

SYNERGY AND SELF-ORGANIZATION IN THE EVOLUTION OF COMPLEX SYSTEMS

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*"From nature's chain whatever link you strike
Tenth or ten-thousandth, breaks the chain alike."*

Alexander Pope

"An Essay on Man"

ABSTRACT

Synergy of various kinds has played a significant creative role in evolution; it has been a prodigious source of evolutionary novelty. Elsewhere it has been proposed that the functional (selective) advantages associated with various forms of synergistic phenomena have been an important cause of the "progressive" evolution of complex systems over time. Underlying the many specific steps in the complexification process, a common functional principle has been operative. Recent mathematical modelling work in biology, utilizing a new generation of non-linear dynamical systems models, has resulted in a radically different hypothesis. It has been asserted that "spontaneous," autocatalytic processes, which are held to be inherent properties of living matter itself, may be responsible for much of the order found in nature and that natural selection is merely a supporting actor. A new "physics of biology" is envisioned in which emerging natural laws of organization will be recognized as being responsible both for driving the evolutionary process and for truncating the role of natural selection. This article describes these two paradigms in some detail and discusses the possible relationship between them. Their relevance to the process of human evolution is also briefly discussed.

SYNERGY VS. SELF ORGANIZATION

It has always seemed to me ironic that we are surrounded and sustained by synergistic phenomena -- combined (or "co-operative") effects that can only be produced by two or more component parts, elements or individuals -- yet we do not, most of us, seem to appreciate its importance; we take its routine miracles for granted. Nor do evolutionists, for the most part, seem to recognize the important *causal* role of synergy in the evolutionary process, despite the fact that we depend upon it in a myriad of ways for our survival and reproductive success, and so do all other living things. Synergy is literally everywhere around us, and within us; it is unavoidable. Here are just a few examples:

- About 2,000 separate enzymes are required to catalyze a metabolic web. But if you were to remove one of the more critical of these enzymes, say the hexokinase that facilitates glycolysis, the process would not go forward.
- Water has a unique set of emergent, combinatorial properties that are radically different from those of its two constituent gases. But if you simply mix the two gases together without a catalyst like platinum, you will not get the synergy.
- Our written language, with well over 300,000 words, is based on various combinations of the same 26 letters. Thus, the letters "o," "p" and "t" can be used to make "top", "pot", "opt" and "p.t.o." (paid time off). But if you remove the vowel, there will be no "pattern recognition" in the reader's mind.
- The humble clay brick can be used to make a great variety of useful structures -- houses, walls, factories, jails, roads, watchtowers, fortifications, even kilns for making more bricks. Truly a synergistic technology. But without mortar and human effort (and a plan), you will have only a pile of bricks.
- A modern automobile is composed of roughly 15,000 precisely-designed parts, which are derived from some 60 different materials. But if a wheel is removed, this incredible machine will be immobilized.
- The African honey guide is a bird with a peculiar taste for bees' wax, a substance that is more difficult to digest even than cellulose. Moreover, in order to obtain bees' wax, the honey guide must first locate a hive then attract the attention of and enlist a co-conspirator, the African badger (ratel)(*Mellivora capensis*). The reason is that the ratel has the ability to attack and dismember the hive, after which it will reward itself by eating the honey while leaving the wax. However, this unusual example of co-operative predation between two different species in fact depends upon a third, unobtrusive co-conspirator. It happens that honey guides cannot digest bees' wax. They are aided by a parasitic gut bacterium which produces an enzyme that can break down wax molecules. So this improbable but synergistic feeding relationship is really triangular. And,

needless to say, the system would not work if any of the partners, for whatever reason, withdrew (Bonner, 1988).

- Economist Adam Smith's classic description in The Wealth of Nations (1776) of an eighteenth century pin factory is often cited as a paradigm example of the "division of labor." Smith observed that 10 laborers, by dividing up the various tasks associated with making pins, were able collectively to produce about 48,000 pins per day. However, Smith opined that if each laborer were to work alone, doing all of the tasks independently, it was unlikely that on any given day the factory would be able to produce even a single pin per man.

THE UBIQUITY OF SYNERGY

Synergy is clearly not a peripheral phenomenon associated only with drug interactions or corporate mergers. Though it often travels in disguise, synergy can be found in the subject-matter of most, if not all of the academic disciplines. In physics, it is associated with the behavior of atoms and subatomic particles, as well as with superconductivity, synchronous light emissions (lasers) and such esoteric molecular phenomena as scale effects -- the "broken symmetries" highlighted in physicist Perry Anderson's classic article "More is Different" (1972). Indeed, the periodic table of elements is a monument to the many forms of synergy that are responsible both for the naturally occurring stable elements and for the more unstable or even transitory creations of modern physics; various combinations of atomic building-blocks produce substances with very different "emergent" properties. Even the "chaotic" phenomena which have been the subject of intensive research by physicists and mathematicians in recent years exhibit many forms of synergy.

Biochemistry and molecular biology are also rife with synergy. Living matter (at least in the form we know it) is composed mainly of a few key constituents -- carbon, oxygen, hydrogen, nitrogen and energy. In various configurations these constituent parts have produced a wondrous array of emergent products, perhaps 10-20 million different species -- nobody really knows. By the same token, as we all know, the DNA that is used to write the genetic code consists of only four nucleotide "letters." With this modest alphabet, evolution has been able to fashion a human genome with perhaps 100,000 genes. During ontogeny, our genome is able co-operatively to fabricate an incredibly intricate emergent product composed of an estimated 500 trillion cells of about 250 different types.

Many individual organisms, from bacteria to humans, also engage in internal or external symbiosis -- synergistic relationships with "dissimilar" organisms -- a subject that will be discussed in more detail below. Sociobiologists, likewise, have documented numerous behavioral synergies among members of the same species, from co-operative

foraging and hunting activities to co-operative defense, reproduction, environmental conditioning and even thermoregulation. (More also about sociobiology below.)

In the social sciences, synergy can be found in many of the phenomena studied by economists -- from market dynamics (demand-supply relationships) to economies of scale, the division of labor and, of course, the influence of technology. Psychologists also deal with synergistic effects, ranging from gestalt phenomena to social facilitation, group "syntality," mob psychology and cult behavior. And political scientists observe synergistic effects in voting processes, interest group activity, coalition behavior, and a host of organizational phenomena, among other things.

The computer sciences are also grounded in synergy. There is, for example, the microscopic complexity of Intel's Pentium microprocessor, which embodies the equivalent of 3.1 million transistors in a substrate that is about 2.17 inches square (it varies with the temperature). There is also the current generation of word processing software, which utilizes -- synergistically -- about two million separate lines of programming code, or instructions. Or consider the multi-leveled synergy that occurs when a computer and its software are combined. We know that the result is synergistic because we also know what happens when the two are not combined, or when the computer and software are incompatible. Similarly, massively parallel computers, which in effect exploit the synergies associated with a division of labor and hierarchical control, offer performance improvements that are many orders of magnitude greater than what can be achieved by conventional sequential processing technology.

THE SYNERGISM HYPOTHESIS

What is the principle underlying such mundane forms of magic? It is not magic at all, of course, but a fundamental characteristic of the material world that things in various combinations, sometimes with others of like kind and sometimes with very different kinds of things, are prodigious generators of novelty. And these novel co-operative effects have over the past 3.5 billion years or so produced at every level of life distinct, irreducible "higher levels" of causation and action whose constituent "parts" have been extravagantly favored by natural selection. Furthermore, in many instances these emergent wholes have themselves become parts of yet another new level of combined effects, as synergy begat more synergy.

The formal hypothesis is that synergistic effects of various kinds have been a major source of creativity in evolution (see Corning, 1983); the synergism hypothesis asserts that it was the functional (selective) advantages associated with various forms of synergy that facilitated the evolution of complex, functionally-organized biological and social systems. In other words, underlying each of the many particular steps in the complexification process, a common functional principle has been at work.

THE SELF-ORGANIZATION PARADIGM

The recently developed theories of self-organization would seem to be orthogonal to this functionalist, selectionist theory. Mathematical modelling work in biophysics, utilizing a new generation of non-linear partial differential equations, has produced a radically different hypothesis about the sources of biological order. As articulated by Stuart Kauffman in an important new synthesis (Kauffman, 1993), much of the order found in nature may be "spontaneous" and autocatalytic -- a product of the generic properties of living matter itself. Kauffman envisions a new physics of biology in which the emerging natural laws of organization will be recognized as being responsible both for driving the process and for truncating the role of natural selection. Natural selection in Kauffman's paradigm is viewed as a supporting actor.

This article will explore the relationship between synergy and self-organization in some detail in the hope of shedding additional light on how complex systems have evolved and how they may be expected to continue doing so over the course of time. The relevance of these two major theoretical paradigms to the process of human evolution will also be briefly discussed.

THE EVOLUTION OF COMPLEXITY AS A THEORETICAL CHALLENGE

Complexity seems of late to have become a buzzword. There have even been popular books chronicling the research and theory that have burgeoned in this category (Lewin, 1992; Waldrop, 1992). Nevertheless, the underlying theoretical challenge is not new. Attempts to explain the origins and evolution of living systems can be traced back at least to the Old Testament. Even a concept as fashionable as autocatalysis can be found in the writings of Aristotle, the first great biologist, who developed what has become an enduring theme in western natural science. Aristotle postulated an intrinsic directionality, or unfolding process in nature (orthogenesis), which was distilled in his concept of *physis*. Aristotle also inspired the concept of an ascending ladder of perfection, or hierarchy, that later came to be associated with the Latin term *scala naturae* (Granger, 1985; Lovejoy, 1936).

At the beginning of the 19th Century, the French naturalist Jean Baptiste de Lamarck postulated a "natural tendency" toward continuous developmental progress in nature, energized by what he called the "power of life" (Lamarck, 1963 [1809]). Likened by Lamarck to a watch spring, it involved the idea that living matter has an inherent developmental energy.

Orthogenetic theories of evolution reached an apogee of sorts during the 19th century with the multi-volume, multi-disciplinary magnum effort of Herbert Spencer, who was considered by many contemporaries to be the preeminent thinker of his era. Spencer formulated an ambitious "Universal Law of Evolution" that spanned physics,

biology, psychology, sociology and ethics. In effect, Spencer deduced society from energy by positing a cosmic progression from energy to matter, to life, to mind, to society and, finally, to complex civilization. "From the earliest traceable cosmical changes down to the latest results of civilization," he wrote in "The Development Hypothesis" (Spencer, 1892 [1852]), "we shall find that the transformation of the homogeneous into the heterogeneous is that in which progress essentially consists." Among other things, Spencer maintained that homogeneous systems are less stable than those that are more differentiated and complex. (It is worth noting that, while Spencer viewed this progression as "spontaneous" in origin, he also believed that it was sustained by the fact that more complex forms are functionally "advantageous.")

There have been many less imposing vitalistic and orthogenetic theories since Spencer's day, ranging from Henri Bergson's *élan vital* to Hans Driesch's *Entelechie*, Pierre Tielhard de Chardin's Omega point, Pierre Grassé's *idiomorphon*, and Jean Piaget's *savoir faire*. However, in this century Darwin's theory of natural selection has cast a long shadow over various autocatalytic theories. Darwin seemed to be rebutting Lamarck and Spencer directly when he wrote in The Origin of Species "I believe in no fixed law of development." And again: "I believe...in no law of necessary development" (1968 [1859]:p.318,348). One of the formulators of the so-called modern synthesis (or sometimes neo-Darwinian synthesis), the late Theodosius Dobzhansky, put the matter succinctly: "Natural selection has no plan, no foresight, no intention" (1975:p.377).

A striking illustration is the eye, that revered object of 19th century natural theology. We now know that the eye did not unfold deterministically or arise full-blown. It developed independently on perhaps 40 different occasions in evolutionary history, utilizing at least three different functional principles -- the pinhole, the lens and multiple tubes. Nor do all the eyes of a similar type work in the same manner.

