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The transition to civilization and symbolically stored genomes

Jon Beach

California State University, Fullerton, CA, USA

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Abstract

The study of culture and cultural selection from a biological perspective has been hampered by the lack of any firm theoretical basis for how the information for cultural traits is stored and transmitted. In addition, the study of any living system with a decentralized or multi-level information structure has been somewhat restricted due to the focus in genetics on the gene and the particular hereditary structure of multicellular organisms. Here a different perspective is used, one which regards living systems as self-constructing energy users that utilize their genome as a library of information, making the genetic system just another component that adds fitness to the overall integrated unit. In this framework, basic fitness is measured as the ability to gather energy for growth and reproduction, and the fitness of the genetic system is broken down into two aspects: first, the effectiveness in searching for new somatic functional information, and second, the effectiveness in searching for better structures to store and process information. With this more generalized perspective, major evolutionary transitions to higher levels of organization become competitions between different information structures; furthermore the functioning and fitness of cultural systems can be more easily described and compared with other modes of information storage within biological systems. Modern technological societies are self-constructing systems that rely on written (symbolic) information storage and very complex algorithms that effectively search for variation with a high probability of successful selection. These systems are currently competing with traditional organic systems, and this competition constitutes the latest major evolutionary transition. Upon comparison of the energy-gathering potential of symbolic-based systems with DNA-based life, it appears that symbolic systems have a tremendous fitness potential and the current shift to a higher level of selection may be as significant and far-reaching as any of the previous major evolutionary transitions.

E-mail address: jonbeach@lycos.com (J. Beach).

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1. Introduction

The rise of civilization marks a major evolutionary transition in the way living systems are organized. J. Maynard Smith and E. Szathmary (1995) characterize a major transition as a change in the way information is transmitted that creates a new higher level of selection. It is certainly the case that language, writing, the printing press and modern information technology have fundamentally changed the way information is transmitted. The goal of this discussion is to compare the current changes in the structure of information systems with past major evolutionary transitions and to show that there are indeed many similarities between modern events and past transitions, and that, in fact, the evolution of life on earth is presently undergoing a fundamental shift to a new higher level of selection due to changes in the way information is stored and transmitted.

Researchers have produced a large body of work that investigates specific pathways of ecological and environmental conditions through which major transitions can be made. Some have studied group selection (Hamilton, 1964; Maynard Smith, 1964; Grafen, 1984; Wade, 1985; Goodnight & Stevens, 1997; Sober & Wilson, 1998), symbiosis (Bremermann & Pickering, 1983; Frank, 1994, 1995a, 1997a; Turner, Cooper, & Lenski, 1998; Chao, Hanley, Burch, Dalberg, & Turner, 2000), and reciprocity (Trivers, 1971; Axelrod & Hamilton, 1981; Alexander, 1987; Taylor & Mcguire, 1988; Kitcher, 1993; Dugatkin, 1997). Others have looked at cultural transmission of information (Cavalli-Sforza & Feldman, 1981; Lumsden & Wilson, 1981; Boyd & Richerson, 1985; Axelrod, 1988; Durham, 1991; Findlay, 1992; Sperber, 1996) or culturally transmitted policing mechanisms (Boyd & Richerson, 1992; Boehm, 1992; Clutton-Brock & Parker, 1995; Gachter & Fehr, 1997; Bingham, 1999) as pathways to group cooperative function. But evolution is both the study of the history of specific lineages or events and the identification of broader trends and principles that affect the overall process. Models of selection for specific traits, however constructed, can still only be used to study specific pathways one event at a time. Recent studies still leave the question unanswered of what the underlying process is that has repeatedly driven evolution through major transitions to higher levels of organization and what it is that is different about certain genetic changes that lead to these major shifts. This paper focuses on identifying the underlying principles that apply to all major transitions and that make these evolutionary jumps more significant and far-reaching than other evolutionary events. The method for accomplishing this is to study quantitative and qualitative properties of the information structure itself, rather than the process of selection that it mediates.

The structure of a genetic system determines its overall potential to accumulate information and instruct a living system. The method of coding determines how much information can be stored, at what cost, and how fast it can be replicated or transcribed. How the coding is linked, packaged and transmitted determines how selection will operate on different groups of genes, what groups will cooperate as a single entity and what other groups will remain as ecologically linked symbionts (Buss, 1987; Sober & Wilson, 1998; Michod, 1999). Finally, how the coding is translated determines what types of functions the coding can access and incorporate into the system it instructs. DNA is translated into RNA and then proteins, and therefore its functional range is limited to the variability of these molecules.

In all these ways the genetic structure creates an information space (Dennett, 1995) within which selection can operate, but it also defines the limits to this space and therefore limits the types of systems and the variability that can evolve. In a sense, a specific genetic structure translated in a specific way to function creates its own universe of possible information and a major transition occurs when there are fundamental changes in this structure that open up significant new organizational possibilities. A major transition is propelled not so much by selection for a specific evolutionary pathway (for there are likely to be many potential pathways to the same major transition) but by the size of the new universe of organizational potential that is accessed and by the overall array of beneficial variation made possible due to a shift in genetic structure. This can be measured by the overall additional free energy available to life due to additional information storage capability and the associated potential energy-gathering functionality. The hypothesis is that each hierarchical level of organization is limited in scope by the information structure that instructs it. The transition to the next level is accomplished because identifiable fundamental improvements are made to the information system that allow the coding for more complex systems to be acquired and translated into function. To better understand major transitions we need to study the relationship between different genetic structures and the range of functionality or energy-gathering abilities they can access. Instead of focusing on the details of specific evolutionary pathways, this discussion tries to identify the relationships between organizational levels, the information structures that regulate them and the dynamics of free energy flows that push evolution through transitions to these different levels. Additional understanding of major transitions can be gained by investigating and comparing these improvements in information capabilities. In particular, this approach will help shed some light on the nature and scope of the current transition to a technological society.

The next section outlines a representation of living systems based on energy flows that also highlights the role of information storage and acquisition. A flow chart model illustrates how a feedback of free energy gain through improved information structure can drive evolution irreversibly through a major transition into a new universe of functional possibilities. Then, using this model, the following sections compare the previous major transitions from RNA replicators to linked DNA genomes, to eukaryotic genomes, and then to cloned multicellular systems. Finally, the last sections evaluate the current transition to symbolic (written) information storage and attempt to make a quantitative comparison with past transitions.

2. The model

The usual formulations of fitness used in population genetics cannot be used for a generalized model of transitions because they always in some way presuppose populations of individuals reproducing through discreet offspring according to fixed rules, which, in itself, constitutes a specific genetic structure. This leads to a logical paradox when studying transitions, because if transitions are primarily the result of changes in genetic structure then the assumptions of the model are themselves being modeled. Another problem that arises when fitness is measured as the number of offspring is that genetic systems operate not just to produce offspring, but also to reshuffle information in a way that is likely to produce a better genotype (Mitchell, 1996). This reshuffling activity requires energy, however, and a choice must be made whether to use all available energy to produce offspring or to reserve some for information search. If fitness is solely the production of offspring, then investing some energy into search algorithms such as sexual reproduction can never be fit. But to survive over the long run, most living systems must compete in the search for new information as well as the production of offspring.

Here, in order to separate a generalized measure of fitness from any sort of particular genetic structure—and therefore to allow for varying fitness of the genetic structure itself—fitness is modeled as changes in free energy utilization rather than as gene frequency or number of offspring. Basic growth or production of offspring (and fitness) of a reproducing lineage as a whole or as an evolving, symbolically informed economic organization is modeled as free energy flowing into self-construction and maintenance. On a higher level, however, reproductive cycles and individual fitness are part of the information-generating process that, if successful, produces additional growth in the long term. This acquisition of new information through the process of either innovation or mutation and selection is modeled as a second separate free energy feedback loop of energy used for information-gathering activities. Finally, the selection of the information-gathering structure itself is modeled as a third loop of energy used to test the modifier genes that can change the genetic structure. This model allows the idea of fitness to apply equally to any informed self-constructing system, and then gains explanatory power by decomposing this fitness into the following three categories: 1) energy gains through reproductive fluctuations due to changes in environmental factors; 2) energy gains from the search for new information; 3) energy gains from the discovery of better ways to search for and store information.

