump sets to decide when *all* the x_i in A^+ undergo undamped oscillations. By Lemma 4, if a given x_i satisfies equation (40) then it undergoes persistent oscillations. Thus we wish to guarantee that $M_i(x(t))$ is sufficiently large whenever $t \in T_i$, and that the total length of intervals in

T_i is infinite. The former constraint can be achieved by repelling the trajectory away from S^+ after positive ignition takes place. Since $M^+ = 0$ on S^+, this will keep M^+ positive at all large times. This can be achieved by letting equations (38) and (39) hold. To guarantee that T_i has infinite length, it suffices to prevent jumps to and from v_i from occurring too rapidly as $t \to \infty$. This can be achieved either if jump sets of the form $J_{ji}(R^*)$ and $J_{ik}(R^*)$ do not intersect, or if they do intersect at any point P, then trajectories within R^* are repelled from P. Consequently we assume that all jump sets of vertices in A^+ are separated; or that, for any distinct v_i, v_j, and v_k in A^+.

$$\text{if } P \varepsilon J_{ij}(R^*) \cap J_{jk}(R^*) \text{ then } S(P) \cap R^* = \phi. \tag{36}$$

Finally, to convert persistent oscillations into undamped oscillations, it suffices to prevent x_i from remaining close to zero throughout the time intervals while $M^+ = M_i$. Hence we assume that if $v_i \in A^+$ then there exists a $v_j \in A^+$ such that

$$J_{ij}(R^*) \cap \{x \varepsilon \mathbb{R}^n_+ : x_i = 0\} = \phi. \tag{41}$$

Because $v_j \in A^+$, equation (41) implies that there exist time intervals when $M^+ = M_i$ and x_i is bounded away from zero. If equation (36) also holds, then the length of these time intervals will have a positive lower bound, so that x_i will undergo sustained oscillations. These observations are summarized below.

Theorem 3 (*Sustained Oscillations*).

1. *Ignition Surface*: Suppose that there are at most finitely many equilibrium points $P_1, P_2, \ldots, P_L$ in S^+. Let

$$S(P_j) \cap R^* = \phi, \qquad j = 1, 2, \ldots, L \tag{38}$$

and suppose that there exist positive δ and ε such that at any nonequilibrium point $y \in S^+$ that is outside the domain of repulsion of the equilibrium points $P_1, P_2, \ldots, P_L$, there exists an $i = i(y)$ such that

$$a_i(y) M_i(y) \leq -\delta, \tag{39a}$$

and

$$\frac{\partial M^+}{\partial x_i}(y) \leq -\varepsilon. \tag{39b}$$

2. *Jump Sets*: Suppose that for any distinct v_i, v_j, $v_k \in A^+$,

$$\text{if } P \varepsilon J_{ij}(R^*) \cap J_{jk}(R^*) \text{ then } S(P) \cap R^* = \phi. \tag{36}$$

Moreover, given any $v_i \in A^+$, there exists a $v_j \in A^+$ such that

$$J_{ij}(R^*) \cap \{x \varepsilon \mathbb{R}^n_+ : x_i = 0\} = \phi. \tag{41}$$

Then given any trajectory that intersects S^+ at a nonequilibrium point, every x_i in its asymptotic graph undergoes sustained oscillations as the system jumps infinitely often among its Eulerian cycles.

The above constraints apply to Volterra–Lotka systems in a natural way, and in fact are all trivially verified in equation (3) if $\alpha+\beta \geq 2$ and $(1-\alpha)(1-\beta) < 0$. In equation (3),