While the evidence for natural selection as a directive agency in evolution is overwhelming, many theorists over the years have felt that the neo-Darwinian synthesis is inadequate, by itself, to account for the undeniable "progressive" trend from the primordial chemical soup to simple one-celled prokaryotes, eukaryotes and, ultimately, to large, complex, socially-organized mammals. The evolution of complexity has seemed to require something more than "random" point mutations in a genetic "beanbag" (to use Ernst Mayr's felicitous caricature). The long-term trend toward greater complexity (in tandem with the many examples of stasis) seems to suggest the presence of some additional mechanism or mechanisms. Some years ago, the late C.H. Waddington articulated these doubts with characteristic bluntness: "The whole real guts of evolution -- which is how do you come to have horses and tigers and things -- is outside the mathematical theory" (quoted in Rosen 1978:p.371).

WHY COMPLEXITY? AND WHAT IS IT?

More broadly, the question is: Why does complexity exist? Why have various parts aggregated over time into larger, more complex wholes? And why have many wholes differentiated into various specialized parts? For that matter, what *is* complexity? And, in the context of modern biology, what *are* wholes, and parts? The accumulating data on mutualism, parasitism, colonialism, social organization, coevolution and the dynamics of ecosystems have revealed many nuanced interdependencies and have blurred the supposedly sharp demarcation lines among various biological units.

Physicist Larry Smarr (1985) has pointed out that complexity is in reality a multi-dimensional, multi-disciplinary concept; there is no one right way to define and measure it. A mathematician might define it in terms of the number of degrees of freedom in computational operations. A physicist might be concerned with the number and frequency of interactions in a system of interacting gas molecules. The systems theorists of the 1960s were fond of using the rubric (suggested independently by mathematicians Alexei Kolmogorov and Gregory Chaitin) of "algorithmic complexity" - the size of the smallest mathematical description of system behavior. Social scientist Herbert Simon (1965) advocated the use of a hierarchical measure -- the number of successive levels of hierarchical structuring in a system, or what biologist G. Ledyard Stebbins (1969) characterized as "relational order." For obvious reasons, biologists have traditionally preferred such biologically-relevant measures as the number of parts (say cells), or types of parts (cell types), or the number of interdependencies among various parts. In recent years there have also been a number of efforts to define complexity in relation to thermodynamics, entropy and information (see especially Wicken (1987); Haken (1988); Brooks and Wiley (1988); Weber et al., (1988) and Salthe (1993)).

John Tyler Bonner, in his recent book on the evolution of complexity (1988) suggests that biological (and by extension social) complexity should also be defined in terms of the functional nature of living systems. What is most salient about biological systems is not just the number of parts, or even the number of interconnections among the parts, Bonner argues, but the division of labor (and the combining of capabilities) which result; these are the distinctive hallmarks of biological complexity. In other words, biological complexity should be associated with the functional synergies that it produces.

In recent years there has also been increasing acceptance of the views of biologists Ludwig von Bertalanffy (1950, 1967), W. Ross Ashby (1952, 1956), C.H. Waddington (1962, 1968), Paul Weiss (1971) and others that biological complexity is characterized by cybernetic properties; it is not just ordered but also organized (see also Norbert Wiener, 1948; William T. Powers, 1973 and James G. Miller, 1978). That is, biological (and social) systems are distinctive in being goal-oriented (or teleonomic), hierarchically-organized and self-regulating (they display processes of feedback control), as well as being uniquely self-developing and self-determining. The physical

chemist Engelbert Broda (1975) stressed the functional imperatives: "The more the division of labor was developed [in evolution], the more important became intercellular and interorganismal communication and control. Hence, for an understanding of more complicated systems, thermodynamics and kinetics must increasingly be supplemented by cybernetics, by applied systems analysis." In hindsight, Broda might have added molecular (morphogenetic) and intracellular communication and control to the list of biological processes with cybernetic properties.

One other distinctive feature of complex living systems is that they cannot be fully understood, nor their evolution and operational characteristics fully explained, by an exclusive focus either on the system as a "whole" or on the component "parts". Though the long-standing "holism-reductionism" debate in the sciences still lingers, chemist Michael Polanyi's classic article "Life's Irreducible Structure" (1968) remains the definitive peace-making effort. Polanyi noted that, in the process of constructing a complex living system, the causal dynamics are in fact multi-levelled. On the one hand, the properties of the whole are constrained and shaped by the properties of the parts, which in turn are constrained and shaped by the lower-level properties of their constituent raw materials, and by the laws of physics and chemistry. To a devout reductionist, this is a truism which modern science daily reconfirms.

On the other hand, the extreme reductionist argument that an understanding of the parts fully explains the whole leads to what C.F.A. Pantin called the "analytic fallacy." Polanyi pointed out that a whole also represents a distinct, irreducible level of causation which "harnesses," constrains and shapes lower level parts and which may in fact determine their fates. In effect, wholes may become both vessels and selective fields for the parts -- and may even come to exercise hierarchical, cybernetic control over the parts.

Moreover, wholes can do things that the parts cannot do alone. An automobile cannot be fully understood or its operation explained by separate descriptions of how each part works in isolation. Not only is the design of each part affected by its role and relationship to the whole but its performance and functional consequences may only be comprehensible in terms of its interaction with other parts and the whole. (See the discussions in Corning, 1983 and Haken, 1973, 1977, 1983; also, cf., the concept of "interactional complexity" in Wimsatt, 1974.)

Thus, an automotive engineer must always look both upward and downward (and horizontally) in the hierarchy of causation when trying to comprehend the operation of any part. And the same applies to the students of living systems. Evolution has produced several emergent levels of wholes and parts. Furthermore, the power and impact of these emergent wholes has greatly expanded over the course of time; complexity has been at once a product of evolution and a cause of evolution (an important point to which we will return below).

And yet, the question remains: Why complexity? How do we account for the "progressive" evolution of complex systems? As noted above, two alternative theoretical approaches are currently in contention -- the somewhat tattered neo-Darwinian (functionalist) theory and the theory of autonomous self-organization (autocatalysis). Until a few years ago, the neo-Darwinian explanation, while subject to vigorous debate over the details, was essentially uncontested; it was assumed that the trend toward biological complexification was functionally-driven. But the nascent science of complexity has challenged the selectionists' hegemony; non-Darwinian vitalistic/orthogenetic theories -- now respectably clothed in a new wardrobe of non-linear, dynamical systems models -- are again in vogue. Let us consider each of these explanatory paradigms in more detail.

SELF-ORGANIZATION AND COMPLEXITY

"Self-organization" is almost as much of a buzzword these days as "complexity". However, it is not a newly discovered phenomenon. Aristotle enshrined it in his classic metaphor about the growth of acorns into oak trees. The pioneering nineteenth century embryologists, such as Karl Ernst von Baer, also appreciated, and observed, self-organization in the process of morphogenesis. But more important, self-organization is also compatible with Darwin's theory. Modern neo-Darwinians, following the lead of Francisco Ayala (1970), Theodosius Dobzhansky (1974) and Ernst Mayr (1974a,b), have generally associated self-organization with Colin Pittendrigh's term "teleonomy" (evolved purposiveness) and the concept of an internal "program" (Roe and Simpson, 1958). In this formulation, self-organization has been equated with the mechanisms of cybernetic self-regulation and feedback. Self-organization is viewed as being a product of, and subordinate to, natural selection.

Darwin also categorically rejected the idea of an inherent energizing or directive force in evolution, as mentioned earlier. However, it is important to note that the theory of evolution via natural selection does not stand or fall on this issue, so long as any autocatalytic processes are (a) of a materialist nature, (b) empirically verifiable and (most important) (c) subject to testing for their functional (fitness) consequences in relation to survival and reproduction.

ILYA PRIGOGINE

In light of these criteria, there is nothing inherently threatening to natural selection theory in the work of physicist Ilya Prigogine and his colleagues on what might be called "orthogenesis through fluctuations" (Nicolis and Prigogine, 1977, 1989; Prigogine 1978, 1980; Prigogine, et al. 1977). Prigogine's frame of reference is non-equilibrium thermodynamics, and his major contribution, which liberated both physics and biology from the thrall of Clausius's Second Law of Thermodynamics [1850],

was to show that there is a class of systems in nature that are able to defy the inherent tendency of the physical world to devolve toward a state of thermodynamic equilibrium, or maximum disorder (entropy).

Prigogine and his co-workers, elaborating on the earlier insights in Erwin Schrödinger's remarkable book What is Life? (1944), developed the theory that "dissipative structures" are able to circumvent the Second Law by being "open" or energy-processing in character. They feed on throughputs of energy to sustain order or "negative entropy" and can remain in a sustained condition of disequilibrium. Dissipative structures, according to Prigogine, are also self-organizing. They arise spontaneously and may also spontaneously evolve toward greater complexity (shades of Lamarck and Spencer). This may occur when an open system is driven so far from an equilibrium condition that nonlinear discontinuities, or threshold instabilities may occur that will transform the system in the direction of greater complexity and more structural stability. In thermodynamic terms, a complex open system such as a human organism is "a giant fluctuation stabilized by exchanges of matter and energy" (Prigogine, et al., 1977:p.18). Moreover, Prigogine envisioned this process as having been cumulative historically. At each branch point, or "bifurcation," existing structures trigger the process that leads to new, more complex and more stable forms of order.

Where is natural selection in this model? Prigogine has not, to my knowledge, addressed explicitly the relationship between his theory and the functional and adaptive characteristics of biological organisms. However, it is obvious that thermodynamic considerations must be one of the priorities of natural selection. Indeed, the thermodynamic nature of living systems imposes the adaptational requirement for energy capture, and living systems have developed a diverse array of mechanisms for doing so. But that's not all there is to the problem of survival and reproduction. Living systems also have a material structure and organization and must earn a living in the environment. Thus, any self-organizing properties in such systems are also subject to the vicissitudes of the environment and the functional requirements for survival. Living systems must adapt; they must submit to the ultimate "censorship" of natural selection.

MANFRED EIGEN ET. AL.

The case for autocatalysis and self-organization in evolution has also been advanced by the important work of biophysicists Manfred Eigen, Peter Schuster and their colleagues (1979, 1981). Their focus is the early stages of prebiotic and macromolecular evolution, and their pioneering use of non-linear dynamical systems models has provided a new perspective on evolution.

Several of their contributions should be noted. First, they recognized that, in the initial stages of evolution, co-operative processes had to predominate; the construction of primitive organic molecules (monomers) required the integration of component materials, just as the creation of more complex polymers required monomer mergers. In

fact, they argue, it was only after the evolution of biochemical structures which possessed the informational capabilities needed for self-replication that Darwinian competition arose.

Eigen, Schuster and their co-workers also developed a case for the proposition that autocatalysis and self-organization were prior to mutations (indeed, prior to genes) and were therefore more fundamental sources of innovation in the formative stages of evolution (though environmental challenges were also obviously a stimulus).

They also identified the existence of what amounts to an evolutionary super-charger -- autocatalytic "hypercycles" that they believe accelerated the start-up phases of evolution. These co-operative phenomena, which have been empirically verified in contemporary examples of viral activity (1981), involve a cyclic coupling of catalytic processes in such a way that they reinforce and augment one another. Eigen and Schuster also proposed that hypercycles may account for how organic substances of increasing complexity have been able to circumvent what is known as the "complexity catastrophe." This constraint might have imposed an organizational ceiling on evolution, they maintain, were it not for hypercycles. If this is so, it provides an important example of the role of synergy in evolution. (However, Stuart Kauffman has a somewhat different view of this issue. See below.)

Finally, Eigen and Schuster developed the concept of what they call a pre-Darwinian phase of natural selection (they equate natural selection with individual competition) in which successful hypercycle participants and rudimentary forms at the viral level of organization formed "quasi species" that were selected as units in what amounted to a series of phase transitions. In other words, selection at this stage may have been more of a collective phenomenon involving categorical "yes-or-no" choices rather than competitive "better-or-worse" choices (but see the critique by Wicken, 1985).

The case for autocatalysis and self-organization has also been buttressed by chaos theory, or more specifically, the aspect that Stuart Kauffman (1991) has called "anti-chaos". Chaos theory is a new scientific paradigm built on non-linear dynamical systems models. It is focussed on a class of phenomena that involve unpredictable but deterministic dynamical interactions.