The structure of living systems is generalized by using a simple abstract representation of function based on three basic components labeled the engine, constructor, and the tape (von Neumann, 1966). The engine gathers energy from the environment for use by itself and the other components. The constructor produces growth by constructing itself and all other components, and the tape stores all the information needed to regulate and instruct these activities. Fig. 1 illustrates these components and the flow of energy among them.

The large arrow represents all free energy entering the system through the activities of the engine. The solid arrows indicate the flow of this free energy from the

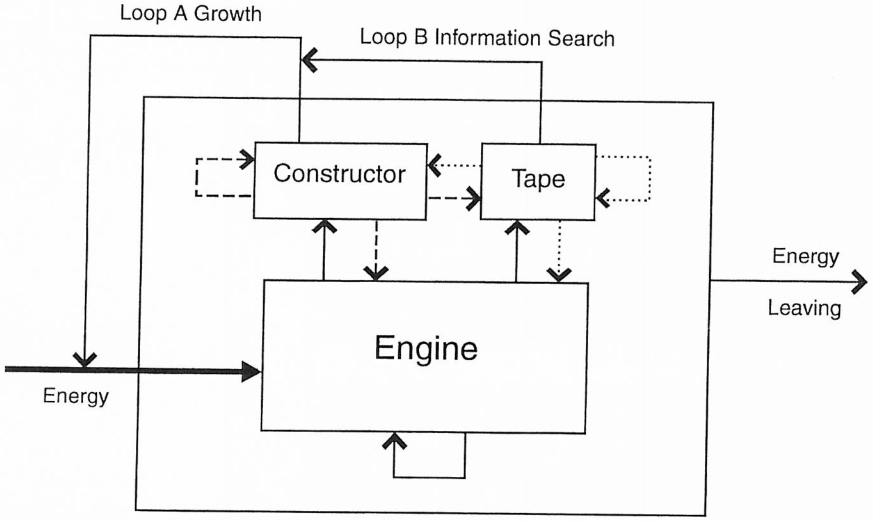

Fig. 1. A basic flow chart representation of a self-constructing system. In some subsequent figures the dashed and dotted flows are not shown, in order to simplify overall flows of energy through the system.

engine to the other components of the system. The dashed arrows show the flow of energy from the constructor used for maintenance and the construction of additional components creating growth. Finally, the dotted arrows represent the free energy used by the tape to supply the information needed to instruct and regulate these activities.

The two feedback loops represent increases in free energy throughput due to growth and information search. These two feedback loops result from cumulative effects of overall energy flows generated by the combined processes of the system. Loop A represents the differential of free energy throughput achieved by the system as it builds more units and as these come on line and gather more energy for themselves, creating a growth feedback. Loop B represents throughput gains achieved by directing energy into the search for better operative information. This is energy consumed by structure or behaviour associated with information search algorithms (including mutation and selection) that produce adaptive changes in somatic structure. This is a more long-term feedback process leading to the expansion and diversification of the lineage over evolutionary time as new or more efficient ways to gather and utilize energy are discovered. The information search arrow points to the growth loop because better information ultimately leads to expansion through enhanced growth and reproduction. The assumption is that the search for information requires energy, and there is a trade-off between using this energy to search for better information that may result in increased future growth or immediately reproducing more with existing information.

The growth loop represents the ability of the existing genotype to compete in the current environment (its fitness) and the information search loop represents the fitness of the genetic system itself—or its ability to compete in the race to adapt to new conditions or acquire new information (Holland, 1975; Frank, 1997b).

These two feedback loops pictured in Fig. 1 illustrate a basic choice confronting every organization, namely how much to invest in research and development. A simple analysis of the system (Beach, 1998) shows that the greatest growth in energy utilization would result from directing all energy exclusively into either information search or growth depending on which path produces the greatest average long-term payback under current conditions. However, since the growth feedback loop involves a much shorter time frame, the growth loop might appear to always produce the highest immediate payback. Even in unfavourable growth conditions, more might be immediately gained by direct investment in reproduction rather than a search for a better technology that could only pay off in the future. This dilemma is the familiar one of when it is prudent to stop working and forego immediate gain in order to find better ways to work.

The stochastic nature of both information search and reproduction, and the emphasis on loop A fitness (immediate reproductive consequences) in genetics, can obscure the overall optimal flow of energy into information search. Research may only occasionally produce a benefit that is then carried on indefinitely into the future producing a cumulative effect. Reproductive effort may immediately produce more offspring, but if the environment is near its carrying capacity this may have little effect on the future. Therefore, optimal flow of energy into research depends on the average benefit of both failed and successful experiments and also on the present value of the cumulative total of information gains into the indefinite future.

On the other hand, frequency-dependent aspects of fitness (Michod, 1999) can make rapid expansion the determining factor in permanently establishing one species and excluding another in a particular location. Continual survival of a lineage in some form defines the winner in the evolutionary game, but is it sheer numbers from successful reproduction or is it variability derived from information search that primarily determines survivability? In fact both factors enhance the other, since larger populations support much greater variability and variability allows a species to succeed in a greater range of environments. This might indicate that the best strategy is indeed to direct energy into either reproduction or information search depending on which is currently providing the greatest average return. Investment in greater numbers may always pay the greatest return when an opportunity to expand presents itself. But once the limits of growth with existing information is reached, investment in new information is the best long-term option for continued growth. However the rigidity and long-term nature of information search may make the redirection of energy between information search and reproduction based on short-term conditions impractical in many cases. But still the genetic structure, mutation rate and variability could be sensitive to the long-term payback of information search and may be selected for at this level (Frank, 1997b).

The debate over the fitness of sex also hinges on these issues. Biologists have variously argued that sex is primarily useful for speeding up evolution, eliminating deleterious mutations, or competing in an arms race with parasites (Kondrashov, 1988; Ridley, 1993), but all these explanations basically involve just the more efficient generation of useful information. Whatever the reason for the fitness of sex may be in a particular case, it is fundamentally due to better information search algorithms, and involves an expenditure of energy in a trade-off with immediate reproduction. The relative fitness of sexual versus asexual reproduction for a species depends on the ecological or environmental factors that determine whether rapid growth or efficient information search is more important for survival. In cases where these factors vary greatly, one might expect to find organisms that can switch from one mode to the other.

So, Fig. 1 illustrates two levels of fitness. The first level is reproduction, and then a second level operates in a longer time frame and creates growth by searching for better technology to carry out first-order activities. In Fig. 2, a third-order feedback is added that represents the free energy throughput differential attributed to energy used in searches for better technology to carry out second-order activities. The search for better information search and storage structure has an even longer time frame (although there must also be immediate payoffs) than the more basic search for better somatic structure, because this has the most far-reaching and enduring pay-

