# Biological competition: Decision rules, pattern formation, and oscillations

(development/cooperation/voting paradox/Volterra-Lotka/self-organization)

#### STEPHEN GROSSBERG

Department of Mathematics, Boston University, Boston, Massachusetts 02215

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ABSTRACT Competition solves a universal problem about pattern processing by cellular systems. Competition allows cells to automatically retune their sensitivity to avoid noise and saturation effects. All competitive systems induce decision schemes that permit them to be classified. Systems are identified that achieve global pattern formation, or decision-making, no matter how their parameters are chosen. Oscillations can occur due to contradictions in a system's decision scheme. The pattern formation and oscillation results are extreme examples of a complementarity principle that seems to hold for competitive systems. Nonlinear competitive systems can sometimes appear, to a macroscopic observer, to have linear and cooperative properties, although the two types of systems are not equivalent. This observation is relevant to theories about the evolutionary transition from competitive to cooperative behavior.

## 1. Biological signal processing and competitive decisions

Darwin's classic work (1) on the survival of the fittest emphasized the importance of competition as a universal principle of biological organization. Darwin's theory was formulated in terms of macroscopic variables such as competing species. More recently, competitive interactions have been shown (2-5) to solve a universal dilemma concerning the processing of patterned information by any noisy system with finitely many excitable sites. All cellular systems are of this type. This dilemma, called the noise-saturation dilemma, notes that small signals to the system can get lost in noise whereas large signals can saturate system response by exciting all of its sites and thereby reducing to zero its sensitivity to signal fluctuations. The dilemma describes a fundamental problem concerning the transmission of information by biological systems because, by trying to avoid noise, the system might amplify the signals so much that saturation occurs, and conversely. The noise-saturation dilemma is solved by competitive systems, and the solution shows how such systems can automatically retune themselves to avoid both noise and saturation. This fact supplies a basic reason for the universal existence of competition on both the microscopic and the macroscopic level and throws a new light on Darwin's concept of biological competition.

Given that competitive systems are ubiquitous, we need a general method for classifying some of the rich variety of their dynamical possibilities. Smale (6) has shown that essentially any dynamical behavior can be embedded in a suitably defined competitive system. The present method reverses his approach by providing a tool for designing, analyzing, and classifying competitive systems that have desirable biological behavior.

This note announces that every competitive system induces a decision scheme that can be used for global analysis of the competition as it evolves through time. The method has been used to explicate radically different types of dynamical behavior within competitive systems. Section 4 below summarizes a result concerning global pattern formation by systems possessing any number of competing populations. This result describes a principle of system design that guarantees the absolute stability of pattern formation; that is, pattern formation occurs no matter how system parameters are chosen within this class of systems. This principle of design means intuitively that the system possesses an adaptation level. Any such competitive system is capable of resolving essentially arbitrary irregularities in local system design into a global consensus or decision among the system's components by balancing these irregularities against the adaptation level. Some systems that arise within Eigen's theory of macromolecular evolution are of this type (7). Neural networks and other cellular and chemical mass action systems are often of this form (3, 4, 8). The systems also suggest new models of stable economic markets (M. W. Hirsch, personal communication).

Section 3 below illustrates how the method can be used to prove global oscillation theorems for systems of arbitrarily many competing populations (9). The oscillations reflect a system's inability to arrive at a global decision. The two types of theorems—pattern formation and oscillations—are extreme examples of a complementarity principle that seems to hold in competitive systems.

In this idea of decision, the decisions are defined by structures that exist far from equilibrium. The method hereby shows that measures of the nonequilibrium behavior of competitive systems often provide a deeper insight into their design than does the traditional local analysis of their equilibrium points.