$$M_1(x) = 1 - x_1 - \alpha x_2 - \beta x_3 \tag{42a}$$

$$M_2(x) = 1 - \beta x_1 - x_2 - \alpha x_3 \tag{42b}$$

and

$$M_3(x) = 1 - \alpha x_1 - \beta x_2 - x_3 \tag{42c}$$

The planar sets $M_i(x) = 0$, $x \in \mathbb{R}^3_+$, $i = 1, 2, 3$, are drawn in Fig. 5(a) under the assumption $\beta > 1 > \alpha$. In Fig. 5(b) and (c), the positive (negative) ignition surface is drawn. In Fig. 5(a), there exist exactly five equilibrium points. Note that only one equilibrium point $P = (\gamma, \gamma, \gamma)$, where $\gamma = (1+\alpha+\beta)^{-1}$, lies in S^+, and that P is the only point of intersection of S^+ and S^-. Region R^* is sandwiched between S^+ and S^-. To verify equation (38), one notes that all solutions of the form $x_1 = x_2 = x_3 > 0$ converge to P whether or not $\alpha+\beta \geq 2$. If $\alpha+\beta \geq 2$, then the stable manifold

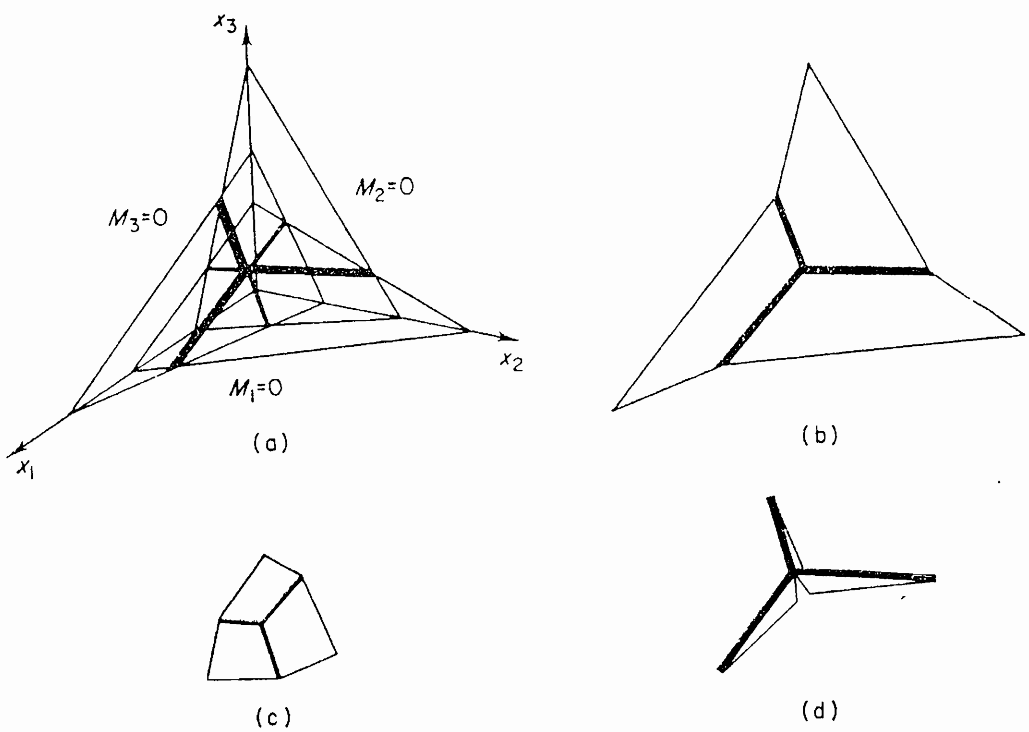

FIG. 5. (a) The sets $M_i(x) = 0$, $x \varepsilon R^3{}_+$; (b) The positive ignition surface; (c) The negative ignition surfaces; (d) The jump sets.