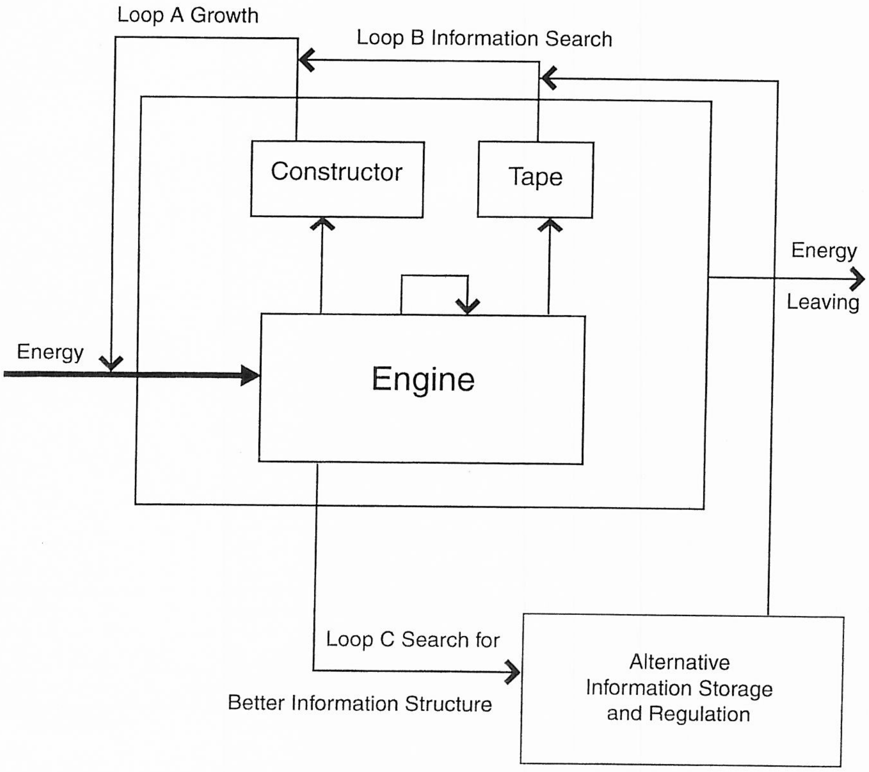

Fig. 2. A system with a third feedback loop (loop C) of energy flow due to fitness gains in the information system itself. This loop could flow through the individual tape component, creating greater complexity in the single individual through internal information system improvements. However transitions are often derived from symbiotic groups, and this requires the development of a new external information centre for the group and external cooperative flows of loop C energy.

off potential. This third-order loop includes the search for better coding, storing and translating structures, and better search algorithms that make the discovery and retention of more sophisticated information possible. Although they occur only rarely, these changes can lead to the expansion of life into entirely new kingdoms due to the creation of a new form of information.

In this simple model the same principles that apply to the first- and second-order loops apply to the third-order feedback (Beach, 1998). The greatest average long-term growth is achieved by directing all energy to the loop that has the greatest average long-term energy feedback under current conditions. When growth opportunities exist, these will have the greatest return, but information search for better ways to grow will pay the best when growth limits are reached. When the limits of useful diversity within an existing information structure are approached, then the most will be gained in the long run by searching for a better information system that can search for and retain otherwise unattainable complex adaptations. Each of these loops feeds into the next lower-level loop, and in actuality they must all operate simultaneously because selection functions only in the present. A new loop C higher capacity information storage structure gains a foothold because of the beneficial loop B somatic improvements it is able to code for, and in turn these improvements survive because of the increased loop A growth and reproduction they stimulate. In the end evolution boils down to loop A reproductive fitness, but this decomposition of the components of both short- and long-term fitness illustrates some of the complexities involved.

Fig. 3 illustrates a process whereby a higher capacity information structure captures a group of symbiotic entities and integrates them into a new higher-level single entity. Theoretically, once a higher capacity information structure is developed, a single organism could expand into a more complex, higher-level being. However, only the transition to multicellularity has followed this path, and in most cases a higher level of organization has arisen from a combination of ecologically linked independent entities with one specializing in the information-storage function. It appears that this pathway may be a shortcut to complexity that takes advantage of the specialization and diversity of function that already exists in a community to create a complex individual out of already partially developed components. In this scenario, the gains in fitness from added complexity cause selection to create a loop C feedback out of free energy flowing from symbiotic individuals to the specialized information-storage individual that tests and develops a more advanced information structure that can store complex information more efficiently. At the same time, selection-driven community-level loop B flows of free energy develop the information needed to regulate the individuals of the community and convert them into specialized components that can take advantage of the energy available through group cooperation (Frank, 1995b). These ongoing gains in fitness from the advantages of added complexity and higher-level cooperation continue to shift energy for information search to the group level until, eventually, enough group-level information is accumulated to operate as a fully integrated higher-level individual.

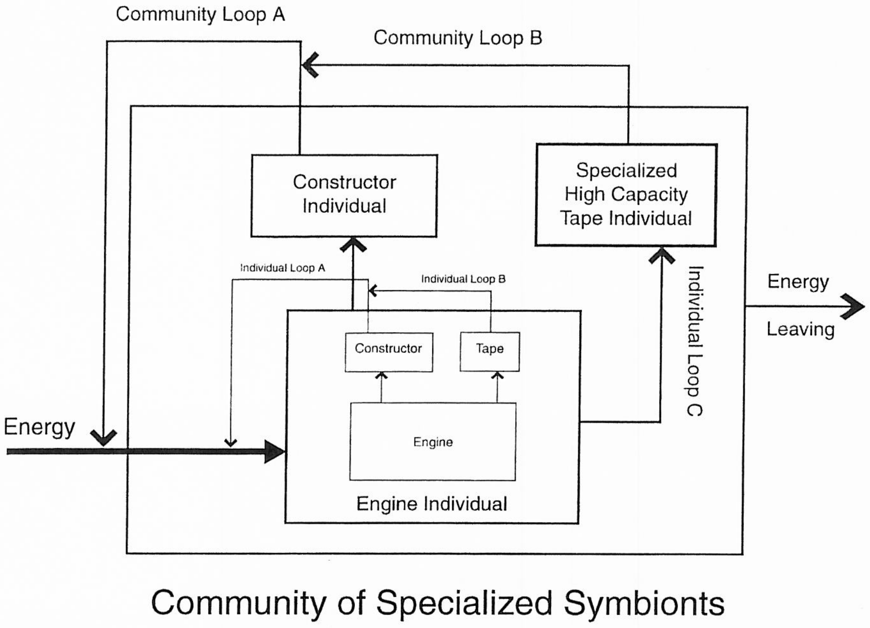

Fig. 3. Selected energy flows among a group of specialized symbionts. Flows from the group constructor or tape to other components are not shown, and also, for simplicity, most flows within the group components are not depicted. The group engine, constructor and tape are made up of one or many individuals. Cooperative effort by these individuals results in loop C energy flows that contribute to the evolutionary improvement of the group information centre (tape) and feed into group level loop B and A energy flows.

3. Some philosophical considerations

This model is fundamentally different from other models of evolution that focus on gene frequencies. Population genetics sees living systems as the expression of a group of genes, and studies evolution from a bottom-up, reductionistic perspective that makes the survival of these genes the primary focus (Dawkins, 1976). The model proposed here sees life from a more holistic perspective as entire systems that gather energy to construct more of themselves. Genes are regarded as a library of stored information for the system, instead of the system being merely a survival vehicle for the genes. This makes the search for better genetic information just another function of the system as a whole and allows this function to be related to flows of energy and overall survival and diversification (fitness). It is this perspective that allows us to make the conceptual distinction between a separate growth and reproductive function, an information search and storage function, and a search for better information searching and storing procedures function. It is the relationships between these three different avenues for investment of energy and the long-term returns on investment that shape the long term trends in evolution. Selection is always the proximate force that guides evolution and reproductive fitness always determines what is selected. *But certain information represented by loop C traits can have a much more profound effect on long term success by controlling access to large classes of lower-level somatic information.* So, in a larger sense, it is the flow of free energy among these three categories of system-wide function that creates the fitness differences of specific structure. Reproductive fitness locally directs selection, but these more global considerations have an impact on what is fit in the most general sense.