#### 2. Decisions in competitive systems

Suppose that a system is defined by n quantities  $x = (x_1, x_2, ..., x_n)$  evolving through time. For example,  $x_t(t)$  might be the population size, or activity, or concentration, etc. of the *i*th species  $v_i$  in the system, i = 1, 2, ..., n. A system

$$\frac{dx}{dt} = f(x), \quad x \in R,$$
<sup>[1]</sup>

is said to be competitive if its ith component

$$\frac{dx_i}{dt} = f_i(\mathbf{x}) \tag{2}$$

satisfies

$$\frac{\partial f_i(x)}{\partial x_i} \le 0 \text{ if } i \neq j \text{ and } x \in R, \qquad [3]$$

and the system remains in a bounded region R of Euclidean n space. In other words, increasing  $x_j$  can only decrease  $x_i$ 's rate of change, but might not change it at all, for all  $i \neq j$ .

The new concept of decision can be motivated in the following fashion. Suppose that an experimentalist is looking at a petri dish filled with an unknown material. What does the experimentalist notice? Usually, one's attention goes to those regions of the petri dish where something is changing. If sud-

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denly a change occurs in a new region of the dish, attention is focused on the new region. Our attention hereby jumps from region to region as new changes appear. Just as our attention jumps to follow the most noticeable system changes, we can formalize the maximal changes in system activity as decisions within the system that regulate which of its regions are active.

Actually, the intuitive notion of decision can be explicated in several directions by using competitive systems as a guide. The decisions to be described below are "local" decisions that might, or might not, terminate as time goes on. When they terminate in pattern formation, the entire system has made a more global decision based on the series of local decisions. If this competitive system is embedded as a component in a hierarchy of competitive subsystems, linked together by adaptive feedback pathways, then the patterns at each level in the hierarchy sometimes mutually reinforce and amplify each other, thereby locking each other into a global activity pattern that represents a functional unit of the entire system and which can thereupon drive adaptive changes in system structure. Such adaptive resonances define a yet higher sense in which competitive systems participate in biological decision-making (5, 10). Each of these levels of decision-making acts on different spatial and temporal scales, and each must be analyzed before decisionmaking by an organism as a whole can be understood.

To see how jumps, or local decisions, are formalized, a competitive system often can be written in the form

$$\dot{x}_i = a_i(x_i)M_i(x), \quad i = 1, 2, \ldots, n.$$
 [4]

For example, in the classical Volterra-Lotka systems

$$\begin{aligned} & \stackrel{\#_i^c}{x_i} = A_i x_i \ (1 - \sum_{k=1}^n B_{ik} x_k), \\ & a_i(x_i) = A_i x_i, \text{ and} \end{aligned}$$
 [5]

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

Intuitively,  $M_i(x)$  defines the competitive balance at the *i*th state  $v_i$ , and  $a_i(x_i)$  is an amplification coefficient that converts the competitive balance into the growth rate  $dx_i/dt$  of  $x_i$ . In particular,  $a_i(x_i) > 0$  unless  $\mathbf{x}_i = 0$ ,  $a_i(0) = \mathbf{0}$ , and

$$\frac{\partial M_i(x)}{\partial x_j} \leq 0 \text{ if } i \neq j \text{ and } x \in \mathbb{R}.$$
 [6]

To track which states are changing fastest and slowest, we define

$$M^{+}(x) = \max_{k} M_{k}(x) \text{ and } M^{-}(x) = \min_{k} M_{k}(x).$$
 [7]

One then proves that there exists a competition threshold; namely, if  $M^+[x(T)] \ge 0$  at some time t = T, then  $M^+[x(t)] \ge 0$  at all times  $t \ge T$ . Thus, if some state  $v_i$  is being enhanced at time t = T [that is,  $d/dt x_i(T) \ge 0$ ], then at every future time  $t \ge T$ , some state  $v_j$  will be enhanced, but possibly different states at different times. In other words, if the competition "ignites" at some time t = T, then it thereafter never turns off. Set

$$S^+ = [x \in R: M^+(x) = 0]$$
 [8]

is thus a competition threshold, and once the *positive ignition* region

$$R^+ = [x \in R: M^+(x) \ge 0]$$
 [9]

is entered, it never can be left. In mathematical parlance,  $R^+$  is a positively invariant region.