is one dimensional and equals

$$S(P) = \{(y, y, y) \neq P : y > 0\}.$$

In fact the eigenvalues at P are

$$\lambda_1 = -1, \lambda_2 = \tfrac{1}{2}\gamma[\alpha + \beta - 2 + (\alpha - \beta)\sqrt{3i}],$$

and

$$\lambda_3 = \tfrac{1}{2}\gamma[\alpha + \beta - 2 - (\alpha - \beta)\sqrt{3i}];$$

cf., May & Leonard (1975). Thus P is a stable critical point unless $\alpha+\beta \geq 2$. In the latter case, only λ_1 has a negative real part and its eigenvector is (1, 1, 1). To verify equation (39), note that $\partial M_i/\partial x_j$ is a negative constant (-1, $-\alpha$, or $-\beta$) for each i and j. To verify equation (36), the jump sets are drawn in Fig. 5(d). They are triangular in shape, intersecting in R^* only at P. Hence equation (36) follows from equation (38) in this case. To verify equation (41), note that since equation (3) is a three-dimensional Volterra–Lotka system, all jumps are directed, and because $\beta > 1 > \alpha$, all jumps proceed along the cycle $v_1 \to v_2 \to v_3 \to v_1$. Thus all populations v_1, v_2, and v_3 are in A^+. It is obvious by inspection of Fig. 5(d) that for any distinct choice of $\{i, j, k\} = \{1, 2, 3\}$, equation (41) holds. These results are summarized in the following corollary.

Corollary 4 (*Volterra–Lotka oscillations*)

Suppose that $\beta > 1 > \alpha$ and $\alpha+\beta \geq 2$ in equation (3). Then in response to any initial data $x(0) \in \mathbb{R}^3_+$ such that $x(0) \notin \{(y, y, y) : y > 0\}$, both positive and negative ignition occur, equation (37) holds, infinitely many jumps occur in the cyclic order $v_1 \to v_2 \to v_3 \to v_1$, and all variables x_i, $i = 1, 2, 3$, undergo sustained oscillations.

Corollary 4 can be generalized to include more general Volterra–Lotka systems than equation (3); for example:

$$\dot{x}_i = x_i\left[1 - \sum_{k=1}^{3} N_{ik}x_k\right], \tag{32}$$

$i = 1, 2, 3$, in which the coefficients 1, α, β are replaced by the inequalities $N_{21} > N_{11} > N_{31}$, $N_{32} > N_{22} > N_{12}$, and $N_{13} > N_{33} > N_{23}$, and it is required that the coefficient matrix $N = \|N_{ij}\|$ be invertible so that only one $P \in S^+$ exists. Again equation (36) follows from equation (38), and equation (39) is obvious, but computing $S(P)$ for these more general choices of competition coefficients is tedious.

The above results provide information about the geometrical designs that can produce global limits or oscillations. These results can, of course, be supplemented by other forms of analysis, as in May & Leonard (1975), where limit cycles are numerically found if $\alpha+\beta = 2$ but non-periodic oscillations are found if $\alpha+\beta > 2$. May & Leonard claim that when $\alpha+\beta > 2$, the non-periodic trajectory approaches the set of straight lines between (1, 0, 0), (0, 1, 0), and (0, 0, 1). This is not correct. Fig. 6 shows the vector field in the two-dimensional invariant region R_{23} where $x_1 = 0$, $x_2 \geq 0$, $x_3 \geq 0$, $M_2 \geq 0$, and $M_3 \leq 0$. Clearly every trajectory that enters R_{23} with $x_2 > 0$ approaches (0, 1, 0) as $t \to +\infty$. It is also clear by the continuity of the flow that there is a heteroclinic trajectory from

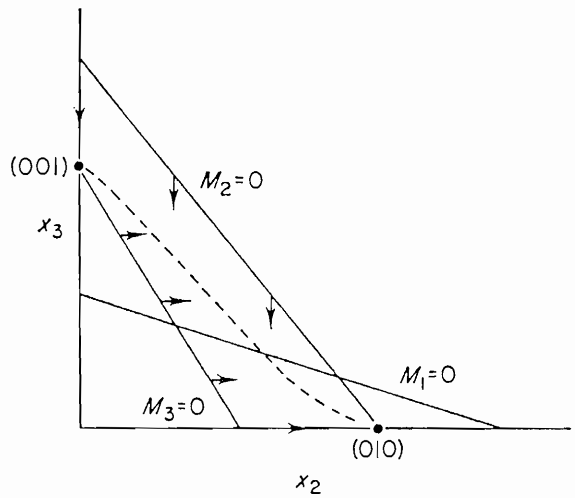

FIG. 6. The vector field in the region R_{23} admits a nonlinear heteroclinic trajectory from (1, 0, 0) to (0, 1, 0) if $\alpha+\beta > 2$.