With fitness based on gene frequency, the emphasis is necessarily on gene-level selection (Wimsatt, 1980), or, in the case of symbolically stored information, at the level of individually competing memes (Aunger, 2001). This approach is natural for multicellular sexual systems which are based on rigid protocols for reshuffling information at the gene level, but, as is argued later in this discussion, this group represents a special case for living systems. For the more normal condition of reproduction by fission and more haphazard (or sophisticated) information exchange through a variety of different methods, it is convenient to identify and delineate a system through common descent and then measure fitness by changes in the ability to gather and utilize energy which directly measures an entire system's ability to compete (Brandon, 1999). Using the energy utilization of a system as a whole to measure fitness allows us to delineate any group of integrated components on any level that is related by descent as the system under study and then to compare its fitness in a holistic sense with other levels and entities based on different scenarios of energy-gathering potential (Lewontin, 1970; Hull, 1980; Sober & Lewontin, 1982; Lloyd, 2000).

Another idea brought forward by the holistic perspective of this model is that DNA or symbolic coding operates as a way to compactly store unused function. This information storage function is a fundamental aspect of living systems that is obscured by the focus on genes as an inheritance system. J. Maynard Smith (2000) has commented on the prospect of living systems existing without stored information as if this were possible. But this is unlikely because the essence of a living system is its ability to call up out of storage the information needed to react to a variety of environmental conditions. Even the simplest bacterium could not possibly have all its metabolic pathways operating at once; it must have some sort of life cycle or resting stage in which some functional structure exists only as inertly coded information. Trees must have a seed stage, butterflies cannot be butterfly and caterpillar at the same time, and the cells of multicellular organizations cannot function as nerves, muscles and blood cells all at once even though they have the information to be all of these. The energy efficiency of storing life's array of function as coded information rather than as actual structure is so pervasive that it is a necessary and defining attribute of all living systems. If information was copied from proteins directly, this would necessitate separate specialized proteins for storing and copying information as opposed to functioning proteins resulting in the same division of labour that exists between nucleic acids and proteins.

Genetic systems transmit information to future generations and mediate the process of evolution, but they are equally fundamental to life as libraries for an array of economically stored function that can be accessed as needed on a day-to-day basis.

This idea is central to the hypothesis that changes in information structure are the primary cause of major transitions because it is the enhanced *information storage* capability that creates a new universe of functional possibilities that these transitions feed on. Selection acts on the inheritance function of genetic systems to determine the specific pathway of a transition, but it is the potential capacity of the information system as a library of stored function accessible on a day-to-day basis that determines where the path will lead.

Because it is based on a generalized, fundamental definition of life, this model has the advantage that it can be used equally well to describe cultural, economic or biological organizations (Wimsatt, 1999). In fact, it is difficult to discuss living systems from this perspective without using terminology from both economics and biology. Some economists (Schumpeter, 1934; Nelson & Winter, 1982; Arthur, 1988; Aldrich, 1999) have looked at growth and economic change as an evolutionary process. Nelson and Winter have identified three levels of growth (productive growth, information search, and the search for better information search) that are identical to the ideas used here (Nelson & Winter, 1982, pp. 17–18), and they have used selection of informational traits of individual businesses as a basis for overall change. But they have not recognized written information as the equivalent of DNA coding and the consequent fundamental changes in information structure that have occurred. If symbolically coded (written) information is recognized as the genetic material of a new class of economic self-constructing organizations that operate with integrated biological and technological structure (which is a hypothesis of this paper), then economics and biology can be merged into different branches of one discipline based on the same underlying principles. But, due to differences in genetic structures of economic organizations, it is difficult to measure gene frequencies. In most organic systems, replication of information follows strict procedures that are closely connected to reproduction. But economic organizations grow continuously without formal reproduction, and information search and exchange is carried out in complex processes that traditional genetic models are not able to cope with. For this reason energy consumption is the most convenient measure of fitness for classes of economic organizations related by descent, and it may be just as fundamental for all living systems in a philosophical sense. Survival involves the continuing existence of the entire system and this requires access to adequate energy supplies. Coded information is the key to instructing these energy-gathering activities, but long-term survival requires that this information is continually updated or expanded and not just rigidly replicated. Fitness is the effective discovery, storage and use of information, not just the act of copying it.

Traditional evolutionary theory was largely developed through the study of eukaryotic and multicellular organisms and their Mendelian genetics. The framework of this study follows from a different perspective; it develops concepts from a fundamental definition of life based on a von Neumann automaton wedded to a thermodynamic component. The concepts of information, heredity, variation, selection, and teleology arise out of the operations and relationships created by this type of system and are necessary results of continued operations. Other concepts such as the genotype/phenotype distinction, gene frequencies, or even the idea of the gene itself, or of discreet offspring, derive at least some of their significance from the particular reproductive processes or coding and translating mechanisms used by multicellular organisms, and are not necessarily so directly connected to a prototypical life form. When viewed from first principles, free energy flows are the raison d'être of the system, and the tape and its information have no special standing or importance compared to the other components. All parts only have meaning and life when functioning together. For this reason it seems justifiable to use free energy throughput as a measure of fitness and to compare the fitness of information systems on this basis. The following sections expand on this line of thought by applying it to past and current transitions.

4. The first transition

One of the most plausible theories for the origin of life is that evolution began with the selection of short RNA replicators that also possesed enzymatic activity (Eigen & Schuster, 1977; Maynard Smith & Szathmary, 1995; Szathmary, 1999). Then the first major transition would have been from individual RNA replicators to organizations of 'ribozymes' regulated by group information stored in higher-capacity DNA coding. The following is a mostly speculative scenario of how this transition could have occurred, one which illustrates our energy feedback model and the central role of changes in genetic structure in initiating this energy feedback.

Studies have shown that RNA can have enzymatic activity and replicate in an appropriate environment (Szathmary & Demeter, 1987; Maynard Smith & Szathmary, 1993, 1995). But to have any significant biochemical effect, these single enzyme replicators must have formed a network of ecological relationships. However, since in this situation selection favors individually selfish molecules, these networks would fall victim to parasitism by any RNA replicator that used the shared resources without contributing anything in return (Bresch, Niesert, & Harnasch, 1980). Entire communities of molecular replicators with primary energy gatherers, grazers, predators, parasites and extensive food chains could have developed, but even with unlimited time for evolution to reach an optimal level of adaptation, a biosphere of single enzyme replicators cannot acquire enough information to evolve beyond a very low level of activity (Maynard Smith & Szathmary, 1995). In other words, the universe of information for RNA replicators connected to only RNA function is very limited. The growth and first order information search loop (loop A and B) can only select among all possible single enzyme replicators and very quickly reaches the limits of energy-gathering and technological discovery for this level of organization. This leaves the search for a better information system (creating a loop C feedback) as the best avenue for expansion, and therefore energy going into mutations exploring innovations of information structure has the highest average return on investment or fitness. If a higher-level universe of information exists (a more sophisticated coding system connected to more potential for technological variability) and there is a viable pathway to this universe, then selection will follow a pathway to higher-level organization and a major transition will occur at this point in evolutionary development.

The first step in this transition is a change in the information structure that creates a spatial association of replicators such as an attachment to mineral substrates or containment within lipid protocells (Michod, 1983; Breden & Wade, 1989; Sober & Wilson, 1998). These changes could have been genetically mediated by RNA replicators that promoted the construction of lipids, or by mutations that gave RNA replicators an affinity for naturally occurring lipid membranes or other surfaces (Maynard Smith & Szathmary, 1995). This change in the spatial association of information allows group selection to act to contain parasites and expand cooperative systems, but as long as there is an significant element of competition within the group, cooperation cannot evolve further into the near total cooperation between components of a higher-level individual (Sober & Wilson, 1998).