Similarly, if  $M^{-}[x(T)] \leq 0$  at some time t = T, then  $M^{-}[x(t)] \leq 0$  at all times  $t \geq T$ . Thus, if some state  $v_t$  is being suppressed

at time t = T [that is,  $d/dt x_i(t) \le 0$ ], then at every future time  $t \ge T$ , some state  $v_j$  will be suppressed, but possibly different states at different times. Set

$$S^{-} = [x \in R: M^{-}(x) = 0]$$
 [10]

defines the threshold at which suppression sets in, and the negative ignition region

$$R^{-} = [x \in R: M^{-}(x) \le 0]$$
[11]

is a positively invariant region.

How are the regions  $R^{\pm}$  and  $R^{-}$  used? Suppose x(t) never enters  $R^{+}$ . Then, by Eq. 4, each  $d/dt x_i(t) \leq 0$  at all times  $t \geq 0$ . Consequently,  $x_i(t)$  monotonically decreases to a limit. In this case, the competition never gets started. The interesting behavior in any competitive system occurs within the invariant region  $R^{+}$ , and really within the smaller invariant region  $R^{*}$  $= R^{+} \cap R^{-}$  because, if x is in  $R^{+}$  but not  $R^{-}$ , all  $x_is$  are increasing and the limit  $x(\infty) = \lim_{t \to \infty} x(t)$  trivially exists.

After ignition takes place [i.e., x(t) is in  $\mathbb{R}^*$ ], we keep track of which state  $v_i$  is being maximally enhanced at any time. That is, we pay attention to the biggest rates of change. If, for example,  $M^+[x(t)] = M_i[x(t)]$  for  $S \le t < T$  but  $M^+[x(t)] =$  $M_j[x(t)]$  for  $T \le t < U$ , then we say that the system jumps from i to j at time t = T. These jumps are the local decisions in a competitive system. A jump from i to j can only occur on the jump set

$$J_{ij} = [x \in R^*: M_i(x) = M_j(x) = M^+(x)].$$
 [12]

Because this set is defined where the  $x_i$ s are changing at a maximal rate, it defines a hypersurface that is far away from the equilibrium points x such that dx/dt = 0 of the system. By studying the geometrical relationships of the jump sets within  $R^*$ , global results have been proved about pattern formation and oscillations in nonlinear systems with any number  $n \ge 2$  of competing states. Below, I briefly summarize two applications of the theory to systems that are, on the surface, very different, although both are amenable to the present method.

#### 3. Oscillations and the voting paradox

In ref. 9, n-dimensional generalizations

$$\dot{x}_i = a_i(x)[1 - \sum_{k=1}^n B_{ik}(x)f_k(x_k)], \quad [13]$$

 $i = 1, 2, \ldots, n$ , of the three-dimensional Volterra-Lotka system

$$\begin{array}{l} \dot{x}_1 = x_1(1 - x_1 - \alpha x_2 - \beta x_3) \\ \dot{x}_2 = x_2(1 - \beta x_1 - x_2 - \alpha x_3) \\ \dot{x}_3 = x_3(1 - \alpha x_1 - \beta x_2 - x_3) \end{array}$$
[14]

are globally analyzed. May and Leonard (11) studied system 14 to illustrate the voting paradox. Namely, if  $\alpha + \beta \ge 2$  and  $\beta > 1 > \alpha$ , then in pairwise competition in system 14,  $v_1$  beats  $v_2$ ,  $v_2$  beats  $v_3$ , and  $v_3$  beats  $v_1$ . When all three populations interact, a global "contradiction" is produced because, if the winning relationship were transitive,  $v_1$  could beat itself, which is absurd. May and Leonard showed that this contradiction produces sustained oscillations in system dynamics. They used computer simulations and local analytic estimates to do this. The present method provides a global analysis of system decisions and hereby shows why the system is forced to jump infinitely often in the cyclic order  $v_1 \rightarrow v_2 \rightarrow v_3 \rightarrow v_1$ , thereby producing sustained oscillations.