(0, 0, 1) to (0, 1, 0), but this trajectory is not a straight line, as can be shown by contradiction. By contrast, if $\alpha+\beta = 2$, there is a straight heteroclinic trajectory from (0, 0, 1) to (0, 1, 0) of the form:

$$x_2(t) = e^{(1-\alpha)t}[A + e^{(1-\alpha)t}]^{-1}, x_3(t) = e^{(\alpha-1)t}[A^{-1} + e^{(\alpha-1)t}]^{-1}.$$

In a similar fashion, there exist heteroclinic trajectories from (0, 1, 0) to (1, 0, 0), and from (1, 0, 0) to (0, 0, 1), neither of which are straight lines. Any trajectory that approaches the union of these heteroclinic trajectories will have an increasing period of oscillation as $t \to \infty$ since each heteroclinic trajectory takes an infinite amount of time to go from its source to its sink.

7. Continuous, Parallel and Microscopic or Discrete, Serial, and Macroscopic?

Several general themes and problems are suggested by the above results. Of central interest is the fact that a continuous competitive system can be analyzed in terms of a discrete series of jumps. The competition is expressed by parallel interactions, yet the jumps occur serially in time. The analysis of a parallel system in terms of serial events can be interpreted in terms of a macroscopic observer as follows: the observer measures the most detectable changes in the system; these appear to be a serial series of enhancement steps. However, accurate prediction of which step will follow the next requires an analysis of the system's microscopic parallel dynamics. This example thus illustrates how a parallel system can appear to be serial when observed through coarse measuring devices that are insufficient to predict the system's temporal evolution.

At least three major problems are suggested by the above results. First, classify the asymptotic graphs that can arise in physically important competitive systems. Second, classify parametric feedback schemes that do generate a definite asymptotic graph as $t \to \infty$ vs. schemes that do not. Third, classify the nested dynamic boundaries that arise due to particular combinations of physical boundaries and nonlinear signals in competitive systems.

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APPENDIX

Lemma 1

It suffices to prove that if $M^+(x(S)) = 0$ at some time $t = S$, then $\mathrm{d}/\mathrm{d}t\, M^+(x(S)) \geq 0$. Suppose that $M^+(x(S)) = M_i(x(S))$. Then

$$\frac{\mathrm{d}}{\mathrm{d}t} M^+(x(S)) = \sum_{k=1}^{n} \frac{\partial M_i}{\partial x_k}(x(S))\dot{x}_k(S)$$

or

$$\frac{\mathrm{d}}{\mathrm{d}t} M^+(x(S)) = \sum_{k=1}^{n} \frac{\partial M_i}{\partial x_k}(x(S))a_k(x(S))M_k(x(S)). \tag{A1}$$

Since $M_i(x(S)) = 0$, the ith term in this sum vanishes. Since each $x_k(S) > 0$, equation (11) implies that each $a_k(x(S)) > 0$. Moreover $0 = M^+(x(S)) \geq M_k(x(S))$, and by equations (14a) and (15a), $\partial M_i/\partial x_k(x(S)) \leq 0$ for $k \neq i$. Consequently, $\mathrm{d}/\mathrm{d}t\, M^+(x(S)) \geq 0$ as desired. A similar proof using equations (14b) and (15b) establishes negative ignition.