For further gains to occur, there must be a higher degree of regulation and policing among members of the group (Ratnieks, 1988) and this requires changes in the information structure that create the capacity for more sophisticated information storage at the group level to instruct this regulating and policing function. *Selection of this linked group-level genome as a unit is the pivotal event that creates a new higher-level individual* (Lewontin, 1970; Hull, 1980; Sober, 1981). The fitness gains that drive this shift in selection mode are from a new universe of energy-gathering technical information that can be discovered at this higher level. The enhanced feedback of *group-level* loop A and B due to this new universe of potential discovery created by individual-level loop C innovation irreversibly establishes this higher level of organization by creating a selective force that continually expands the lineage of group-level information to create an array of new species. To take advantage of the opportunity at a higher level, the lower-level individuals become more specialized (Anderson & McShea, 2001) and individual reproduction of these specialized individuals becomes regulated in order to produce the right kind of components at the right time. Individual reproduction is converted to regulated production of parts, selection shifts almost entirely to the group genome, and the group changes into an integrated whole evolving at a higher level. The key idea is that loop C flows of energy into the search for a new linked site for group-level information storage, driven by fitness gains from the previously inaccessible information available at this level, are what irreversably shifts selection to the higher level and creates a new, more complex individual.

Fig. 4 illustrates the feedback of free energy during this process of transition. Selection creates a loop C energy flow into the search for any individual replicator that has some attribute that makes it a good site for group information. In a group of replicators this may have been a more stable individual DNA replicator. Due to its advantage in information storage capability, selection gradually shifts this function entirely to DNA. In a concurrent process, this DNA group information centre is connected to an expanded universe of functional variability, because once DNA assumed the information storage role for the group, RNA was available to become the translational connection to protein function and to assume other specialized tasks. A pathway to this might be imagined in the following way (Szathmary, 1993; Maynard Smith & Szathmary, 1995): transfer RNA were originally functionally independent ribozymes with attached amino acid co-factors. Ribosomal RNA developed

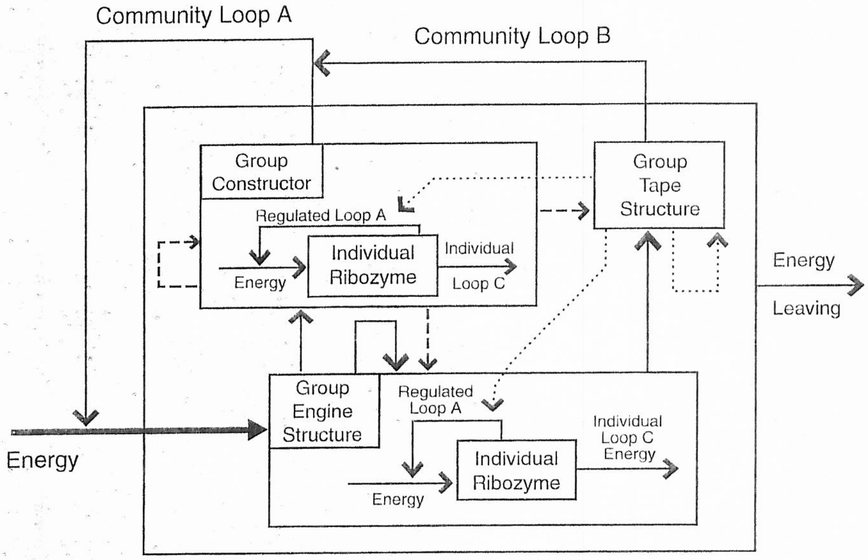

Fig. 4. A group of individuals (ribozymes in this case) cooperating in a way that creates a higher level individual. The dashed and dotted flows of energy between components are added back in to show how overall group flows of energy create a new individual similar to Fig. 1. Individual loop A reproduction becomes regulated and policed by group information. Individual loop B nearly disappears because strong group loop A and B flows shift selection to the group genome. Individual loop C flows are part of an intricate web of altruistic behavior that supplies energy for integrated group function, including variation and selection of the group information centre.

to combine separate transfer RNA and their cofactors into enzyme complexes, but as the complexes became larger and the protein component became the centre of function, these protein cofactors split off to function independently, converting RNA into a translator. This is purely speculative, but the point is that the coordination of this highly cooperative translation process and the conversion of RNA from information storage to translation that opened up life to the tremendous potential variability of proteins could never have occurred without the initial conversion of the information storage system into a higher capacity, linked, group-level DNA structure with the capacity to contain the coded information needed for this degree of cooperation and regulation.

This outline of the origin of life using an energy feedback model illustrates the fundamentally different, more holistic view of living systems with fitness decomposed into three levels. Evolution is regarded as the search through a finite information space (Dennett, 1995) driven by the feedback of free energy capture that is the result of technological discovery within the information space. This loop B search is eventually exhausted, and then the highest feedback gain is through a loop C search for a better information system that can open up a new group-level loop B search through an untapped new information space. Selection and individual fitness make up the search process and are the proximate causes of evolutionary change, but the overall trends are caused by feedback flows of free energy that are the result of the investment returns from information search and the discovery of better information systems that have a greater capacity to store information for more complex technology and organization.

5. The transitions to eukaryotic and multicellular systems

The second and third transitions to eukaryotic cells and to multicellular systems can be thought of as one continuous transition made possible by the increased capacity of the eukaryotic information structure. The eukaryotic structure features multiple linear chromosomes and polyploidy for increased storage capacity (Maynard Smith & Szathmary, 1995), the process of mitosis to efficiently replicate this larger body of information, a nuclear structure to manage information-processing, and a fair meiosis leading to sexual reproduction for an efficient search through this larger information space. This more sophisticated information structure is what allowed the original eukaryotic host cell to accumulate and store sufficient information to act as the group information centre for its bacterial partners converting these symbionts into regulated, non-competitive mitochondria and plastids. Just as the greater information capacity of DNA enabled the information storage function to migrate out of RNA to group DNA storage in protocells, so the higher capacity nuclear system allowed information to migrate out of the bacterial symbionts and to accumulate as a group-level genome in eukaryotic cells (Margulis, 1970, 1993; Margulis, Dolan & Chapman, 2000). The efficiency and capacity of the nuclear system opened up the increased energy-gathering potential of group-level systems which created selective pressure to centralize the reproductive and functional control of members of the group in the nucleus, creating a higher-level individual (Frank, 1995b, 1996). This new, more complex individual then became available for further development as a multicellular system.

The emergence of multicellular individuality is a fascinating contrast to the first and second transitions which both combined symbionts under a higher capacity group-level genetic structure. This third transition was built on the expansion of the internal (eukaryotic) information centre combined with various strategies for elaboration of the individual cell structure. Therefore, in this case, the loop C arrow in Fig. 2 should point to the internal tape rather than to alternative external information storage. Since greater complexity was developed from within rather than from a group of ready-made cooperating symbionts, the engineering problem was then how to construct multiple specialized components and expand functionality and information-processing capacity from the structure of a lone eukaryotic individual.

One answer could have been to greatly expand and diversify the eukaryotic cytoplasmic elements and bacterial symbionts. Under this plan, symbionts or other organelles become the “cells” of multicellular groups, the eukaryotic cell membrane becomes the outer covering and the nucleus becomes the central information site. Advanced protozoans, fungi and especially the slime moulds have used this plan (Luyet, 1940; Martin, 1957), becoming mobile, sometimes macroscopic, “multicellular”, systems with an outer covering derived from a cell membrane. One drawback of this strategy may have been the limitations of a single nucleus as a group information centre and its slow chemical communication links with the cytoplasm. Ciliates have a special polyploid macronucleus to expand information processing, but in most groups it seems that multiple nucleii and decentralized control have been substituted for a central expanded nucleus. However, multiple nucleii in acellular systems create the same potential for intragenomic conflict and somatic parasitism as in multicellular groups. For this reason information exchange follows rigid protocols that limit the access of exchanged information to somatic structure and life cycles include a stage that requires that new systems arise from a single genome selected at the group level. As in multicellular systems, sex is followed at some point by a single nucleus stage that ensures high relatedness between all nucleii of a newly developing individual.