Below are intuitively summarized some of the ideas that yield pattern formation and oscillation theorems. First, one observes that given initial data x(0) such that

$$\int_0^\infty M^+[x(t)]dt < \infty, \qquad [15]$$

then the limit  $x(\infty)$  exists, and we say that pattern formation occurs in response to x(0). It is also shown that if, starting at x(0), there ensue only finitely many jumps, then relationship 15 holds, and consequently  $x(\infty)$  exists. Intuitively this means that, after all local decisions have been made, the system can form a well-defined pattern  $\mathbf{x}(\infty)$ . For example, suppose, starting at x(0), all jumps are partially ordered so that no jump cycles (e.g.,  $v_1 \rightarrow v_2 \rightarrow v_3 \rightarrow v_1$ ) exist. Then, only finitely many jumps can occur, so pattern formation occurs. Moreover if relationship 15 holds, because  $M + [x(t)] \ge 0$  at all large times, it follows that  $\lim_{t\to\infty} M^+[x(t)] = 0$ . Consequently, x(t) approaches an equilibrium point that lies on S<sup>+</sup>. For example, in Volterra-Lotka systems 5 with n = 3, to find the jump sets  $J_{ii}$  defined by Eq. 12, one first notes if the planes  $M_i(x) = 0$  and  $M_i(x) = 0$ intersect on  $S^+$ . The intersection is a line segment  $L_{ii}$  except in trivial cases. Then, one defines the planar region interpolated between  $L_{ii}$  and the point x = 0 and intersects this planar region with  $R^*$  to find  $J_{ij}$ . Because n = 3, no jump cycle exists unless there are three line segments  $L_{i_1i_2}$ ,  $L_{i_2i_3}$ , and  $L_{i_3i_1}$  on S<sup>+</sup> with  $i_1$ ,  $i_2$ , and  $i_3$  distinct. If not, given any x(0), the limit  $x(\infty)$  exists; that is, global pattern formation occurs. Moreover the limit  $\mathfrak{x}(\infty)$ lies on  $S^+$ . Fig. 1 illustrates some Volterra-Lotka systems that undergo global pattern formation.

The starting point for studying oscillations is the converse statement:

$$\int_0^{\infty} M^+[\mathbf{x}(t)]dt = \infty \qquad [16]$$

implies that infinitely many jumps occur. For example, the jump sets of the Volterra-Lotka system 14 are depicted in Fig. 2. One finds that, if  $\beta > 1 > \alpha$ , jumps must cycle in the order  $v_1 \rightarrow v_2 \rightarrow v_3 \rightarrow v_1$  if they occur at all. To show that this jump cycle recurs infinitely often, we must prove relationship 16, given prescribed initial data x(0). To do this, one studies the ignition surface  $S^+$  defined by [8] to test which x(0)s generate trajectories that penetrate  $S^+$  and which of these trajectories will satisfy  $M^+[x(t)] \ge \epsilon$  for some  $\epsilon > 0$  and all times t that are sufficiently large. Then [16] readily follows. In system 14, all trajectories penetrate  $S^+$  except those that have uniform initial data  $x_1(0) = x_2(0) = x_3(0)$ . The latter trajectories remain uniformly distributed and approach the equilibrium point  $P = (1 + \alpha + \beta)^{-1}(1, 1, 1)$  that lies at the intersection of the dark lines



FIG. 1. The sets  $S_i = [x \in \mathbb{R}^3_+: M_i(x) = 0]$  are planar segments in the case of three-dimensional Volterra-Lotka systems. (a) All three  $S_i, i = 1,2,3$ , form part of  $S^+$ . Because only two intersections  $S_1 \cap S_3$ and  $S_1 \cap S_2$  are nonempty in  $S^+$ , there are no jump cycles. Global pattern formation therefore occurs. Moreover, there are two equilibrium points (filled circles) on  $S^+$ , but only the one on  $S_1 \cap S_3$  is stable. (b) Only one intersection  $S_1 \cap S_3$  is nonempty in  $S^+$ . Again, global pattern formation occurs. The equilibrium point on  $S^+$  is stable.