Among the important discoveries made by chaos theorists is the fact that dynamical systems have many emergent, systemic properties that arise from the interactions among the parts -- properties that cannot be predicted or observed by isolating the parts (synergy). But more important for our purpose, chaotic systems may also spontaneously "crystallize" stability and order under various circumstances. Indeed, in certain configurations of random Boolean (or on-off switching) networks, dynamical systems may spontaneously evolve stable patterns. In the three-dimensional "state spaces" that are used to model Boolean network processes, these steady states are zero-dimensional points that are referred to as "dynamical attractors." In effect, these are models of self-organized synergy.

HERMAN HAKEN

The work of the physicist Herman Haken and various colleagues over the past 20 years in the science of "synergetics" should also be mentioned (1973, 1977, 1983, 1988). Synergetics is defined as the science of co-operation, and Haken pioneered the scientific analysis of hierarchically organized co-operative phenomena in physics, with applications also in biology and the social sciences. He was one of the early workers also in chaos theory and self-organization and was one of the first to recognize co-operative self-ordering in various kinds of dynamical systems. A contribution of particular importance was a recognition that complex dynamical systems are Janus-faced. In some circumstances, the introduction of small changes can enhance the stability of the system or cause no significant disturbance. Yet, in other circumstances, a small change can completely destabilize the system -- a phenomenon subsequently developed by other workers and given the name of "self-organized criticality" (Bak and Chen, 1991). Haken also pioneered in the study of hierarchical control in dynamical systems. In particular, he identified two very different kinds. One involves distributed, mutual control among system parts in order to maintain a stable collective state (homeostasis). The other involves the introduction of superordinate "order parameters."

STUART KAUFFMAN

The recently published volume by Stuart Kauffman, The Origins of Order: Self-Organization and Selection in Evolution (1993), deserves special attention. Not only is this magnum opus an imposing, even daunting guided tour of the rapidly developing science of complexity but it goes well beyond the claims of other workers in this vineyard. In fact, Kauffman's thesis is nothing less than subversive to natural selection theory. Natural selection is not the primary source of biological organization, he asserts, but a supporting actor that fine-tunes a self-organizing natural world. As Kauffman puts it: "Much of the order found [in nature] is spontaneously present... Such order has beauty and elegance, casting an image of permanence and law over biology. Evolution is not just 'chance caught on the wing.' It is not just a tinkering of the ad hoc, of bricolage, of contraption. It is emergent order honored and honed by natural selection" (1993:p.644).

The origins of order are to be found, he says, in the generic properties of living matter itself, which he characterizes as an "invisible hand." Natural selection is portrayed as being subordinate to these self-organizing principles. "Vast order abounds [in nature] for selection's further use" (1993:p.235). Indeed, Kauffman suggests that biological order may exist sometimes "despite" natural selection. He speaks of a new physics of biology that requires us to view natural selection as being highly constrained by the natural laws of organization. Natural selection is "privileged" to improve upon the imminent order that exists in biological systems.

The basis for Kauffman's heretical conclusion is the broad-ranging application (by himself and other workers) of dynamical systems models to various domains of biology, including the origins of life, the process of adaptive evolution, ontogeny, metabolism, differentiation, protein evolution and the immune system, among other things.

Some of Kauffman's results are not particularly controversial, because they build on a long tradition in biology that has had as its focus the elucidation of various laws, constraints and emergent properties associated with complex systems. The assertion that natural selection is constrained by the laws of physics and thermodynamics challenges no orthodoxy. What Kauffman adds to this tradition are some law-like constraints associated specifically with the dynamics of complex systems.

On the other hand, Kauffman's overarching conclusion *is* controversial, even gratuitously so. The proposition that autonomous, autocatalytic processes are the primary sources of order in nature, and that natural selection merely fine-tunes the results, represents a radical reformulation of evolutionary theory. Yet this conclusion is not the ineluctable result of the work Kauffman so carefully explicates. It is, as he acknowledges, a "bold leap" beyond the models (and a limited body of empirical support). Nor, as we noted above, is his hypothesis new. The vision of evolution as being self-propelled, or as a self-determined unfolding process, is a venerable theme in natural philosophy, tracing its roots at least to Empedocles. (Indeed, Kauffman's effort is only the most extensive and rigorous of a skein of more or less explicitly orthogenetic, anti-Darwinian theorizing in recent years. See, for instance, Jantsch, 1980; Csányi, 1989; Salthe, 1993.)

BROOKS AND WILEY

Another variation on the non-selectionist theme is the thermodynamic *cum* informational theory of evolution developed by Daniel Brooks, E.O. Wiley (1988) and various colleagues (1989). These theorists propose an explanation for biological evolution that relegates natural selection to the role of facilitating non-essential "enhancements". The three "essential" attributes of living systems, they claim, are relative autonomy from the environment ("phase separation"), the ability to replicate and the production of structural information. "Evolution is quite possible without natural selection and adaptation" (cf., Wicken, 1987; Fivaz, 1991; Salthe, 1993).

NATURAL SELECTION VS. SELF ORGANIZATION

Many years ago, Theodosius Dobzhansky voiced what still stands as the most important scientific objection to such orthogenetic and non-selectionist visions. The basic problem, he noted, is that these theories implicitly downgrade the contingent nature of life and the basic problem of survival and reproduction. In fact, they explain away the very thing that requires an explanation: "No theory of evolution which leaves the phenomenon of adaptedness an unexplained mystery can be acceptable" (1962:p.16). There's the rub. Order is not a synonym for adaptation, and adaptation in nature depends on functional design.

Nor can the need for adaptation be so lightly dismissed as Brooks and Wiley do. For one thing, energy is not a free good; it must be captured and converted to various organic uses. Also, the thermodynamic processes and structures that characterize living systems are never "autonomous," or independent of environmental contingencies. It matters a great deal whether or not these systems are located on land or in water, in the Arctic or the tropics, in an oxygenated or anoxic environment, and whether or not they are subject to competition, or predators, or parasites. Life in the real world is always contingent and context dependent. Indeed, orthogenetic theories are often obtuse, or cavalier about the prevalence in evolutionary history of extinctions. Finally, "information" and "structure" are not functional equivalents; what gets tested in the environment are the properties of the structures themselves, not their informational "content". (See the discussion in Section VII below.)

Self-organization is an undisputed fact, and the case for autocatalysis, especially in the early stages of evolution, is compelling. Indeed, Kauffman's work strengthens the case. His formulation suggests that life may have "crystallized" initially in a collective phase transition leading to connected sequences of biochemical transformations -- an alternative to the hypercycle concept. (Elsewhere, Kauffman likens the process to a set of pegs scattered on a floor that are gradually tied together to form a net.) If this scenario is correct, life may have an "innate holism" (synergy); it began as an integrated, emergent property of complex systems of polymer catalysts. Also, it may have been more easily achieved than we have heretofore imagined. However, Kauffman's vision does not extend very far up the phylogenetic tree, to the point where morphology, functional design and a division of labor begin to matter.

Equally important, much of Kauffman's case, despite its admirable rigor, rests on the models themselves -- on hypotheses that still require testing. At this point, some are little more than mathematical "just-so" stories. The jury is still out on a key question: To what extent are the models isomorphic with the dynamics of the real world? What is the relationship between these computer-driven equations and concrete, feedback-driven, cybernetic systems with specific functional properties and requirements? Do the *quantitative*, numerical relationships in the models map to the *qualitative* functional interactions (and logic) within and between living systems?

This issue is of crucial importance. In its original (Darwinian) formulation as a functional theory of evolution, natural selection referred to those functional effects (adaptations) of all kinds, and at various levels of biological organization, which in each successive generation influence, if not determine, differential survival and reproduction. It is the functional effects produced by a gene, or a genic "interaction system" (in Sewall Wright's felicitous term), or a genome, or phenotype, or an interdependent set of genomes (symbionts, socially organized groups, coevolving species) in relation to the contingencies of survival and reproduction that constitute the directive (causal) aspect of natural selection. Neither randomness (strictly speaking), nor incrementalism, nor even competition (strictly speaking) are indispensable. Natural selection can also be a party to synergistic autocatalytic processes. It can be a party to discontinuous ("catastrophic") symbiotic functional fusions. And it can be a party as well to novelties that create new niches and mitigate competition. Natural selection becomes a co-conspirator whenever an innovation has functional consequences for survival and reproduction. Likewise, natural selection re-confirms existing adaptations in each new generation via "normalizing" or "stabilizing" selection.

In this broader, functional conceptualization, which (contrary to some slanderous caricatures) was clearly articulated by the developers of the so-called "modern synthesis," natural selection is superordinate to all proximate forms of functionally-significant causation, including those that may be autocatalytic and self-ordering (see Huxley, 1942; Dobzhansky, 1962; Simpson, 1967; Wright, 1968-1978; Mayr, 1982; Stebbins and Ayala 1985). In this formulation, natural selection often plays the role of an "editor" or a "censor".

Accordingly, Kauffman's models, and various related efforts, beg the question: Do the dynamical attractors in a Boolean network model represent autonomous self-ordering processes? Or do they perhaps model stable combinations of polymers, genes, cells or organisms which, in the real world, would be likely to be favored by natural selection? The answer may be both. The ordering observed in evolution may have been a trial-and-success process in which the stable attractors identified in dynamical systems models also happen to simulate functionally viable synergistic combinations -- the material entities that must survive in the real world. In this vision, natural selection is not simply the interior decorator who was brought in to hang the curtains after the house was built. From the very outset, natural selection was posing the question to both the architect and the builder: Does it work?

SOME CONCLUSIONS

Several conclusions can be drawn from this important body of theory and research, and from the convergent efforts of many other workers in this area. First, it would appear likely that order was prior to selection and arose through autonomous

self-organizing processes; natural selection did not create order *ab initio*. It may only have bestowed a blessing on it. Nor was natural selection the exclusive designer of biological organization later on. (Indeed, I will argue below that the products of evolution have themselves become increasingly important co-designers over time, though often inadvertently, in a process that has been interactive.)

A second conclusion, one that will also be discussed further below, is that "wholes" may have been more fundamental biological entities than "parts" in terms of the process of biological complexification. In the earliest stages of evolution, the parts in fact had no meaning, no directional consequences and no selective value until they were combined into functional units. Classical competitive selection began to play a shaping role when the first self-organized reproducing wholes appeared, and it intensified in proportion to the increasing organizational and functional capabilities of various combinations of parts. It was the emerging functional capacities for replication, metabolism, damage repair, mobility, predation, defense -- all of which are products of more complex organization -- that accelerated the evolutionary arms race.

Finally, we can discern at an early stage of the evolutionary process a principle which will be elaborated upon below, namely: "competition via co-operation." Co-operation is not a peripheral survival strategy in a world governed by competition. The synergy resulting from co-operative interactions of various kinds provides the functional *raison d'etre* for biological organization, and for the observed evolutionary trend toward greater complexity. In many but obviously not all cases, synergy has given more complex forms a competitive edge. Let us turn then to a consideration of the role of synergy (and symbiosis) in evolution.

SYMBIOSIS VS. SYNERGY: A NOTE ABOUT TERMINOLOGY

Before proceeding further, the relationship between synergy and symbiosis should be clarified. Both are relevant to the process of complexification, but their relationship is often misunderstood.

The word synergy is derived from the Greek word *synergos*, meaning "to work together." As noted above, it connotes combined effects, or the functional outcomes of co-operative interactions of all kinds. (In this context, co-operation is strictly a functional term; it has nothing to do with "altruism".) Though it is often associated with the slogan "the whole is greater than the sum of its parts," it would be more accurate to say that synergy refers to effects that the parts (or individuals) cannot achieve alone, effects that are interdependent. Wholes are not necessarily greater than the sum of their parts, just different.

Among biologists, use of the term synergy has been limited until recently mainly to certain specialized areas, such as neurochemistry, cell biology and endocrinology. (A

recent literature search of these sub-disciplines for the past five years produced some 10,958 "synergy" citations.) On the other hand, most biologists recognize the subset of synergy known as "emergent effects," as well as the synergies associated with coevolution. The term has been used somewhat more broadly in other fields, however, ranging from economics and psychology to architecture and philosophy.