Another option for constructing components and expanding function seems to have been cloning and then diversifying the single cell, creating true multicellularity. This option provides a far more complex basic fabric for the development of higher-level structure. However, the presence of many complete, potentially competitive cells makes the integration of the higher-level individual problematic (Michod, 1999). This problem is solved by the existence of a single cell stage somewhere in the life cycle, making this feature the key to multicellular individuality. This single cell stage serves the same purpose as linked DNA storage and translation of all ribozyme function in primitive cells, namely, to create a single site for the storage and selection of the master genome of the new higher-level individual. Just as central DNA storage in primitive cells ensured that ribozyme replication originated from a single noncompetitive template, so the single cell stage of multicellular systems ensures that all multicellular components are selected as a unit and all component information is derived from this group-level master genome. The group information is disseminated from this single source to specialized cells using a combination of mitosis and the epigenetic, cytoplasmic switching systems which turn on the relevant bits of the master code for each specialized cell as it develops, mimicking the transcription and translation of DNA information into functional proteins. At the multicellular level, specialized cells are the basic functioning component analogous to single cell proteins, but they have their own component-level information centre and it is this cytoplasmic switching system that effectively translates relevant bits of the group-level master code into these operating somatic structures.

It has been suggested that the germ line/soma distinction was an important innovation that had the effect of preventing competition between cloned cells (Buss, 1987; Michod, 1999). However plants have no such division, and for them a structure of cloned cells with a zygote stage seems to be adequate protection against intercellular conflict (Maynard Smith & Szathmary, 1995, p. 244; Maynard Smith, 2000). The germ line is a necessary outgrowth of the single cell stage for some groups simply because undifferentiated cells must be stored somewhere in a convenient way for use in the future. Plants grow continuously throughout their life cycle; therefore they have continuously operating stem cells and no need for the storage of dormant germ line cells. In contrast, most metazoans have a distinct, highly structured construction phase followed by an operating stage in which totipotent dividing cells are generally not needed except for occasional reproductive activities; this creates the need for specialized storage of a germ line connected to the reproductive organs.

The differences in the occurrence of asexuality in multicellular groups can also be explained by the differences in their construction strategies.The modular, iterated design of plants (and colonial invertebrates) lends itself to continuous meristematic construction that makes asexual reproduction through propagules just a simple extension of individual growth. Because plants are non-mobile, sexual exchange of information is difficult, and therefore one might expect to see the elaboration of growth through asexuality between episodes of sexual reproduction (Cohen & Zohari, 1986). On the other hand gaining the advantage of information exchange through sex is easy for mobile metazoans, but maintaining viability during an extended non-functional construction stage is a more difficult problem. So, for metazoans with a unitary, integrated design, when the difficult process of reproduction is attempted one would always expect the easily gained information-generating advantages of sex to be included.

But, irrespective of these details of storage and utilization of inherited information, stem cells, the germ line and a single cell stage are the group information centre for the multicellular unit because they contain the inertly stored single copy of all group information that is selected and passed on to the future as a unit. As these totipotent cells became the group information centre and as they accumulated the information necessary to regulate the translation of their information to somatic components, the emergence of multicellular individuality followed the same pattern of free energy feedback among symbionts that produced integrated DNA-instructed cells. The loop C traits that enabled the storage and translation of the group-level information of the zygote into specialized somatic structure opened up the energy-gathering potential of multicellular complexity and propelled an adaptive radiation of higher-level organization.

6. The metazoan split personality

The single cell stage (and therefore somatic mortality) is necessary for group cooperative function in multicellular systems, but in metazoans this requirement presents two major engineering challenges. The first is how to manage quickly and efficiently the construction of a complex multicellular organism from a single cell. New unicellular organisms can be made simply by constructing excess parts inside existing cells and then dividing these parts among two daughter cells. This simple and logical method of reproduction is possible because the reproduction of RNA replicators has been completely replaced by translation of RNA function from the single group 'external' (from the ribozyme's point of view) DNA information centre. In unicellular eukaryotes, the genes for reproductive control of mitochondria and plastids are also located in the 'external' nucleus (from the point of view of bacterial symbionts) allowing reproduction by fission because of this centralized group-level control. But for metazoans the separate 'external' germ line (from the point of view of the somatic cell), which stores the master genome, is isolated from day-to-day operations and therefore cannot also serve as the control centre that coordinates function. The group storage function is separated from the group coordination and control function (the brain and nervous system), and for this reason the germ line cannot directly transcribe information for production of specialized organ tissue and centrally direct the assembly of whole new organisms. Thus the strange metazoan system of reproduction and development through interactive signalling between parts (self-organization) had to be invented (Wolpert, 1991; Lawrence, 1992; Theraulaz & Bonabeau, 1995). Often metazoan offspring are constructed internally (as in mammals) and budded off just as in unicellular reproduction, but because of the separation between central control and the inheritance of information this internal construction still cannot be directed centrally. Mammals have the advantage of a controlled factory environment for constructing offspring, but the construction is still an autonomous process directed by the parts themselves.

The second engineering problem created by the metazoan strategy of cloning is also related to the fact that storage of the group genome is separated from central coordination and control of the group. In unicellular systems group information is stored in the same structure that coordinates and controls the group, and these two functions are integrated in the nucleus. In metazoans, however, the nucleus is cloned along with the rest of the cell, and then specialized to act only as a local information and control centre for the cellular component. This requires the development of a brain and nervous system to act as a coordination and control centre for the entire system; but this physical separation of the storage and inheritance of group information (the germ line) from its use by the central coordination centre (the brain) creates barriers both to the inheritance of information and its direct use for central coordination and control (Rushton, Fulker, Neale, Nias, & Eysenek, 1986). Information encoded in DNA cannot easily be transcribed into complex behavioural instructions, and phenotypic differences in detailed behaviour due to mental characteristics cannot be reliably correlated with DNA inheritance. Metazoans have been denied the extraordinary fitness benefits of complex learned behaviour simply because there is no way to encode this type of information reliably into DNA and pass it on to future generations. This deficiency in metazoan information structure set the stage for learning and the cultural inheritance of traits, and this is the reason that the recent appearance of a truly independent, extra-cellular method for storing coded information is so significant. Language allows a limited amount of complex information to be transferred from brain to brain, but it is writing that more fundamentally changes the relationships and design potential of living systems by allowing the absorption of DNA-coded information (and also technological information) into a combined external central storage and coordination centre with efficient and accurate replication. Just as DNA absorbed and linked the diverse functions of ribozymes (and proteins) into a centrally controlled higher-level selection unit, so external symbolic coding can coordinate and link the diverse functions of humans (and technology or any unrelated organic species) into a new selection unit regulated by an integrated central information storage and processing centre. Incidentally, this also enables the return of reproduction by the simpler, more efficient method of centrally controlled construction and division of parts, and eliminates the need for the rigid sexual protocols for information exchange or the somatic cycle of mortality necessary in multicellular systems.

7. The transition to civilization

The hypothesis of this paper is that advanced civilization is the result of the development of new external symbolic information storage structures that serve as the group information centre for human social organization. Written symbols are the first new high-fidelity mode for coding information to appear since the switch from RNA to DNA, and this new information structure makes it possible to regulate multicellular individuals as non-competitive components of a higher-level unit.

In contrast to earlier genetic modifications, the pathway to this transition is fairly well-known. The brain developed originally in multicellular systems to process sensory information and co-ordinate activities. But once memory became developed the brain could also store learned information and transmit small amounts of this information from parent to offspring.

In primates, social behaviour and cooperation probably developed in conjunction with kin selection among bands of related individuals (Sober & Wilson, 1998). Cellular DNA may have been the best way to lock in cooperative personality traits among primates, but more detailed technical information about tool-making or specific adaptations to a specialized environment are probably much more easily stored in memory (Boyd & Richerson, 1985). The invention of language vastly increased both learning capacity and the ability to transmit cultural information to the next generation, and consequently made the brain into a viable group information centre for group-level policing and integrated function (Sober & Wilson, 1998; Bingham, 1999). However language turned out to be only a pivotal stepping stone that supported the development of a series of increasingly powerful group information storage structures that were entirely external, such as writing, paper, the printing press, libraries and modern information technology. Writing was the first new purely coding structure that allowed group information to be stored accurately and transmitted independently from individual DNA and individual selection. Now, the existence of powerful high-capacity independent group-level inheritance of information is changing the relationships among components of technological societies in the most profound ways.