FIG. 2. (a) Sets  $S_1 \cap S_2$ ,  $S_2 \cap S_3$ , and  $S_3 \cap S_1$  are nonempty in  $S^+$ . (b) Positive ignition surface with equilibrium point  $P = (1 + \alpha + \beta)^{-1}$  (1,1,1). (c) Negative ignition surface with equilibrium point P. (d) Jump sets form a jump cycle  $v_1 \rightarrow v_2 \rightarrow v_3 \rightarrow v_1$  if  $\beta > 1 > \alpha$ .

in Fig. 2b. What prevents other trajectories from approaching P after they penetrate  $S^+$ ? The condition  $\alpha + \beta \ge 2$  guarantees that P is an unstable equilibrium point with respect to the directions lying within  $R^*$ .

After one is sure that x(0) generates infinitely many jumps, how does one know which  $x_i$  oscillate persistently as  $t \to \infty$ ; that is, which  $x_i$  oscillate at arbitrarily large times and in such a way that the limit  $x_i(\infty)$  does not exist? To study this, one defines an *asymptotic graph* that decomposes the jumps that reoccur infinitely often into a collection of jump cycles among certain of the states  $v_i$ . In system 14, all of the  $v_i$ , i = 1, 2, 3, are in the asymptotic graph if  $\alpha + \beta \ge 2$  and  $\beta > 1 > \alpha$ . One then shows how those  $x_i$  whose  $v_i$  are in the asymptotic, graph cannot stop oscillating as  $t \to \infty$  without contradicting [16].

It does not follow that persistently oscillating  $x_t$ s approach a periodic solution as  $t \rightarrow \infty$ . For example, May and Leonard (11) numerically demonstrated oscillations of ever-increasing period in system 14 when  $\alpha + \beta = 2$ , and Grossberg (9) showed that such oscillations can occur when the trajectory approaches a union of heteroclinic orbits (namely, orbits between two equilibrium points) as  $t \rightarrow \infty$ .

#### 4. Absolute stability of global pattern formation

In ref. 8 it is shown how a large class of systems defined by mass action, or kinetic laws, and subjected to feedback excitatory and inhibitory interactions undergo global pattern formation. That is, given any initial data x(0), the system approaches a limiting pattern  $x(\infty) = \lim_{t\to\infty} x(t)$  as time goes on. In general, there can be infinitely many possible  $x(\infty)$  in a given system, but the analysis of jumps provides considerable information about how  $x(\infty)$  depends on x(0).

The systems covered by this analysis include examples of neural networks with recurrent on-center off-surround anatomies, biochemical mass action interactions, developmental decisions, and interpopulation competition (see refs. 5 and 12 for the general theory). The theorem describes the behavior of systems that can be written as

$$\dot{\mathbf{x}}_i = a_i(\mathbf{x})[b_i(\mathbf{x}_i) - c(\mathbf{x})]$$
 [17]

where, by [3],  $\partial c / \partial x_i \ge 0$ , i = 1, 2, ..., n. The results about [17] suggest a solution to a dilemma that has interested philosophers and scientists for hundreds of years: How can arbitrarily many individuals, populations, or states, each obeying unique and personal laws, ever interpret each other's signals or communications well enough to ever agree about anything? Leibniz has met this dilemma by developing his theory of monads (13). The

theorem suggests a different solution. In [17], each  $v_i$  can have an essentially arbitrary signal function  $b_i(x_i)$  as well as an arbitrary amplification function  $a_i(x)$ . Global consensus, or pattern formation, can be achieved despite these local irregularities because there exists a commonly shared *adaptation level* c(x)against which to evaluate local irregularities. The adaptation level c(x) defines a type of symmetric long-range order that is shared by the populations.