Theorem 1

If the system never positively ignites, then all x_i monotonically decrease to non-negative limits. If the system does ignite, then the integral

$$\int_0^\infty M^+(x(t))\,\mathrm{d}t$$

can be broken into two parts, one negative, say from time 0 to S, and one positive, from time S to ∞. Hypothesis (19) says that this latter integral is finite. Let $S = 0$ for definiteness. Define:

$$N(T) = \int_T^\infty M^+(x(t))\,\mathrm{d}t. \tag{A2}$$

Because $M^+(x(t)) \geq 0$ for $t \geq 0$, hypothesis (19) implies that $N(T) < \infty$ and that $N(T)$ decreases monotonically to zero as $T \to \infty$. By equation (10), for every $i = 1, 2, \ldots, n$,

$$\dot{x}_i = a_i M_i \leq a_i M^+. \tag{A3}$$

Since $a_i(x)$ is a continuous function on the compact set R, there exists a $\delta > 0$ such that $a_i(x) \leq \delta$, $x \in R$. By equation (A3),

$$\dot{x}_i \leq \delta M^+. \tag{A4}$$

Integrate equation (A4) from any time T to any time U. Then:

$$x_i(U) - x_i(T) \leq \delta \int_T^U M^+(x(t))\,\mathrm{d}t. \tag{A5}$$

By equations (A2) and (A5),

$$x_i(U) - x_i(T) \leq \delta N(T). \tag{A6}$$

Since $\lim_{T\to\infty} N(T) = 0$, equation (A6) shows that $x_i(t)$ is essentially monotone decreasing as $t \to \infty$. Since also $x_i \geq 0$, the limit $x_i(\infty)$ exists, $i = 1, 2, \ldots, n$.

Corollary 1

Suppose that no jump occurs after $t = T$. Let $M^+(x(t)) = M_1(x(t)) \geq 0$, $t \geq T$, for definiteness. By equation (10), $\dot{x}_1(t) \geq 0$ for $t \geq T$, and since x_1

is bounded above, $x_1(\infty)$ exists. Also by equation (10), $\dot{x}_1 = a_1 M^+$ for $t \geq T$, so that for any $U \geq T$,

$$x_1(U) - x_1(T) = \int_T^U a_1(x(t)) M^+(x(t))\, dt. \tag{A7}$$

Since $x_1(T) > 0$ and $x_1(t)$ is monotone increasing for $t \geq T$, it follows that $x_1(t) \geq x_1(T) > 0$ for $t \geq T$. Thus by inequality (11), there exists a $\delta > 0$ such that $a_1(x(t)) \geq \delta$ for $t \geq T$. By equation (A7),

$$x_1(U) - x_1(T) \geq \delta \int_T^U M^+(x(t))\, dt. \tag{A8}$$

Let $U \to \infty$ and use the fact that $x_1(\infty)$ exists and is finite to conclude from equation (A8) that:

$$\int_T^\infty M^+(x(t))\, dt < \infty,$$

and thus that equation (19) holds.

Theorem 2

Since all jump sets are directed and no jump cycles exist, there must exist finitely many jumps, in fact no more jumps than the number of jump sets given any $x(0)$. By Corollary 1, the limit $x(\infty)$ exists.

Corollary 2

The conditions on f_i allow us to transform equation (21) to equation (22) by substituting equation (21) into $\dot{x}_i = f_i'(y_i)\dot{y}_i$, and writing $y_k = f_k^{-1}(x_k)$ wherever y_k appears, $k = 1, 2, \ldots, n$. Boundedness follows from equation (27) which implies inequality (12b). The main constraint is condition (28). To check whether jumps between v_i and v_j are directed, suppose that

$$M^+(x(T)) = M_i(x(T)) = M_j(x(T)) \geq 0, \tag{A9}$$

at some time $t = T$. Since

$$M_p = 1 - \sum_{k=1}^n N_{pk} x_k. \tag{A10}$$

equation (A9) implies that

$$\sum_{k=1}^n (N_{ik} - N_{jk}) x_k(T) = 0. \tag{A11}$$

To test the direction of jumps, we check the relative sizes of $\dot{M}_j(x(T))$ and $\dot{M}_i(x(T))$. By equation (A10) and (10),

$$\dot{M}_j(x(T)) - \dot{M}_i(x(T)) = \sum_{k=1}^n (N_{ik} - N_{jk}) a_k(x(T)) M_k(x(T)).$$