An external group-level site for information storage is the critical structure that allows the creation of a higher-level individual. The brain alone cannot serve this function for a society of multicellular components because there is no way to reliably replicate the mental make-up of an individual that might serve as the storage site for group information. Memory is not directly accessible for replication, and transmission through language is plagued by errors, has limited capacity and is influenced by personality and DNA-controlled mental characteristics. Externally stored symbolic information such as written records or more modern information storage technologies have none of these drawbacks. Information structures of this type can be accurately and cheaply replicated, have nearly unlimited capacity, and can be combined into integrated central storage and control centres with sophisticated regulation and processing. Memory and language were the bridge that opened the pathway to higher-level organization, but more modern methods of truly external information storage such as writing constitute the critical loop C advance that opens the door to a new world of group-level information storage, variability and selection.

The greater power of symbols to store information is what is propelling the current transition and opening up a new universe of energy-gathering possibilities. As a comparison to symbolic (written) storage, it is possible to conceive of an enhanced DNA structure becoming a central integrated information and coordination center for a group of multicellular components. Insect societies are mostly just an extension of multicellular specialization based on de-centralized interactive signalling (Bourke & Franks, 1995; Bonabeau, Theraulaz, Deneubourg, Aron, & Camazine, 1997), but the queen is already a specialized reproductive and information storing unit, and this individual could evolve further into a more advanced, fully functional information centre. DNA capacity in the queen might expand to program for many types of workers or other even more specialized structures derived from workers, and sex with haploid males could be reduced to merely transporting information between regenerative queens of continuously evolving colonies. Only the pertinent fragment of DNA would need to be transferred from the queen to each type of worker, making the queen resemble a nucleus with a single master genome where information is transcribed for use by the society as a whole. Greater DNA capacity in the queen and rapid communication links made possible by transmission through a nervous system could also allow the queen to store regulatory information that directly controls the activities of the group. At this advanced stage of integration the colony would begin to again resemble a single cell, with the queen as the advanced nucleus and the workers making up a "cytoplasm" constructed and operated with messages sent from the queen's genome. But this advanced "nuclear" controlled organization would avoid the limitations of the expanded single cell of the mycota and protozoa, because "smart" components derived from differentiated workers have their own local DNA information storage and processing and a nervous system that can communicate rapidly with the queen. Thus these "single-celled" insect societies would have a system coordinated by a single "nucleus" with all component information translated from a single template, and also have advanced components with their own local DNA information processing and high-capacity rapid communication links with the central information centre through the component nervous systems. These integrated groups could then reproduce through fission and simple replication of the single combined information storage and control center embodied in the queen. The limitations of somatic mortality and construction through interactive signalling alone could be eliminated, and the opportunities of possible shifts away from sexual recombination towards more efficient information search algorithms could be explored.

Insect societies may be heading in this direction, but the point is that they would still be limited by a slow and cumbersome chemical coding system that can only be translated into protein function. The power of symbolic coding comes not only from the advantages of a structural shift to central integrated inheritance and control, but also from more energy-efficient information storage, replication and transcription, transmission at the speed of light over great distances, and, most importantly, *direct translation mediated by humans into a vast potential of mechanical functionality never before available to living systems.*

The differences between DNA and symbolic (written) coding are reflected in the differences between organic and technological organizations. Both types of living systems have the same functional mechanisms that store, translate and replicate information, gather energy, transport materials, construct new components, sense and react to environmental conditions, and otherwise carry out all the processes of life. However, technological organizations operate in a spatial mechanical world that through humans can utilize nearly any sort of material or process or domesticate any other existing organic system (including humans themselves). Organic life is chemical and is restricted to materials that are chemically compatible and also must be physically connected (at least periodically) to function as a unit. Human organizations can communicate rapidly over great distances; they therefore can be physically disconnected and still function as a unit over global distances. Most importantly, the basic functional unit of cellular life is the versatile but still simple protein molecule, whereas the functional unit for symbolic systems is the much larger and more complex human being. A comparison can be made with the switch from proteins as the functional units of prokaryotes to entire cells as functional units for eukaryotes and muticellular systems. As higher levels are created in any hierarchy, the systems become much larger and the components and interactions among them become slower but much more complex (Pattee, 1973). This added complexity can allow new capabilities and new properties to emerge. Eukaryotic cells are much larger than prokaryotes, and multicellular organisms are much larger still (Schmidt-Nielsen, 1984). Eukaryotic structure allowed sexual reproduction to emerge, and multicellular systems gave rise to the brain and consciousness. Symbolically informed systems can be global in scale, but the most important manifestation of the greater complexity of these systems may be our emerging, more efficient algorithms that search for new information. The loop C changes that improve the efficiency of information search and storage are the pivotal events that create the long-term trends in evolution. Loop C innovations have given human organizations the ability to acquire and retain new information at an unprecedented rate (Campbell, 1990), and this advantage is leading to an equally unprecedented major transition in evolution.

8. What are symbolically informed systems?

Any organized group operating with an even rudimentary symbolically stored body of rules, policies, or procedures qualifies as a selection vehicle for the evolution of symbolically informed traits (Hull, 1980). Because of the existence of this inertly stored, language-based coding, modern organizations have the three generally accepted characteristics of a Darwinian system: heredity, variability and a competitive struggle to survive (Lewontin, 1970). Many of these systems have continuity and identifiable lineages that can be traced back for thousands of years, but because of extensive exchange of information between most groups a strictly phylogenetic classification of organizations would be difficult.

DNA code can also be considered symbolic (as is any coded information stored on the "tape" of a living system) and the use of this word to characterize only language-based information storage needs to be clarified. The phrase 'symbolically informed systems' is used in this study to refer to organizations that rely on some form of inert replicable coding (this could be written documents, microfilm, videotape, digital records or any other type of data storage) to store information that is translated into function through a language-based input into human consciousness. This is in contrast to DNA, which is chemically translated into protein function and then more or less unconsciously translated into an organism's actions due to the operation of proteins.

Several other words are given a specific meaning in this study. 'Reproduction' refers to the construction of an entirely new system complete with an engine, tape and constructor, as opposed to 'replication', which is simply copying the tape. 'Transcription' is the process of converting coded information from one code to another such as from DNA to RNA, while 'translation' is the overall process of converting stored information into active function. With these definitions, we might label printing a copy of a textbook for storage in a university library as replication, while printing copies of the same textbook for use in a classroom could be labelled as a transcribing process that is part of a larger mechanism for translating stored information into function. All the stored information of various types that trains and instructs engineers and workers on how to build a power plant (for example), including information still only stored in memory and handed down verbally, is the genotype, whereas the plant itself, which has local environmental conditions and contingencies factored in, is the phenotype.

McKelvy (1982) has made an extensive but inconclusive effort to develop a taxonomy of human organizations. Here, we classify these systems ecologically into a governmental/territorial class, a functional/mutualistic class, and a predator/parasitic class. Government systems are characterized by distinct borders that circumscribe a specific territory where their regulatory regime is enforced. As with all true organizations, the rulers and other personnel come and go while the entity remains the same due to the stability of its stored body of information. Governments have the most formalized information system of rigidly maintained laws or policies and formal procedures for interpreting or adding to the body of law. The genetic system of most industrialized nations is democracy, which is an elegant set of procedures and institutions to maximize potentially useful variability within the genome and minimize the invasion of selfish traits (Buchanan, 1954; Boehm, 1997). Special interest groups, government leaders, and voters all can be expected to act selfishly, but in a well-functioning democracy a complex system of checks and balances, government-sponsored education, and policing by the media can allow even selfish actors to produce and maintain a body of law that benefits the entire group. A population genetics of democracy would need to handle all of these factors, and would be very different from the traditional formulations developed to handle multicellular search algorithms. Selection at the group level still determines survival, but a system that filters mutations for a higher probability of success (as research institutions do for technological innovation) has a powerful loop C fitness advantage. Government and legal systems are the genetic systems of territorial organizations, but their information search algorithms are so much more sophisticated than those of organic genetic systems that they are generally not recognized as serving the same function.