There seems to exist a complementarity, or trade-off, between how freely one can choose local parameters ("individual differences") and how global the adaptation level ("communal understanding") must be chosen to achieve global consensus (8, 9). For example, in the Volterra-Lotka system 14 there is no adaptation level, and even linear feedback signals can produce sustained oscillations. By contrast, a large class of generalized Volterra-Lotka systems [13] do undergo global pattern formation. These are the systems whose interaction coefficients  $B_{ik}(x)$  are determined by statistically independent factors at  $v_i$  and  $v_k$ —namely,  $B_{ik}(x) = g_i(x_i)h_k(x_k)$ . Then [13] can be written in the form of [17] and hence undergoes global pattern formation. Thus, within Volterra-Lotka systems, only deviations from statistically independent interactions can produce sustained oscillations.

An important class of mass action systems undergoing competitive feedback can be written in the form of [17]. To illustrate this, consider the usual voltage law that underlies the circuit diagrams of nerve cell membranes (14, 15):

$$C \frac{\partial V}{\partial t} = (V^{+} - V)g^{+} + (V^{-} - V)g^{-} + (V^{P} - V)g^{P}$$
 [18]

in which C is capacitance, the constants  $V^+$ ,  $V^-$ , and  $V^p$  are excitatory (usually Na<sup>+</sup>), inhibitory (usually K<sup>+</sup>), and passive saturation points, respectively; and  $g^+$ ,  $g^-$ , and  $g^P$  are excitatory, inhibitory, and passive conductances, respectively. The voltage V(t) is variable, and stays between  $V^+$  and  $V^-$  because  $V^- \leq V^P < V^+$ . Let  $y_i(t)$  be the voltage of the *i*th cell (or cell population)  $v_i$ . Let C = 1 (that is, rescale the time variable), and introduce the notation  $V^+ = B$ ,  $V^P = 0$ , and  $V^- = -D$ , in which B > 0 and  $D \ge 0$  because  $V^- \le V^P < V^+$ . Suppose that the *i*th excitatory conductance  $g_i^+$  is influenced by a constant, or tonic, external input  $I_i$  and by a positive feedback signal  $f_i(y_i)$  from  $v_i$  to itself. Thus,  $g_i^+ = f_i(y_i) + I_i$ . Let the *i*th inhibitory conductance  $g_i^-$  be influenced by a constant, or tonic, input  $J_i$  and by competitive or inhibitory signals  $f_k(y_k)$  from all cells  $v_k$ , k  $\neq$  i. Thus,  $g_i^- = \sum_{k \neq i} f_k(y_k) + J_i$ . Actually, one can think of  $I_i$  and  $J_i$  as varying slowly compared to the reaction rate of  $x_i$ . Let the passive conductance  $g_i^p$  equal the constant A. In all, the feedback interactions define a recurrent on-center (v, excites itself) off-surround ( $v_k$  inhibits  $v_i$ ,  $i \neq k$ ) anatomy. Eq. 18 then becomes

$$\dot{y}_{i} = -Ay_{i} + (B - y_{i})[f_{i}(y_{i}) + I_{i}] - (y_{i} + D) \left[\sum_{k \neq i} f_{k}(y_{k}) + J_{i}\right].$$
 [19]

Now generalize [19]. Let each  $v_i$  have an arbitrary decay rate  $A_i$ , an arbitrary excitatory saturation point  $B_i$ , and an arbitrary inhibitory saturation point  $D_i$ . Then [19] becomes

$$\dot{y}_i = -A_i y_i + (B_i - y_i) [f_i(y_i) + I_i] - (y_i + D_i) \left[ \sum_{k \neq i} f_k(y_k) + J_i \right]$$
which is an *n*-dimensional mass action as kinetic network with

which is an *n*-dimensional mass action, or kinetic, network with arbitrary parameters, tonic inputs, and feedback signals  $f_k(y_k)$ . To write [20] in the form of [17], first let  $x_i = y_i + D_i$  and  $h_i(x_i) = f_i(x_i - D_i)$ . Then,

$$\dot{x}_{i} = -A_{i}x_{i} + (B_{i} + D_{i} - x_{i})[h_{i}(x_{i}) + I_{i}] + x_{i}\left[\sum_{k \neq i} h_{k}(x_{k}) + J_{i}\right] + A_{i}D_{i}.$$
 [21]