The term symbiosis is also of Greek origin; it means "living together." Its use as a technical term in biology traces to the German mycologist Anton de Bary (1879), who employed it to denote the living together of "dissimilar" or "differently named" organisms in lasting and intimate relationships. His focus was on relationships, and the paradigm examples, both in de Bary's time and ever since, are the roughly 18,000 different species of lichen -- mutualistic partnerships between some 300 genera of fungi and various species of cyanobacteria (formerly known as blue-green algae) and green algae -- although de Bary also included in his definition what would now be called parasitic relationships.

Some biologists still treat symbiosis as a curiosity rather than as a major theme in evolution and its status remains a matter of contention. Indeed, the very definition of the term has been subject to disagreement, and there are an array of conflicting definitions in the literature. Among other things, this etymological anarchy reflects important differences about how the subject matter of the field should be defined, and about which phenomena should be included. Adding to the confusion is the fact that symbiologists are not always consistent in practice even with their own definitions.

SOME ADVANTAGES OF "SYNERGY"

Even if there is no consensus about how to define it, symbiosis is firmly established in biology, both as a concept and as an area of active research and theorizing; it is unlikely to be displaced by any alternative. Nevertheless, the term "synergy" may have more utility as an umbrella term for co-operative interactions. Some of the reasons are as follows:

- Synergy is a room without walls in terms of which kinds of co-operative relationships are applicable; combined effects of all kinds and at every level of living systems are relevant, from enzymes to ecosystems; indeed, the term can even accommodate such unconventional but important biological phenomena as animal-tool "symbioses," not to mention the relationships between humans and their technologies.
- Synergy can comfortably handle both mutualistic and parasitic combinatorial effects, as well as various asymmetrical distributions of costs and benefits and even some co-operative effects which defy the conventional categories. For instance, the humus soils upon which many plants and, indirectly, insects,

herbivores and humans depend, are the combined effects of biological activity over many millions of years. This biologically-important medium exhibits synergy, but it is not the direct product of mutualism or parasitism. It is an incidental combined effect resulting from the aggregation of many incremental contributions by countless individual organisms.

- By focussing on co-operative effects of all kinds, synergy is a more pan-disciplinary and inclusive term; it even encompasses an array of non-living phenomena, from "Bucky Balls" (Buckminster Fullerenes) in physics to the synergy-rich realm of human technology.
- Synergy also focuses our attention on the *functional effects* produced by co-operative phenomena, including symbiosis. This is important because it is the functional effects associated with a novel adaptation that are the locus of natural selection.

All symbioses produce synergistic effects, but many forms of synergy are not the result of symbiosis (see Section VI). One example will perhaps illustrate the problem with using symbiosis as an inclusive term for co-operative phenomena, and ultimately as a conceptual framework for explaining the evolution of complexity. The eukaryotic cell, with its intricate structure of differentiated organelles, is a model of micro-level synergy (Adam Smith's famous pin factory writ small) and one of the great breakthroughs in the evolution of complexity. During the past decade, new evidence of nucleic acid sequencing homologies with free-living bacteria, among other developments, has convinced many skeptics that some of the key organelles -- the mitochondria, undulipodia (cilia) and chloroplasts -- may indeed have evolved in accordance with the so-called SET (serial endosymbiosis theory) espoused by Lynn Margulis and others (1970, 1981, 1993). While it remains less certain, it is also possible that the centrioles/kinetochores and spindle apparatus in eukaryotes may have derived from symbiotic (or parasitic) relationships with spirochetes. In short, the eukaryotic cell may be a "federation" -- an obligate union of several once independent genomes.

However, there are a number of other organelles in this remarkably complex division of labor that most likely evolved through internal processes of compartmentalization, differentiation and functional specialization, rather than via symbiosis. Some candidates for the "autogenous" theory of eukaryote evolution include the nucleus, the Golgi bodies (dictyosomes), vacuoles, ribosomes and endoplasmic reticulum (Margulis and McMenamin, eds., 1993). Indeed, Thomas Cavalier-Smith (1981, 1987) has proposed a scenario for eukaryote evolution that stresses internal structural developments as prerequisites.

Whatever their origins, these organelles provided the evolving eukaryotic cells with a potent set of functional capabilities -- the ability to engage in metabolism and manufacture (and repair) structural components, the capacity to resist various environmental insults, motility, the ability (in plants) to conduct photosynthesis, and, not least,

the ability to reproduce. It was the co-operative effects -- the synergies -- produced by these organelles *in combination* that explains, ultimately, the evolutionary success of the eukaryotes. Symbiosis played an important role in the "how" part of the story, while the concept of functional synergy speaks to the "why" question.

Thus, in this instance as in many others, the term symbiosis (in any of its diverse definitions) does not provide a large enough umbrella to cover the full range of co-operative phenomena in nature. On the other hand, the term synergy has no such connotative constraints. It can comfortably accommodate both incremental evolution via classical neo-Darwinian point mutations and more punctuational changes via genomic fusions, which Robert Haynes (1991) has characterized as "megamutations". Likewise, it is equally at home with both of the two different modes of complexification in evolution, namely, "integration," (aggregation, fusion or "alliances" of various kinds) and internal "differentiation". (More on this subject below.) Synergy also directs our attention beyond relationships to the functional properties and fitness consequences of co-operative phenomena of all kinds -- to the data associated with a causal explanation for the evolution of complexity.

THE REDISCOVERY OF SYMBIOGENESIS

Symbiosis in general and mutualism in particular (to say nothing of the broader concept of synergy) represented at best a minor theme in biology until recently, and it certainly played no role in mainstream evolutionary theory. Some theorists considered symbiosis to be a "myth"; others viewed it merely as a small class of anomalies or oddities that in no way challenged the dominant neo-Darwinian synthesis (competition and mass selection among point mutations in individual genes); still others recognized that mutualistic, co-operative relationships might provide organisms with a competitive advantage under some circumstances (even Darwin appreciated that), but it was assumed that such phenomena are relatively rare.

During the past decade, however, a dramatic change has occurred. There has been an upsurge in research and theorizing about symbiosis, mutualism, co-operation and even synergy. Among the major developments:

- Growing acceptance of the endosymbiotic theory of eukaryote evolution, indisputably one of the major benchmarks in biological complexification;
- A flowering of research and publications on symbiosis across more than a dozen subdivisions of biology, along with a growing number of courses and textbooks on symbiosis, a new international journal called Symbiosis and several conferences devoted to the subject;

- A parallel upsurge of interest in mutualism and coevolution among ecologists, with special reference to the application of co-operative versions of the well-known Lotka-Volterra equations, as well as various cost-benefit models;
- A recognition of the importance of co-operation among hard-core neo-Darwinians in general and sociobiologists in particular, in part due to the iterated prisoner's dilemma model developed by Robert Axelrod and William Hamilton (Axelrod, 1984; Axelrod and Hamilton, 1981) and the supporting research that it has spawned (Axelrod and Dion, 1988; Lima, 1989);
- Work in Europe on symbiosis and the emergence of a new academic subspecialty, endocytobiology, which is devoted to cellular symbioses (Schwemmler and Schenck, eds., 1980; Schwemmler, 1989);
- The belated discovery in the west of an entire school of "Symbiogenesis" theorists, dating back to a group of late 19th and early 20th century Russian botanists (but including also a few advocates in the west), who advanced the hypothesis that symbiosis has played a major causal role in evolution (according to some, in opposition to natural selection) (Khakhina, 1979, 1992; Margulis and McMenamin, eds., 1993);

THE 1989 INTERNATIONAL CONFERENCE

A culmination of this process was a landmark international conference in 1989 on symbiosis as a source of evolutionary innovation, at which some 20 participants documented the ubiquity of symbiosis and developed the case for Symbiogenesis as a significant factor in evolution (Margulis and Fester, eds., 1991). Among the evidence presented:

- Symbiosis is a far more widespread phenomenon than is generally appreciated. Mutualistic or commensalistic associations (not to mention parasitism) exist in all five "kingdoms" of organisms (Margulis and Schwartz, 1988) and in 37% of the 75 phyla associated with the four eukaryotic kingdoms.
- Over 90% of all modern land plants establish mycorrhizal associations, which are essential to their survival.
- Land plants may have arisen through a merger between fungal and algal genomes -- as sort of inside-out lichens. In any case, it is now generally accepted that land plants represent a joint venture between fungi and green algae.

- Almost one-third of all known fungi are involved in mutualistic symbioses, many of which have conferred on their partnerships the ability to colonize environments that would otherwise have been inaccessible to them (e.g., lichen).
- Virtually all species of ruminants, including 2,000 termites, 10,000 wood-boring beetles and 200 Artiodactyla (deer, camels, antelope, etc.) are dependent upon endoparasitic bacteria, protocists or fungi for the breakdown of plant cellulose into usable cellulases.
- Given the fact that parasitic relationships are very often "building blocks" that facilitate a symbiotic interaction, it is estimated that over half of all the animal species on earth have feeding relationships that are mediated by symbionts. (For example, nematodes that are parasitic on beetles survive only when there are bacteria present that can prevent the decay of host tissue by producing an antibiotic.)
- Though still speculative, it has been seriously proposed that angiospermous flowers and fruits are derived from arthropod-induced galls via the incorporation of microbial or fungal DNA into plant genomes.
- Also speculative at this point is the intriguing hypothesis that plant and animal chromosomes have symbiotic origins.
- There is accumulating evidence that symbiosis may play a direct role in the process of speciation. Many symbionts produce "emergent" new synthetic products that are important to their mutual survival.
- The startling discoveries of symbioses associated with sea floor hydrothermal vents provide additional evidence of Symbiogenesis as a factor in evolution. Within the abundant communities of organisms discovered at these vents are symbiotic partnerships between chemoautotrophic (sulfur-oxidizing) bacteria and various invertebrates, which rely on the bacteria for their carbon and energy requirements.
- Many organisms are more promiscuous with their genes, both as donors and as recipients, than the "selfish gene" model of the genome suggests; we now know that DNA travels easily, even across taxonomic boundaries, in the form of small replicons (plasmids, viruses, transposons, etc.). Bacterial communities provide an important example. Most bacterial cells congregate and reproduce in large, mixed colonies with many endosymbionts (virus-like plasmids and prophages) and ectosymbionts (metabolically complementary bacterial strains). These congregations call into question the classical notion of a species, in the sense of competitive exclusion and reproductive isolation.

- Finally, there was discussion at the conference of the hypothesis advanced by Bernstein et al., (1985) and Margulis and Sagan (1986) that sexual reproduction, one of the major remaining conundrums in evolutionary theory, may trace its roots to symbiotic damage repair mechanisms among ancestral prokaryotes of 3 billion years ago.

SOME TENTATIVE CONCLUSIONS

Though much work still remains to be done by symbiologists on the costs and benefits, and evolutionary implications, of symbiosis, a number of tentative conclusions are possible. First, there can be no doubt that the synergies associated with symbiosis have played a significant role in the evolution of complexity. Symbiosis is implicated in the emergence of the first living organisms, as well as mergers among primitive prokaryotes with complementary functional specializations, the development of complex nucleated cells, the emergence of land plants and ruminant animals, the colonization of various aquatic and terrestrial environments, and the "progressive" coevolution over time of both aquatic and terrestrial ecosystems.

A second conclusion is that symbiosis is clearly a robust phenomenon. Not only is it found within and between all five kingdoms but functionally similar kinds of symbiosis have evolved repeatedly and independently within (and across) various taxa. For instance, the lichen taxon, which has no common ancestor, includes 16 of the 46 recognized orders of ascomycetes fungi (as well as some basidiomycetous and conidial fungi) and over 30 types of algae and cyanobacteria (Hawksworth, 1988). By the same token, cyanobacteria, which are photosynthesizers, form symbiotic relationships not only with fungi but also with some algae, Bryophytes, aquatic ferns (*Azolla*), Cycads and angiosperm (*Gunnera*) (Ahmadjian and Paracer, 1986). Similarly, many species of cleaner fish and cleaner birds provide services opportunistically for an array of fish, alligators, crocodiles, iguana, elephants, rhinos and many other species of herbivores. The multiple, independent evolution of symbiotic relationships has also been documented in corals, legumes, ruminant gut symbionts and hydrothermal vent species, among others.