By equation (A9),

$$\dot{M}_j(x(T)) - \dot{M}_i(x(T)) = M^+(x(T)) \sum_{k=i\,j} (N_{ik} - N_{jk}) a_k(x(T)) + \sum_{k \neq i\,j} (N_{ik} - N_{jk}) a_k(x(T)) M_k(x(T)).$$

By equations (A11) and (28b),

$$\dot{M}_j(x(T)) - \dot{M}_i(x(T)) \geq \sum_{k \neq i\,j} (N_{jk} - N_{ik}) a_k(x(T)) \left[M^+(x(T)) - M_k(x(T))\right]. \qquad \text{(A12)}$$

Clearly $a_k(x(T)) > 0$ and $M^+(x(T)) \geq M_k(x(T))$, for $k = 1, 2, \ldots, n$. By inequality (28), also $N_{jk} \geq N_{ik}$ for $k \neq i, j$. Consequently $\dot{M}_j(x(T)) \geq \dot{M}_i(x(T))$ so that, given any $i < j$, jumps can only go from i to j no matter how $x(0)$ is chosen, and at most $n-1$ jumps can occur.

Corollary 3

We already know that property (2) implies property (3), and that property (3) implies property (1). To prove that property (1) implies property (2), it suffices to show that $x(t)$ must travel at least some positive distance δ before a jump can occur. Separating the jump sets accomplishes this by preventing $x(t)$ from getting arbitrarily close to the intersection of any pair of jump sets that represent a possible jump transition.

Lemma 1

If there are only finitely many jumps, then inequality (19) holds.

Lemma 2

If negative ignition does not occur, then $\dot{x}_i(t) \geq 0$ for all $i = 1, 2, \ldots, n$ and $t \geq 0$. Since there exist only finitely many x_i, equation (37) implies that there exists some x_i, say x_1, such that:

$$\int_{T_1} M_1(x(t))\,\mathrm{d}t = \infty, \qquad \text{(A13)}$$

where

$$M^+(x(t)) = M_1(x(t)) \text{ if } t \,\varepsilon\, T_1. \qquad \text{(A14)}$$

By constraints (10), (11), and the fact that x_1 is monotone increasing, there exists a $\delta > 0$ such that $\dot{x}_1 \geq \delta M_1$. By equation (A13) and the fact that x_1 is monotone increasing, it follows that $x_1(\infty) = \infty$, which is impossible.

Lemma 3

By inequalities (39), after $x(t)$ intersects S^+, it is repelled away from all P_i, $i = 1, 2, \ldots, L$. Consequently, $x(t)$ can only approach S^+ from within R^+ at a nonequilibrium point y that is as least some distance α away from any

P_i, $i = 1, 2, \ldots, L$. At any such y, $M^+(y) = 0$ so that all $a_i(y)M_i(y) \leq 0$, $i = 1, 2, \ldots, n$. If $x(t)$ could intersect S^+, say $x(T) = y$ when $M^+(x(T)) = M_j(x(T)) = 0$, then

$$\frac{dM^+}{dt}(x(T)) = \sum_{k \neq j} \frac{\partial M_j}{\partial x_k}(x(T))a_k(x(T))M_k(x(T)).$$

By equation (39), $dM^+/dt\,(x(T)) \geq \delta\varepsilon$. Consequently, $x(t)$ can never reach S^+, and remains uniformly bounded away from S^+ in R^+. Thus there exists an $\beta > 0$ and a T_β such that $M^+(x(t)) \geq \beta$ if $t \geq T_\beta$, which implies equation (37).

Lemma 4

If not, then all x_i are monotonic after a prescribed time $t = T$. The proof of Lemma 2 can now be imitated to prove that some $x_i(\infty) = \infty$, which is impossible.

Lemma 5

The proof is an obvious consequence of the definition of A^+.

Theorem 3

The proof is outlined in the text.

Corollary 4

The proof is outlined in the text.