System 21 can be written in the form of [17] by using the definitions  $a_i(x) = x_i$ ,

$$b_i(x_i) = -A_i - I_i - J_i + x_i^{-1} [A_i D_i + I_i + (B_i + D_i)h_i(x_i)], \text{ and } c(x) = \sum_{k=1}^n h_k(x_k).$$

Clearly [17] is vastly more general than [20]; for example, it permits nonlinear combinations of the signals, rather than merely additive ones, as well as state-dependent changes in the parameters. Because global pattern formation obtains given any choice of parameters in [17], I call the system absolutely stable. Any mechanism that changes system parameters can cause dramatic changes in the underlying decision scheme without destroying the system's ability to reach a new global consensus. The theorem thus constrains possible bifurcations in the space of decision schemes. This subject should be studied further.

For example, the system

$$\dot{x}_i = -Ax_i + (B - x_i)f(x_i) - x_i \sum_{k \neq i} f(x_k)$$
 [22]

describes the simplest competitive mass action feedback network. If the signal function f(w) is chosen so that b(w) = $w^{-1}f(w)$  is strictly increasing, then the system chooses the population  $v_i$  possessing the maximal initial data and concentrates all system activity at  $v_i$ . By contrast, if b(w) is a concave function with a flat plateau between its increasing and decreasing values, as when f(w) is a sigmoid or S-shaped signal function, then a quenching threshold exists: initial activities that are smaller than the quenching threshold are suppressed, whereas the spatial pattern of initial activities that exceed the quenching threshold is contrast-enhanced and stored (3, 16). These results illustrate how a competitive system can sometimes. but not always, behave, like a finite state machine. In particular, a "hill" or "hump" in the graph of b(w) can significantly alter system dynamics. Mimura and Murray (17) have noted the importance of hills in determining the qualitative behavior of prey-predator reaction-diffusion systems. Their goal was to understand spatial heterogeneity, or patchiness, in these systems. In a neural context, analogous effects occur and are called disinhibition or lateral masking (18, 19).

Global pattern formation in [17] is proved by first analyzing how the hills in the functions  $b_i(w)$  influence system dynamics. It is shown how the decision rules sense these hills by causing a nested series of decision boundaries to be laid down as time goes on. These decision boundaries suddenly appear at prescribed times and, after they appear, each  $x_i(t)$  can fluctuate only within the intervals that are defined by the boundaries. Once all the boundaries are laid down, the decision process is essentially complete, except for a possible series of minor system adjustments. The concept of decision boundary is reminiscent of the compartmental boundaries that Kauffman et al. (20) have modeled for the development of the Drosophila embryo. However, the Kauffman et al. model describes a linear threshold phenomenon that is due to the existence of a physical boundary-in their case, an elliptic boundary. A decision boundary is caused by nonlinear suprathreshold interactions even if no physical boundary effects occur.

To illustrate how hills are related to decision boundaries, choose all  $b_t(w) \equiv b(w)$  and let b(w) possess finitely many local maxima and minima. Consider the abscissa values of the hill peaks of highest height. There exists a time  $T_1$  after which each  $x_t(t)$  is trapped within an interval between a pair of such abscissa values. These abscissa values are the first decision boundaries to appear. To prove this fact, the ignition property

is used. If at any time  $t, x_t(t)$  equals one of these abscissa values, then  $M_i[x(t)] = M^+[x(t)] \ge 0$ . Consequently  $\dot{x}_i \ge 0$ , so that once  $x_t$  crosses an abscissa value, it can never cross back. Further analysis shows that there exists a time  $T_2 > T_1$  after which no  $x_t(t)$  can cross the abscissa values between either the highest or the next-highest hill peaks. This process of laying down decision boundaries continues until each  $x_t(t)$  is trapped in the "bowl" between a pair of successive hill peaks. The first stage of pattern formation is then complete.