A third conclusion is that symbiosis has provided many opportunities for organisms to occupy ecological niches that would not otherwise have been viable. The lichen that are often the first living forms to colonize a barren environment provide an example. And so also do the richly populated coral communities that are frequently found in what would otherwise be unproductive tropical waters. Likewise, gut symbiosis is indispensable for the niche occupied by ruminant animals. (The hydrothermal vent species, which occupy a unique niche, were also noted earlier.)

It should also be evident that symbiosis may serve a number of highly survival-relevant purposes, including defense and protection, nutrition, mobility and

reproduction. The character of these relationships can also vary widely across a number of different "parameters," including: duration, persistence, specificity, universality, level of dependency, type and level of integration, mode of transmission and the distribution of costs and benefits. For instance, many flowering plants are completely dependent on their animal symbionts for reproductive assistance, but the relationships are transitory and promiscuous. By contrast, some cattle egrets, oxpeckers and other bird species may form more or less permanent attachments to one or a few ruminant animals but may not depend for their nutritional needs on the animals' parasites; they may be diversified ground foragers as well.

Another point is that symbiosis typically precipitates the coevolution of various facilitative adaptations -- morphological structures, chemical substances, communications modalities and even cybernetic regulatory mechanisms. There are, for example, the specialized organs that accommodate the light emitting bacteria in luminescent pony fish (Ruby and Morin, 1979); there is the "honeydew" that aphids produce for their ant hosts (Wilson, 1975); there are the hollow thorns and glycogen-rich nectar that attract *Pseudomyrmex* ants to *Acacia* plants, where, in return, the ants provide protection from harmful parasites and disperse the plants' seeds (Ahmadjian and Paracer, 1986); there are also the nectar and honey guides produced by flowering plants; and there are the bicarbonate ions produced in abundance in the saliva of ruminants, which help to maintain an acceptable pH for their gut symbionts (Smith and Douglas, 1987). Perhaps most significant is the evidence that symbiont hosts may regulate the growth and reproduction of their partners, presumably in the interest of preserving the integrity of the whole (Smith and Douglas, 1987). As Margulis (Margulis and McMenamin, eds., 1993) truly observes, the reproductive rates of symbionts must of necessity be synchronized.

As noted earlier, it is also evident that symbiosis frequently involves more than two species and may constitute some of the key building blocks of an ecosystem. One of the most extraordinary examples is the single celled eukaryotic protist *Mixotricha paradoxa* (Margulis and McMenamin, eds., 1993; Mayr, 1974a). In fact, each cell represents an association of at least five different types of organisms. In addition to the host cell, there are three surface symbionts, including large spirochetes, small spirochetes and bacteria. The function of the large spirochetes, if any, is not clear; they may even be parasites. However, the hair-like small spirochetes, which typically number about 500,000 *per cell*, provide an unusually effective propulsion system for the host through their highly coordinated undulations, the control mechanism for which is still obscure. Each of these spirochetes, in turn, is closely associated with another surface symbiont, a rod-shaped "anchoring" bacterium. Finally, each *Mixotricha* host cell contains an endosymbiont, an internal bacterium that may serve as the functional equivalent of mitochondria, removing lactate or pyruvate and producing ATP.

What makes this partnership all the more extraordinary is the fact that *Mixotricha* is itself an endosymbiont. It is found in the intestine of an Australian termite, *Mastotermes darwinensis*, where it performs the essential service of breaking down the

cellulose ingested by its host. Indeed, these and other symbionts may constitute more than half the total weight of the termite.

Perhaps the most impressive form of multiple symbioses, though, can be found in coral communities. A single coral reef may encompass millions of organisms from dozens of different plant and animal species, many of which are symbiotic with one another, as well as with the coral outcropping itself. The coral provides oxygenated water and shelter. The plants and animals consume the oxygen, plankton and organic debris and deposit calcium to build the coral. In addition, there are many kinds of symbioses between the creatures that are associated with the corals -- among others, clams and algae, crabs and sea anemone, fish and sea anemone, shrimp and sea anemone, and sea urchins and fish. The functions associated with these relationships include nutrition, protection from predators, mobility, mutual defense and parasite removal (Perry, 1983).

Some Implications

Among the implications of symbiosis for the science of complexity, three should be mentioned at this point.

1. Fusion, or the *functional integration* of *various elements, parts*, or organisms via symbiosis, is one of the major "mechanisms" of complexification. However, the pattern can be extremely varied and the functional consequences are neither straightforward nor fixed.
2. Evolutionary complexification via fusion or integration has a distinctive causal dynamic in which behavioral changes (broadly defined) precipitate new options for selection. These changes are sustained in the short term by *proximate* mechanisms -- direct "rewards" or "reinforcements" (real-time payoffs and feedback). However, the *ultimate* cause of the process -- natural selection -- is the fitness and reproductive consequences of the short-term functional effects. Another way of putting it is that, in evolutionary change, effects are causes. (More on this below.)
3. This dynamic suggests a different approach to the modelling of evolutionary change. In effect, a coupling of two (or more) separately evolved genomes creates a new selective unit that may or may not compete directly with other organisms or with non-symbiotic siblings. Yet, so far as I know, there has been little if any effort to incorporate symbiotic relationships into formal models of evolution, or of complexity. For instance, the word symbiosis does not even appear in the index to Kauffman's recent volume. And his NK models of correlated fitness landscapes are designed to model alternative epistatic interactions among the genes in a single genome. One possible approach might be to modify Sewall Wright's "peak shift" model (Wright,

1968-1978), in which alternative genic "interaction systems" can move abruptly between the peaks on an adaptive "surface".

A final point, to reiterate what was said earlier, is that symbiosis, or *integration*, represents only one of two very different modes of evolutionary complexification. Under the broader umbrella of synergy there are also the multifaceted processes of *differentiation*, which occur at many different levels and involve a very different sort of causal dynamic. We will consider this mode of complexification further below.

SYNERGY AND EVOLUTION

Synergy exists in so many different forms that it defies efforts to develop an exhaustive typology. I will list below some of the more common and functionally important categories (although these are not all mutually exclusive).

1. Linear effects: synergy that arises from additive or multiplicative phenomena. For instance, size is often an advantage in nature (and in human societies); a bigger organism, or a bigger group of organisms, may be able to do things that smaller ones cannot. And, for the most part, larger size is a cooperative effect that is achieved by the aggregation (or multiplication) of many component cells, parts or individuals.
2. Threshold phenomena: what might be called "catastrophic" forms of synergy. Many of these are linear in origin, but their effects are systemic and depend on the specific context. The paradigmatic example is the old-fashioned tug-of-war, but there are many examples with more theoretical significance. For instance, over the course of millions of years, various anaerobic organisms were able jointly to produce an oxygenated atmosphere that was capable of supporting aerobic organisms. This involved an aggregation of like-kind effects, but what is relevant for understanding the evolution of aerobes are the combined properties of the medium itself.
3. Phase transitions: a form of synergy that is a special case of threshold phenomena. Phase transitions are abrupt changes of state, or of functional properties, that occur in many physical and dynamical systems; they are cooperative effects. Physicists often use as examples the crystallization of water into ice, the loss of magnetic properties in a ferromagnet at extremely high temperatures or the onset of superconductivity in various materials at extremely low temperatures. In biology, phase transitions can be observed in such phenomena as seed germination, the mammalian birthing process and the onset of the seasonal transformations in deciduous trees.

4. Emergent phenomena: when two or more "parts" merge in such a way that a new whole arises with distinctive chemical, physical, functional and/or causal properties. Thus, when the light metal sodium and chlorine gas, two elements that are normally poisonous to humans, are combined they form a compound (NaCl) with new properties which, in moderate amounts, are beneficial to humans. But the functional effects of table salt cannot be understood in terms of the properties of its constituent elements; the parts lose their identities and combine to create a new substance.

Another form of emergent synergy can occur through the co-operative interactions among parts that do not surrender their physical identities. Automobiles, computers and symphony orchestras fall into this category. And so do many of the products of social organization in animal and human societies (e.g., the nests of army ants, which are composed of the interlinked bodies of many thousands of the colony-members.)

5. Functional complementarities: a form of synergy that often overlaps with the emergent effects described above. One type of functional complementarity involves a melding of functionally different components. A low-tech example is Velcro. A middle-tech example is a piano. And a high-tech example is a computer. Or, consider this example of nutritional synergy. One-half cup of beans provides the nutritional equivalent of two ounces of steak, while three cups of whole wheat flour provides the equivalent of five ounces of steak. Eaten separately, they amount to the equivalent of seven ounces of steak. But because of the complementarity of their constituent amino acids, if the two substances are consumed together they provide the equivalent of nine ounces of steak, or 33 percent more usable protein.

6. Augmentation and facilitation: co-operative effects that enhance or in some cases make dynamic processes possible. One class of examples is the catalysts that decrease the activation energy required in various inorganic chemical reactions while themselves remaining unchanged. Another class of examples is the catalytic activity of enzymes in biochemical processes, which differ in that the surface geometry of these substances is what determines their functional properties. The enhancement of mutation rates by gamma rays and metallic salts is yet another example. And so are the oxygen-binding properties of hemoglobin. Hemoglobin is a tetrameric protein, and each of its four monomers bind oxygen. But their binding behavior displays positive cooperativity; binding by one monomer increases the binding affinity of the others.

7. Environmental conditioning: a special case of the augmentation and facilitation effects cited above. Emperor penguins (*Aptenodytes forsteri*), for instance, are able to buffer themselves against the intense Antarctic cold by huddling together in dense heat-sharing colonies numbering in the tens of thousands. Experiments have shown that, in so doing, the penguins are able to

reduce their energy expenditures by as much as 50 percent (Le Maho, 1977). Similarly, Warder C. Allee showed that aggregations of flatworms are able jointly to detoxify a hypotonic solution (Allee, et al., 1949). And honey bees, through joint heat production or fanning activities, as the need arises, are able to maintain the internal temperature of their hives within a narrow range (Wilson, 1975).

8. Risk and cost sharing: reductions in risks and costs through various forms of co-operation, including flocking, schooling, synchronized breeding, joint nest-building and communal nesting, collective foraging and migration, pack hunting, and a variety of other co-operative behaviors. Risk-sharing in human societies can be found in such familiar institutions as insurance systems and mutual funds, and cost-sharing is even more widespread.

9. Information sharing: a subcategory of risk and cost sharing but worthy of being singled out because of its obvious importance in human societies. Perhaps the best-known example in nature is the honeybee waggle dance, which facilitates collective foraging (Wilson, 1975). However, there are also many less renowned examples.

10. Social behavior and organization: Though various examples of social co-operation among members of the same species (as distinct from symbionts of different species) have already been cited under other headings above, social synergy is important enough to our purpose to be singled out. A number of different survival-related synergies have been identified by ethologists and sociobiologists, including: (1) hunting and foraging collaboratively, which may serve to increase capture efficiency, the size of the prey that can be pursued, or the likelihood of finding food patches, (2) joint detection, avoidance of and defense against predators, the forms of which range from mobbing and other kinds of coordinated attacks to flocking, communal nesting and synchronized reproduction, (3) co-operative competition, or "coalition" behavior, particularly in relation to obtaining food, territory, social dominance and mates, (4) shared protection of jointly collected food caches, notably among many insects and some birds, (5) co-operative movement and migration, including the use of formations that increase aerodynamic efficiency and reduce individual energy costs and/or facilitate navigation, (6) co-operation in reproduction, which can include joint nest building, joint feeding and joint protection of the young, and (7) shared environmental conditioning and thermoregulation, as described above.

11. Functional Convergences: There is, in addition, a broad category that can be called "functional convergences." Sometimes this category is included in the "division of labor," but it is more accurate to limit it to fortuitous combinations of labor undertaken by the relevant actors independently of any regard for the combined result. For instance, it is a platitude these days to observe that most ecosystems are replete with relationships in which the participants, while in the

process of pursuing their own survival and reproduction, also unwittingly contribute to an unplanned but integrated "web" of functional interactions -- predatory, parasitic, commensalistic, mutualistic -- along with more subtle forms of interdependency. Combined effects of various kinds are woven through every ecosystem. Although some of the patterns that result from these interactions may mimic dynamical models of spontaneous self-ordering, they are in fact the products of functional self-ordering processes; what may look like a dynamical attractor is in fact a functional convergence -- a functionally-induced dynamic stability.

This may not be difficult to imagine in an ecosystem, but such functional convergences also exist at the level of individual organisms and even individual cells. Robert Haynes (1991) has provided an excellent example. The observed error rate in normal cellular DNA replication is remarkably low (about 10^{-10} to 10^{-8} per base pair) compared with the theoretical potential, given the ambient sources of decay, damage and copying errors, of about 10^{-2} . The explanation for this fortunate discrepancy is that it is the convergent result of a complex set of mechanisms that "work together" to prevent what would otherwise be far more frequent genetic "meltdowns". These mechanisms include proofreading by DNA polymerases, methylation-instructed mismatch correction, enzymatic systems that repair or bypass potentially lethal or mutagenic DNA damage, processes that neutralize or detoxify mutagenic molecules, the regulation of nucleotide precursor pools and, of course, the redundancy achieved by double-stranded genetic material. The combined, synergistic result of this functional convergence is an improved reproductive "bottom-line."

Another type of functional convergence, of a very different sort, can be found in Adam Smith's (1964 [1776]) classic description of a complex human economy, the workings of which (as we all know) Smith characterized as "an invisible hand." A microcosmic example is the daily dance of the New York stock market. There is no superordinate price-setting mechanism in the market; it does not work at all like a thermostat. Rather, the market's often unpredictable changes are the fortuitous combined result of many thousands of individual decisions, each of which is oblivious to its impact on the market as a "whole".

SYNERGY AND DIFFERENTIATION

Several of the categories described above overlap with what traditionally has been termed the "division of labor." Plato discoursed on the subject in *The Republic*. Adam Smith appreciated it's central importance to the economy of Eighteenth Century England. And in light of modern biology, we now know that the division of labor is also an important evolutionary phenomenon. At the micro-level it is evident in the

exquisite complexity of the eukaryotic cell, and at the macro level it can be observed in the behavior patterns of socially-organized species.

One of the most impressive examples of the latter is *Eciton burchelli*, a species of army ants found in Central and South America. *E. burchelli* have four morphologically distinct castes (in addition to the queen) which share the responsibility for colony defense, foraging, transport, nest-making and "child care." The result is a super-efficiency that rivals Adam Smith's pin factory. The so-called submajors (or porters), for instance, team up to carry sometimes very large prey which, if split up into pieces, would be more than each individual ant could carry alone (Franks, 1989).

The synergies associated with functional differentiation may take either of two forms. One type involves the disaggregation of a single complex task into a set of specialized sub-tasks. The human immune system -- one of the marvels of nature -- provides a micro-level illustration. As described by immunologists Ivan Roitt (1988) and Gustav Nossal (1993), The system which defends us against the enormous number and variety of potentially pathogenic microbes in our environment consists of at least nine different types of mechanisms, some of which are localized at vulnerable places in the body and act more or less independently while others range throughout the body and are highly interactive with other elements of the system. Perhaps most impressive is our "acquired" immune system, which consists of a widely dispersed network of primary and secondary organs (the thymus and bone marrow, and the lymph nodes, spleen and tonsils) which orchestrate a highly coordinated defense of the body using an array of functionally-specialized cells and molecules that are distributed via our lymphatic and circulatory systems. These specialized agents include, among others, Presenting Cells that identify antigens, MHC (or Major Histocompatibility Complex) cells that display antigen pieces (peptides), T lymphocytes that "read" the antigen peptides and signal other components of the system (such as macrophages), and B lymphocytes that produce a prodigious variety of antibody proteins. (And this is only an abbreviated outline of a much more complex story.)

The second type of functional differentiation arises from the fact that the survival problem is usually multi-faceted, and that the various subtasks associated with survival and reproduction may be allocated to specialists of various kinds (*viz.*, *Eciton burchelli*). In either case, functional differentiation in turn creates a need for cybernetic regulation; the "parts" must be coordinated to achieve the objectives of the "whole". Accordingly, the synergies associated with functional differentiation (or symbiotic integration) create selective contexts that in turn favor the evolution of cybernetic regulatory mechanisms (see below).

THE BIOECONOMICS OF SYNERGY

As the foregoing suggests, synergy can produce a variety of measurable, quantifiable benefits -- economies of scale, increased efficiency, improved benefit-cost ratios, the melding of functional complementarities, reduction or spreading of costs and risks, augmentation effects, threshold effects, and the emergence of novel functional effects. Thus, information sharing by weaver birds can measurably reduce individual energy expenditures for foraging, and the huddling behavior of emperor penguins measurably reduces individual energy expenditures for thermoregulation.

Other examples include Bonner's (1988) observations that aggregates of myxobacteria which move about and feed en masse secrete digestive enzymes that enable them collectively to consume much larger prey. Similarly, Schaller (Schaller, 1972) found that the capture efficiency (captures per chase times 100) and the number of multiple kills achieved by his Serengeti lion prides increased with group size -- although a later study by Caraco and Wolf (1975) found that these results were dependent on the size of the prey. In the highly social African wild dog (*Lycaon pictus*), overall kill probabilities in hunting forays were found to be vastly superior (between 85 and 90 percent) to those achieved by less social top carnivores (Estes and Goddard, 1967). Kummer (1968) found that collective defense in hamadryas baboons (*Papio hamadryas*) is highly successful and reduces the net risk to each individual troop member. Ligon and Ligon (1978, 1982) analyzed the remarkable communal nesting behavior of the green woodhoopoe (*Phoeniculus purpureus*) and discovered that the extensive pattern of helping behaviors, even among unrelated individuals, markedly increased their likelihood of survival and reproductive success in their harsh Kenyan environment. Partridge (1982) and his colleagues have shown that fish schooling, which may include active forms of co-operation, is highly adaptive for the individual members. For instance, evasive maneuvers utilized by dwarf-herring against predatory barracudas dramatically reduces the joint risk of being eaten. And H.O. Wagner (1954) observed that the Mexican desert spiders (*Leiobunum cactorum*) cluster together in the thousands during the dry season, enabling them to avoid dehydration.

In all of these cases, and in countless human analogues, there were synergies -- co-operative economies -- that could not otherwise be achieved. However, as noted earlier, synergy is always context-specific and contingent. Consider again the examples cited above. Weaver birds have nothing to gain from information sharing when food is plentiful and widely distributed; huddling behavior by emperor penguins is not functional -- and is not done -- during the warm summer months; myxobacteria would find it dysfunctional to feed in large aggregations if their food sources were all small and widely dispersed; African lions would do better to hunt small, slow-moving prey alone; if wild dogs were ruminants, sociality would most likely not provide any nutritional benefits; collective defense by hamadryas baboons is relevant only because there are dangers to defend against; in more salubrious environments, green woodhoopoes would probably not find it advantageous to feed unrelated nestlings;

dwarf-herring might not find it advantageous to school if there were not barracudas about; and desert spiders have nothing to gain by congregating during the wet season.

Economic activity in human societies exhibits many of the same properties, and synergies. One important distinction has to do with the role of technology (which is often likened to a form of symbiosis) in driving the evolution of human cultures. Thus, for example, a native Amazonian using a steel ax can fell about five times as many trees in a given amount of time as could his ancestors with stone axes. Likewise, a farmer with a horse can plow about two acres per day, while a farmer with a modern tractor can plow about 20 acres per day. One New Guinea horticulturalist can produce enough food to feed himself and about four or five other people; an American farmer can produce enough to feed 45-50 people. And when the Mobil Oil Corporation recently purchased a Thinking Machines CM-5 computer to replace its existing super-computer, the time (and cost) required to process a major batch of seismic data dropped from about 29 weeks and \$2.8 million to 10 days and \$100,000.

THE CAUSAL ROLE OF SYNERGY IN EVOLUTION

A second point has to do with the nature of evolutionary causation and the causal role of synergistic phenomena. Earlier it was asserted that synergistic effects have played a significant role in the well-documented "progressive" emergence of more complex systems, both in nature and in human societies. (We will use the rubrics of size, functional differentiation, interdependence and hierarchical ordering as our measuring rods.) That is, the functional effects produced by synergistic phenomena of various kinds have been an important "mechanism" of complexification. In order to appreciate how this mechanism has worked, some further clarification of the concept of natural selection is necessary.

Evolutionists often speak metaphorically about natural selection (as did Darwin himself) as if it were an active selecting agency, or literally a mechanism. Thus, Edward O. Wilson (1975:p.67) assures us that "natural selection is the agent that molds virtually all of the characters of species." Ernst Mayr (1976:p.365) tells us that "natural selection does its best to favor the production of programs guaranteeing behavior that increases fitness." And George Gaylord Simpson (1967:p.219) asserted that "the mechanism of adaptation is natural selection." The problem is that natural selection does not *do* anything; nothing is ever actively selected. In fact, natural selection refers to whatever factors are responsible in a given context for causing the differential survival and reproduction of genes, genic interaction systems, genomes, populations and species. It is the functional effects produced by various "units" of selection that matter. Thus, as noted earlier, evolutionary causation runs backwards from our conventional notion of cause and effect; in evolution, functional effects are the causal "mechanisms".

Evolutionists have tended to focus on a particular factor, or "selection pressure," or on the functional properties of a "gene". This has proven to be a useful heuristic device, but in fact the dynamics of evolutionary causation is always interactional and relational. To cite a textbook example, genetically-based differences between the light, "cryptic" strain of the peppered moth (*Biston betularia*) and the darker melanic strain played a role in the documented change in their relative frequencies in the English countryside during the Industrial Revolution. But their color differences became significant only because industrial soot progressively blackened the lichen-encrusted tree trunks that were the moths' favored resting places. Moreover, this change in background coloration was significant only because the moths were subject to avian predators that used a visual detection system (as opposed, say, to the sonar systems used by bats) (Kettlewell, 1955, 1973). In other words, the "mechanism" that was responsible for this micro-evolutionary change was the functional relationship between genetically-determined traits, the background coloration of the trees, the behavior of the moths and the nature of their predators.

Accordingly, any factor that precipitates a change in functional relationships -- that is, in the viability and reproductive potential of an organism or the pattern of organism-environment interactions -- represents a potential cause of evolutionary change. It could be a functionally-significant gene mutation, it could be a chromosomal rearrangement, a change in the physical environment, or (most significant for our purpose here) a change in behavior. In fact, a sequence of changes may ripple through an entire pattern of relationships: Thus, a climate change might alter the ecology, which might induce a behavioral shift to a new environment, which might lead to changes in nutritional habits, which might precipitate changes in the interactions among different species, resulting, ultimately, in morphological changes and speciation.

CREATIVITY IN EVOLUTION

What, then, are the sources of creativity in evolution? There are many different kinds, but the role of behavioral changes as a "pacemaker" of evolutionary change should be emphasized. To quote an authority on the subject, Ernst Mayr (1960:p.373, 377-78):

A shift to a new niche or adaptive zone requires, almost without exception, a change in behavior... It is very often the new habit which sets up the selection pressure that shifts the mean of the curve of structural [or functional] variation... With habitat selection playing a major role in the shift into new adaptive zones and with habitat selection being a behavioral phenomenon, the importance of behavior in initiating new evolutionary events is self-evident... Changes of evolutionary significance are rarely, except on the cellular level, the direct result of mutation pressure.

However, this model also begs the question: What causes behavioral changes? While this is a vastly complicated subject, one important underlying principle can be identified. In fact, behavioral changes often involve a proximate causal "mechanism" -- the immediate rewards and "reinforcements" that psychologist E.L. Thorndike (1965 [1911]) associated with his famous Law of Effect, which forms the backbone of behaviorist psychology. At the behavioral level, in other words, there is a *proximate* selective "mechanism" at work that is analogous to natural selection. Moreover, this "mechanism" is very frequently the initiating cause of the *ultimate* changes associated with natural selection (see Corning, 1983; also, Plotkin, 1988; Bateson, 1988; cf., Skinner 1981).

This is where the phenomenon of functional synergy (and the subcategory of symbiosis) fits into the evolutionary picture: It is the immediate, bottom-line payoffs of synergistic innovations in specific environmental contexts that are the causes of the biological/behavioral/cultural changes that, in turn, lead to synergistic longer-term evolutionary changes in the direction of greater complexity, both biological and cultural/technological.