The second stage is analyzed by keeping track of that  $x_i(t)$ whose hill height  $b[x_i(t)]$  is maximal. Denote the maximal hill height by B[x(t)]; that is,  $B[x(t)] = \max_i b[x_i(t)]$ . By [17], B(x) $= M^{+}(x) + c(x)$ . After all dynamic boundaries are laid down, jumps can occur among descending slopes of the hills (slopes to the right of hill peaks) as B[x(t)] decreases monotonically through time; or jumps can occur among ascending slopes of the hills (slopes to the left of hill peaks) as B[x(t)] increases monotonically through time; or a jump can occur from a descending slope to an ascending slope but not conversely; or the variable  $x_t(t)$  such that  $B[x(t)] = b[x_t(t)]$  can increase continuously as B[x(t)] moves from a descending slope to an ascending slope, but not conversely, because the  $x_t(t)$  variables are trapped within their bowls. In all, B[x(t)] can oscillate at most once after the dynamic boundaries are laid down. Consequently, the limit  $B[x(\infty)] = \lim_{t \to \infty} B[x(t)]$  exists. Using this fact, it is then shown that the limit  $c[x(\infty)] = \lim_{t \to \infty} c[x(t)]$  of the adaptation level also exits and equals  $B[\mathbf{x}(\infty)]$ . In other words, the local decisions among system components ultimately lead to the choice of a set-point or asymptotic adaptation level  $c[x(\infty)]$ . Then each  $x_t$ adjusts itself via [17] to this set-point as the limit  $x(\infty)$  is approached.

The above analysis reveals that B[x(t)] is monotonic at large times; that is, it is an asymptotically Liapunov function. Function B[x(t)] only becomes Liapunov, however, after the decision boundaries have been laid down. Thus, the system approaches a "classical limit" only after its initially nonstationary dynamics of decision-making is over. A similar trend often occurs in learning networks: *after* the nonstationary phase of learning is over, the system settles down to a memory phase, which is described by a stationary Markov chain (21).

### 5. Evolutionary switch from competition to cooperation?

By analogy with [3], a cooperative system is one in which

$$\frac{\partial f_i}{\partial x_i}(x) \ge 0 \text{ if } i \neq j \text{ and } x \in R.$$
[23]

A competitive system can sometimes appear to be cooperative. For example, Grossberg (3) proved that competitive schemes, such as [22], can amplify the activities of all the competing populations, thereby making it appear that an increase in one population's activity has increased other populations' activities. This property can drive all system activities into the range where they are most sensitive to each other's signals. Grossberg (5, 22) argued that this self-tuning, or normalization, property lies behind a wide variety of biological phenomena such as sensory adaptation and self-regulation. Nonlinear interactions are required to achieve self-tuning, but the system's properties can look linear to a macroscopic observer (see ref. 5, section 8). A similar dilemma can occur in learning systems (21). Thus, a system that looks linear and cooperative to an untutored observer can, in reality, be nonlinear and competitive. Such an observer will not be able to understand how the system automatically tunes its sensitivity to match fluctuating external demands, among other properties, and efforts to model the system out of linear components can lead to umphysical instabilities (23).

This situation can create major conceptual difficulties when one considers the evolution of biological order. How do components that compete at early stages of evolution ultimately cooperate to establish a more complex structure, such as an organ? Does this switchover imply that the laws of interaction change from a condition like [3] to a condition like [23]? Or do the components compete throughout all the evolutionary stages. but in such a fashion that earlier stages of competition alter system parameters so that later stages can yield ostensibly cooperative macroscopic properties? For example, if [22] has a sigmoid signal f(w) and system sensitivity is modulated by a variable arousal or enzymatic level, the system can choose a winning population at low arousal levels and amplify all activity levels at higher arousal levels (5). Interacting competitive subsystems can also begin to resonate when their feedback signals match and amplify each other (5, 10, 12).

Such considerations make it plain that the collective properties that define the evolutionary success of biological systems often cannox be reliably guessed from a study of their isolated components and indicate an important role for mathematical analysis in understanding the principles of design on which evolutionary success is founded.

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