Consider these two illustrations, one from each realm. *Anabaena* is a single-celled cyanobacterium that engages in both nitrogen fixation and photosynthesis, a dual capability that gives it a significant functional advantage. However, these two processes happen to be chemically incompatible. The oxygen produced by photosynthesis inactivates the nitrogenase required for nitrogen fixing. *Anabaena* has solved this problem by complexifying. When nitrogen is abundantly available in the environment, all the cells are uniform in character. When ambient nitrogen levels are low, however, specialized cells called heterocysts are developed that lack chlorophyll but synthesize nitrogenase. The heterocysts are then connected to the primary photosynthesizing cells by filaments. Thus, a compartmentalization and division of labor exists which benefits the "whole" (Shapiro, 1988).

The second illustration involves another well-known example from The Wealth of Nations. Adam Smith drew a comparison between the transport of goods overland from London to Edinburgh in "broad-wheeled" wagons and the transport of goods by sailing ships between London and Leith, the seaport that serves Edinburgh. In six weeks, two men and eight horses could haul about four tons of goods to Edinburgh and back. In the same amount of time, a merchant ship with a crew of six or eight men could carry 200 tons to Leith, an amount that, in overland transport, would require 50 wagons, 100 men and 400 horses.

The advantages of shipborne commerce in this situation are obvious. Indeed, shipmen over water has almost always been an advantageous form of long-distance transport, as many different societies have demonstrated historically. But the causal explanation for Smith's paradigmatic example is not so obvious. In part it involved a division of labor and the merging of an array of different human skills; in part it involved the fairly sophisticated technology of late eighteenth century sailing vessels; it

also required the capital needed to finance the construction of the ships; it required a government that permitted and encouraged private enterprise and shipborne commerce (including the protection afforded by the British navy); it also required a market economy and the medium of money; in addition, it required an unobtrusive environmental factor, namely, an ecological opportunity for waterborne commerce between two human settlements located (not coincidentally) near navigable waterways with suitable tidal currents and prevailing winds.

In other words, the causal matrix involved a synergistic configuration of factors that "worked together" to produce a favorable result. And the result -- which played an important role in the rise of the British Empire -- represented a significant step in the ongoing process of technological, economic and societal evolution. However, it should also be reiterated that, if any major ingredient were to be removed from the recipe, the result would not have occurred. Take away, say, the important component technology of iron smelting. Or, in like manner, take away the baggage handling system from the new Denver Airport, or the power supply from Jurassic Park. Synergistic causation is always configural, and relational, and interdependent; the outcomes are always co-determined.

SYNERGY AND THE EVOLUTION OF COMPLEXITY

The relationship between synergistic effects and the evolution of complexity should now be more apparent. The process of complexification in evolution has been closely linked to the production of novel, more potent forms of synergy. That is, the "progressive" *differentiation* and/or *integration* of various "parts," coupled with the emergence of cybernetic regulation and the development of hierarchical controls, has been driven by the "mechanism" of functional synergy; synergistic effects of various kinds have been a primary cause of the observed trend toward more complex, multi-functional, multi-leveled, hierarchically-organized systems. Furthermore, the same "mechanism" is applicable both to biological complexification and to the evolution of complex human societies -- though (quite obviously) both the sources of innovation and the selective processes involved differ in some important respects.

Returning to another point raised earlier, we can now also see why it may be said that, at least in the process of evolutionary complexification, wholes have been more important units of selection than parts (see Sewall Wright 1980). It is wholes of various sorts that produce the synergies that then become the objects of positive selection (ie., differential survival and reproduction); synergistic relationships -- of various kinds and at various levels of organization -- have been important "units" of evolution. In other words, the Synergism Hypothesis is a theory about the causal role of the *relationships* among biological phenomena; it is a theory about relationships. Synergistic combinations, whether they arise through an integration of various parts (symbioses) or through

the differentiation and "progressive" specialization of an existing whole (or for that matter through various agglomerative processes with synergistic outcomes), may provide a competitive advantage. Measurable proximate functional benefits may translate into measurable ultimate selective benefits. Thus the slogan "competition via co-operation."

Biologists David Sloan Wilson and Elliott Sober (1989), in the course of their argument for a multi-leveled model of evolution, have provided an elegant example. They note that many species of beetles in the family Scolytidae have adopted the strategy of tunneling under the bark or into the heartwood of various trees to create "galleries" for laying their eggs and protecting their larva. Normally, these invaders would be thwarted by the trees' defensive measures (which include filling the cavities with resin). However, the beetles are able to overcome the trees' defenses with the assistance of a symbiont -- a pathogenic fungus that kills the wood in the vicinity of the gallery. Meanwhile, a separate community of non-pathogenic fungi and yeast bacteria are also deposited by the beetles, and these symbionts produce a thick lining for the gallery which, among other things, serves as a food supply for the beetle larva. Not only are these symbionts functionally interdependent but, significantly, the beetles have also evolved a specialized structure, called a mycangium, which enables them to carry their symbionts with them when they mature and leave their natal galleries.

In this example, there is a *de facto* partnership -- a functionally interdependent "unit" whose survival and reproductive success is a product of the joint contributions of each of the partners.

SYNERGY AND SELF-ORGANIZATION

What is the relationship, then, between synergy and self-organization? In fact, these two paradigms may not be contradictory but complementary. The process of evolutionary complexification may well have had autocatalytic aspects and certain inherently self-organizing properties that were independent of Darwinian selection processes, at least initially. But the "wholes" that resulted ultimately had to be functionally efficient as well. They had to pass the test of fitness. And, in fact, the most significant thing about organization, however it arises, is the synergy it produces. Thus, synergy is found at the heart of self-organizing phenomena; in effect, synergy may be the functional bridge that connects self-organization and natural selection in complex systems.

However, it should be stressed that synergy is not the same as *functional* synergy in terms of the problem of survival and reproduction, and self-organization is not equivalent to functional organization. Since there is no theoretical restriction on how synergy may arise in evolution, the only issue is whether or not self-organizing phenomena are exempted from, or conform to, the imperatives of functional viability;

are these self-organized synergies compatible with the functional requirements for survival and reproduction, or do they exist "despite" natural selection, as we have defined it here? I believe that, for the most part, it will prove to be the case that autocatalytic and self-organizing phenomena are also subject to the editorial screening of natural selection. Thus, to reiterate, functional synergy may be the bridge that connects self-organization and natural selection. Prigogine's "dissipative structures," Eigen and Schuster's "hypercycles" and Kauffman's "dynamical attractors" -- insofar as they exist in the phenomenal world -- can also be expected to produce synergies that are subject to differential selection in relation to their functional (adaptive) fitness.

In sum, a fully adequate theory of evolution must encompass both self-organization and selection.

SELF-DETERMINATION IN HUMAN EVOLUTION

A common source of confusion in the contemporary literature on self-organization has to do with a widespread failure to differentiate between the two radically different kinds. One form of self-organization is non-purposive in nature and should be called "self-ordering," while the other form is ends-directed; it has a systemic purpose. The former may arise through a fortuitous concatenation of factors, forces or materials (viz., the functional convergences described above or Prigogine's "dissipative structures"). In contrast, the latter implies functional design -- "adaptations" (and structures) that are either directly or indirectly products of natural selection (cf., Banerjee et al., 1990).

"Self-determination," likewise, is often conflated with self-ordering and self-organization. However, as I interpret the term, self-determination involves a phenomenon that transcends *both* the mechanism of spontaneous self-ordering and of self-organization via natural selection. Self-determination implies a degree of autonomy -- the ability to (a) establish goals, (b) make choices (decisions), and (c) exercise control over the conditions that are required to actualize those choices. Theodosius Dobzhansky, one of this century's leading evolutionists, noted that:

Purposefulness, or teleology, does not exist in nonliving nature. It is universal in the living world. It would make no sense to talk of the purpose or adaptation of stars, mountains, or the laws of physics. Adaptedness of living beings is too obvious to be overlooked.... Living beings have an internal, or natural teleology. Organisms, from the smallest bacterium to man, arise from similar organisms by ordered growth and development. Their internal teleology has accumulated in the evolutionary history of their lineage. (Dobzhansky, et al., 1977:p.95-96).

All self-organization (as defined here) has internal teleology, but self-determination implies some degrees of freedom, the potential for creativity and innovation

and the ability to exercise a measure of self-control over the process of adaptation. Self-determining systems can actualize their purposiveness in ways that can contribute significantly to the dynamics of evolutionary change (Corning 1983; Bateson 1988; Plotkin 1988).

SELF-DETERMINATION AND CYBERNETICS

Self-determining systems are also cybernetic systems. And cybernetic systems are controlled by the *relationship* between endogenous goals and the external environment. Consider this problem: When a rat is taught to obtain a food reward by pressing a lever in response to a light signal, the animal learns the instrumental lever-pressing behavior *and* learns to vary its behavior patterns in accordance with where it is in the cage when the light signal occurs, so that whatever the animal's starting position, the outcome is always the same. Now, how is the rat able to vary its behavior in precise, purposeful ways so as to produce a constant result? Some behaviorists postulated environmental cues that modify the properties of the main stimulus acting on the animal and so modify the animal's behavior. But this is implausible. It requires the modifying cues to work with quantitative precision on the animal's nervous system; these cues are hypothetical and have never been elucidated; and most important, this model cannot deal with novel situations in which the animal has had no opportunity to learn modifying cues. A far more parsimonious explanation is that the animal's behavior is purposive: The rat varies its behavior in response to immediate environmental feedback in order to achieve an endogenous goal (food), which in this case also involves a learned subgoal (pressing the lever).

The systems theorist William T. Powers (1973) has shown that the behavior of such a system can be described mathematically in terms of its tendency to oppose an environmental disturbance of an internally controlled quantity (Figure I). That is to say, the system will operate in such a way that some function of its output quantities will be nearly equal and opposite to some function of a disturbance in some or all of those environmental variables that affect the controlled quantity, with the result that the controlled quantity will remain nearly at its zero point.

((FIGURE I. GOES ABOUT HERE))

Needless to say, the model described above is greatly simplified and portrays only the most rudimentary example. More complex cybernetic systems are obviously not limited to maintaining any sort of simple and eternally fixed steady state. In a complex system, overarching goals may be maintained (or attained) by means of an array of hierarchically organized subgoals that may be pursued contemporaneously, cyclically, or seriatim. Furthermore, homeostasis shares the cybernetic stage with

"homeorhesis" (developmental control processes) and even "teleogenesis" (goal-creating processes).

Cybernetic mechanisms are not limited only to one level of organization. Over the past decade or so we have come to appreciate the fact that they exist at many levels of living systems. They can be observed in, among other things, morphogenesis (Shapiro 1991,1992; Thaler 1994), cellular activity (Hess and Mikhailov 1994) and neuronal network operation, as well as in the orchestration of animal behavior. Also, it should be noted that the cybernetic model encompasses processes that conform to Haken's paradigm of "distributed control." Some examples include bacterial colonies (Shapiro, 1988), cnidaria (Mackie, 1990), honeybees (Seeley, 1989), army ants (Franks, 1989) and, of course, humans.

It should also be noted that cybernetic control processes may produce results that resemble Boolean dynamical attractors, but they are achieved in a very different way. By the same token, the cybernetic model, properly applied, calls into question the hypothesis (e.g., Lovelock (Lovelock, 1990) that the biosphere is controlled by "automatic" non-teleological feedback relationships. Without some internal "reference signal" (teleonomy), there can be no feedback control, although there can certainly be self-ordered processes of reciprocal causation at work, or perhaps Darwinian processes of "coevolution" and "stabilizing selection." Indeed, the existence of systemic purposiveness (teleonomy) is what distinguishes organisms (and "superorganisms") from ecosystems (see Wilson and Sober, 1989). The mere fact of functional interdependence is insufficient to justify the use of an organismic/cybernetic analogy.

SELF-ORGANIZATION VS. SELF-DETERMINATION

With the emergence and increasing scope of cybernetic self-control, a subtle but important dividing line was crossed in evolution; self-organization was augmented by self-determination. Accordingly, a fundamental challenge for autocatalytic, self-ordering theories of evolution is this: Can hierarchical, cybernetic controls evolve spontaneously (ie., without reference to their functional properties and performance)? Stuart Kauffman (1993:p.202) suggests as much. He makes the surprising claim that Boolean networks are "functionally equivalent" to cybernetic regulatory systems. However, this does not seem possible because (a) the causal factors underlying the two types of processes are obviously very different and (b) the critical property of teleonomy -- constant outcomes that are achieved or maintained by variable, feedback-driven behavior -- do not appear to be present in these models. Once again, a quote from Dobzhansky may be relevant here:

The origin of organic adaptedness, or internal teleology, is a fundamental, if not the most fundamental problem of biology. There are essentially two alternative approaches to this

problem. One is explicitly or implicitly vitalistic. Organic adaptedness, internal teleology, is considered an intrinsic, immanent, constitutive property of all life. However, like all vitalism, this is a pseudo-explanation; it simply takes for granted what is to be explained. The alternative approach is to regard internal teleology as a product of evolution by natural selection. Internal teleology is not a static property of life. Its advances and recessions can be observed, sometimes induced experimentally, and analyzed scientifically like other biological phenomena. (Dobzhansky, et al., 1977:p.96).

Dobzhansky did not live to witness the recent discoveries in molecular biology that are revolutionizing our conception of evolution. It is becoming evident that even DNA acts in "purposeful", feedback-dependent ways not only to control morphogenesis but, more important, to shape the dynamics of natural selection itself (Cairns, et al., 1988; Shapiro 1991,1992; Thaler 1994). To quote Thaler: The environment not only selects among preexisting variants, it also interacts with the organism in sophisticated ways to generate the variation on which selection acts....The components exist for feedback between the generators of genetic diversity and the environment that selects among variants."

In any event, the evolutionary emergence of self-determination over the course of time has had two implications. One is that self-determining processes have gained increasing ascendancy over the "blind" processes of autocatalysis and natural selection. And the second is that, as noted earlier, the partially self-determining organisms that are the products of evolution have come to play an increasingly important causal role in evolution; they have become co-designers of the evolutionary process.

Recall our earlier discussion of the "pacemaker" role of behavior in evolution. It is now widely recognized (Ayala, 1970; Dobzhansky, et al., 1977; Mayr, 1974b; Rosenbleuth, et al, 1943) that teleonomy, or purposiveness is an important property of the behavior of living systems, with roots that can be traced far back in evolutionary history. Even primitive *E. coli* bacteria, planaria (flatworms) and various insects (*Drosophila* flies, ants, bees, etc.,) can adapt and learn novel responses to novel situations and even, in some cases, engage in "creative" problem-solving.

An unambiguous illustration involves the honey bee's aversion to alfalfa, whose flowers possess spring-loaded anthers that deliver a sharp blow to any bee that attempts to enter. Experienced bees normally avoid alfalfa altogether, but modern, large-scale agricultural practices sometimes leave the honeybee with the choice of alfalfa or starvation. In such situations, the bees have learned to avoid being clubbed by foraging only among flowers where the anthers have already been tripped or by eating a hole in the back of the flower to reach the nectar (Pankiw, 1967; Reinhardt, 1952).

In recent years it has become clear that the learning capabilities of animals go well beyond the simplistic behaviorist paradigm. They include specific learning predispositions, selective attention, stimulus filtering and selection, purposive trial-and-error learning, observational learning and even capabilities for benefit-cost estimates, risk-assessments and discriminative choice-making.

TELEONOMIC SELECTION

Thus, it may be useful to introduce the notion of *teleonomic selection* to characterize the proximate "mechanism" of value-driven, self-controlled behavioral changes. As the evolved products of evolution have gained greater power to exercise teleonomic control over their relationships to the environment (and to each other), natural selection has become a dog that is increasingly wagged by its tail. Teleonomic selection has become an important instigator of evolutionary change, and complexification.

One example of this "mechanism" is the evolution of giraffes, which are frequently cited in elementary biology textbooks as illustrations of the distinction between Lamarckian and Darwinian evolution. Evolutionists like to point out that the long necks of modern giraffes are not the product of stretching behaviors that were somehow incorporated into the genes of their short-necked ancestors (as Lamarck posited). Instead, natural selection favored longer-necked giraffes once they had adopted the "habit" of eating tree leaves. And that's the point. A change in the organism-environment relationship among ancestral giraffes, occasioned by a novel behavior -- a teleonomic selection -- precipitated a new "selection pressure" for morphological change.

A contrasting example involves one of Darwin's Galapagos Islands finches, the so-called woodpecker finch (*Carmarhynchus pallidus*). In order to excavate the bark of trees in search of insect larva, this remarkable bird has been able to circumvent the need to evolve the kind of long, probing tongue that is characteristic of the classic mainland woodpeckers by "inventing" a digging tool -- a cactus spine or small twig, which it holds lengthwise in its beak and carries from tree to tree. In other words, a "creative" behavioral adaptation has enabled *C. Pallidus* to mitigate what would otherwise have resulted in a "selection pressure" for morphological change.

Teleonomic selection is also implicated in the process of evolutionary complexification. Many of the synergistic/symbiotic phenomena that were described above most likely were the result initially of *behavioral* innovations -- ranging from the earliest bacterial colonies to eukaryotes, lichen symbioses, coral communities, land plants, ruminant animals and the division of labor in socially-organized insects and mammals. Synergy provided the proximate rewards, or payoffs, and natural selection affected the appropriate longer-term biological changes.

A similar linkage between synergy and self-determination (teleonomic selection) can be observed in the evolution of human societies. (For a detailed review, see Corning, 1983; also, Hallpike, 1986; Johnson, 1987; Scott, 1989; Durham, 1991; Howells, 1993; also see the work of economist Brian Arthur (1988, 1990) and others on the role of "positive feedback" in economic evolution and the important work on self-determination in human psychology by Deci and Ryan, e.g., 1985.)

One example, from the California Gold Rush era, illustrates not only the role of technological innovation in human evolution but also the economic and organizational (social cybernetic) concomitants. Over a five-year period, from 1848-1853, the ontogeny of gold-mining technology in effect recapitulated our entire technological phylogeny up to that time. Within the first year, the classic model of individual prospectors wading in mountain streams with tin pans was largely supplanted by three-man teams using shovels and "rocker boxes," an innovation that also increased the quantity of material that could be processed in a day from 10 or 15 buckets to more than 100 buckets, or at least twice as much per man. Shortly thereafter, the wooden sluice made its appearance. Though it required six- to eight-man teams (with an associated ownership and management structure), a sluice could handle 400 to 500 buckets of material per day, or about twice as much per man as a rocker box.

When hydraulic mining was introduced in 1853, teams of 25 or more men were required to process and haul the materials and manage the water pumps, hoses, etc., that were used to blast away the faces of entire hillsides. A relatively large amount of capital was needed and an organization was required to manage the technology and the large work force. However, the amount of material processed daily also jumped to 100 tons or more. Again, the functional consequences of synergistic phenomena can be measured and quantified.

Many other examples could be cited, but perhaps this one will suffice to illustrate some of the major features of the process of complexification in human evolution. The process has included purposive innovation, cybernetic social control, the production of synergistic (co-operative) effects, teleonomic selection and, in its train, micro-evolutionary biological changes via natural selection. Much of our early history as a species remains shrouded and subject to varying interpretations as to the particulars, but the overall pattern described above seems valid. Indeed, supporting evidence can be found among contemporary human populations living in extreme environments -- deserts, the arctic, high altitudes -- where distinct cultural and morphological adaptations have followed the teleonomic selections associated with migration into these environments.

SELF-DETERMINATION AND INFORMATION

One other aspect of self-determination in evolution should be mentioned here. It has to do with the role of "information". As Robert Rosen (1985) has pointed out, information is one of the most widely used, exhaustively analyzed and theoretically muddled concepts in all of science. In physics (and electronics) the classic Shannon-Weaver formulation -- the *quantity* of binary "bits" associated with a given communications transaction -- has provided a convenient and durable measuring rod (Shannon, 1948; Shannon and Weaver, 1949). But this also skirts the issue of how to

define information. Furthermore, in living systems the quantity of information is very often less relevant than the *quality*; cybernetic information is not created equal. Nor is there any single "unit" of information that can give quantitative precision to the concept. Information takes different forms at different levels of biological organization. Although there have been numerous efforts in recent years to develop a theoretically useful definition for the life sciences (see Rosen, 1985; Banerjee, 1990; Salthe, 1993; Weber et al., 1988 and the references therein), none has won a consensus.

The definition I favor is perhaps the most radical of all. I have proposed (1983, 1992) that information does not in fact exist; in reality it is an umbrella concept like "natural selection" that we use to characterize certain properties, or functional aspects, of a wide variety of phenomena associated with the construction (ontogeny, phylogeny) and operation of thermodynamic/cybernetic systems. The cybernetics pioneer, Norbert Weiner (1948), equated information with the degree of organization (or negative entropy) in a cybernetic system. However, I prefer to define information *functionally* as: *The capacity to exercise cybernetic control over the acquisition, disposition and utilization of matter/energy in and by living systems.*

David Layzer (1988) has provided a compelling illustration (albeit inadvertently, because it unintentionally contradicts his own thermodynamic definition of information). Layzer's example involves a modification of 19th century physicist James Clerk Maxwell's famous thought experiment. Maxwell proposed that the Second Law of Thermodynamics could be violated if a "demon" were positioned so that he (she?) could sort out a disorganized (entropic) flow of fast and slow gas molecules as they were about to enter the trap door of a divided box. Subsequently, physicist Leo Szilard appeared to demolish Maxwell's reasoning by calculating that the entropy produced by the sorting activity of the hypothetical demon would be sufficient to offset the entropy reduction that resulted, thus preserving the inviolability of the Second Law.

What Layzer has added to the argument is the idea that the entropy resulting from the demon's actions could be reduced significantly (enough to validate Maxwell's original claim) if a robot could be programmed with advance "information" (Layzer's word) that would enable it to predict the sequence of fast and slow molecules approaching the box and do the sorting automatically. Exactly so! Information can provide the functional means to "economize" -- to organize a thermodynamic process in order to reduce entropy and harness energy for useful work. (As an aside, the prevailing focus on entropy has obscured the fact that the most important aspect of thermodynamics has to do with synergy -- the work that energy can do when it is aggregated or concentrated. There may be a new science waiting to be born that could be called "thermoconomics".)

Information in the above definition describes the functional properties of many different kinds of mechanisms, but it can only be measured in terms of the results it achieves for specific living systems. An amino acid sequence that does not code for anything is not information. And neither, by this definition, is the DNA in a sperm that

does not fertilize an egg; nor the insect pheromone (or chemical "signal") that elicits no response; nor, for that matter, an unread book. Indeed, the quantity of what we call information in various contexts is much less important than its "power" -- its ability to exercise cybernetic control over matter/energy (a relationship that *is* quantifiable).

Yet, paradoxically, everything in the universe has, potentially, an informational aspect -- the latent capacity to influence in some way the organization and behavior of living systems. (Witness the vast enterprise associated with the cosmic quest of the Hubbell Telescope). But information only exists in the context of specific real-world transactions within a thermodynamic/cybernetic system, or between such a system and its environment (inclusive of other living systems, of course). Thus, it is both inaccurate and confusing to characterize various non-teleonomic, non-cybernetic physical or thermodynamic interactions as "informational" in nature. Or to suggest that evolution is focussed on the accumulation of information. Or to propose that complexity can be equated with the "quantity of information" (or vice versa).

A CONCLUSION AND A VISION

Nevertheless, "information" in the cybernetic sense is vitally linked to the future of our capacity for self-determination and self-control, both individually and collectively. Much will depend upon the evolving technologies of communications. But, equally important, much will depend upon the capacity of the sciences (and the humanities) to contribute to the development of more powerful and effective "information". The future of self-determination, then, is also tied to the acquisition (and application) of useful knowledge.

It may well be the case that the primordial origins of complexity in evolution were rooted in self-ordering processes; living systems may indeed have been energized and catalyzed by spontaneous biophysical and biochemical activity. However, the trajectory of evolution has moved the causal dynamics inexorably away from autocatalytic phenomena toward purposive and functional phenomena. Accordingly, the future lies with self-determination -- that is, information-based, purposive innovations. And it can safely be predicted that new forms of synergy will play a central role in shaping our future evolution as a species, for good or ill.

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