Government organizations evolve in a close symbiotic relationship with the many economic entities that exist within their borders. Businesses, non-profit organizations, and religious or social groups all belong to the class of functional/mutualistic systems. All produce a product, and all trade with other entities in the environment for other products, forming a complex ecological web. Some associations between mutualists are intimate, resembling the association of plant roots and mycorrhizae (Lewis, 1991) or flowers and their sometimes very specific insect pollinators, and other relationships are more open market, resembling the food chains of biological communities.

Government/territorial systems provide a framework in which economic entities exist, much like a forest canopy creates the environment for the species that live within it, but just like forest dwellers, business or religious groups can overlap between different governments and may evolve separately or have different degrees of co-evolutionary connection to their territorial symbionts (Hannan, Carroll, Dundon, & Torres, 1995). Like governments, economic or religious organizations have a stable and perpetual existence and evolve independently from any particular person or generation (Haveman, 1993). Their character and stability depend on their symbolic genome, which evolves in response to the environment in which it exists (Tucker, Singh, & Meinhard, 1990; Swaminathan, 1996). As with governments, both religious and business organizations have strict rules for preserving and adapting their body of inherited information. These structures, along with capital markets, trade associations, research institutions and government research funding, constitute the genetic systems of mutualistic organizations and are loop C traits that have evolved to maximize the fitness of information search and preservation (Simon, 1990).

Predator and parasitic organizations are economic entities that are outside the mutualistic web of product exchanges. Criminal organizations are obvious predators, but the classification of other associations may be a matter of degree or perspective. Drug cartels, gambling enterprises, corrupt governments or opportunistic businesses are all to different degrees parasitic or predatory. These associations are continually shifting in a co-evolutionary arms race, and, just as in nature, the relationship can switch back and forth from parasitic to mutualistic depending on virulence or on spatial and reproductive factors (May & Anderson, 1982; Bremermann & Pickering, 1983; Frank, 1991, 1992; Herre, 1993).

People live and reproduce within these enveloping, symbolically informed organizations. They most often belong to multiple organizations, and they can switch allegiances at will or they can drop out and survive independently without any significant connection to larger groups. Humans still evolve independently, but the information they are fed and their productive activities are increasingly specialized and determined by the needs of group structures. Symbolically coded information is increasing rapidly while genetic changes are occurring at the usual imperceptible pace, and this differential discovery rate is the reason why symbolic evolution will overwhelm organic genetic systems. The sophistication of symbolic systems has reached at the point where they can absorb and regulate the use of DNA code, turning organic genetic systems into regulated components of higher-level systems. All these events signal a major transition, and this is where the energy feedback model of change can help to clarify an understanding of trends. Symbolic entities lack reproductive cycles or discrete generations, but still their information search mechanisms are much more sophisticated than the sexual or recombinational search algorithms of organic systems. The use of free energy feedback as a more general measure of fitness and evolutionary change makes the comparison of these disparate types of organizations possible.

The flow chart representation of the transition from individual RNA replicators to DNA informed cellular systems (Fig. 4) could just as well describe our own transition to industrial organization. The only difference is that the 'individuals' labeled as ribozymes are human individuals, and, instead of a chemically constituted cellular group with DNA instructions, we work in consciously formed economic groups with symbolically coded instructions. Cellular function operates in a world of chemical connections and interactions, but, in contrast, *humans operate in a spatial mechanical world where relationships and connections are established in a reality projected by our consciousness* (Hegel, 1807; Parsons & Shils, 1952; Berger & Luckmann, 1966; Karniol, 1982; Meyer & Scott, 1983; Frank, 1988; Gibbard, 1990; Barkow, Cosmides, & Tooby, 1992). The information in symbols is translated into activity in this spatial mechnical world through the ability of our brain to receive transcribed information and our body to put it into action. In the same way that DNA instructions coordinated ribozyme activity in protocells, our new external instructions increasingly direct our activities into specialized group-level tasks that have no direct connection to individual survival or reproduction. The difference between being a hunter-gatherer or even a farmer compared to having a job in an industrialized society is profound in an evolutionary sense. This difference marks the boundary between spending our time and energy in the individual pursuit of survival and reproduction or alternately directing our energies into collective survival using an alternate external set of instructions, as illustrated in Fig. 4. In the long run these activities create a feedback of energy that determines what sort of instructions survive, fundamentally altering our mode of existence.

At the same time, new information on birth control techniques and knowledge of genetics and the human genome has profoundly lessened the influence of DNA-programmed reproductive patterns (Fisher, 1992; Ridley, 1993). We now have much more conscious control over reproduction, but at the same time our conscious ideas about reproduction (and our ability to put them into practice) are shaped by symbolically instructed culture and education. As would be expected in a major transition, reproductive competition is being replaced by institutionally controlled reproductive fairness in industrial societies (Alexander, 1987). Not only is reproduction institutionalized, but our educational system is able to program the memory of each new generation, producing engineers, accountants, or whatever other type of specialized actor is currently needed. What was once individual competition to survive is changing into regulated procedures to efficiently produce components to enhance the survival of the group.

The transfer of the genomes of humans and other species into the group symbolic genome now allows 'single cell' reproduction by centrally coordinated construction of parts and division into daughter cells. This shift back to central inheritance through integrated information storage and coordination centres is what makes traditional fitness formulations based on the sexual exchange of information inapplicable to symbolic systems. Information exchange and reproduction of symbolic organizations more closely resembles that of prokaryotes, where lineages are made up of dividing cells with varying mechanisms for occasional information exchange. As in prokaryotes, the species concept cannot be as well defined because symbolic organizations are no longer constrained by the multicellular necessity of reproduction through the fusion of gametes in a zygote stage (McKelvy, 1982).

These changes are made possible by loop C innovations that improve the information structure and feed potential energy gains into loop B information search. In other words, our new way of storing information connected to human activity opened up a new universe of technological variability that can be searched through. This untapped universe of potential information yields extremely high returns on energy invested in information search because there is no competition in this realm and all the easily obtained innovations are still waiting to be discovered. This unprecedented loop B gain feeds into loop A construction and growth, causing the rapid physical expansion of human organization.

The capabilities of symbolic information structure are still increasing, indicating that we are still in the earliest stages of this current transition. Our group information centres are still in the formative stages, and they have just begun the integration of lower-level units into a new higher-level entity. A reasonable extrapolation of current trends into the future would create a jump in information capacity that would exceed the jump from RNA to DNA capacity that made cellular life possible. The world of unlimited technological variability should more than match the reservoir of protein variability that DNA tapped, possibly leading to an expansion of symbolically informed systems on a scale similar to the expansion of cellular and multicellular life.

9. Conclusion

Biological literature discussing the evolution of civilization has focused almost exclusively on the interplay between biological and cultural evolution in populations of individuals. Culture has been treated as behaviours or ideas that are centred in the mind and passed directly from one generation to another. Sociobiologists view culture as a secondary body of individual traits that co-evolve with the DNA genome but are ultimately held on a leash by DNA-specified human characteristics (Wilson, 1978). Boyd and Richerson (1985) gave cultural evolution a more equal role; they make culture a separate inheritance system with its own unique properties, but still do not consider the integrated nature of human organization, technology and group-level symbolically coded information as a higher-level selection vehicle. The models presented by Boyd and Richerson only consider cultural or genetic transmission as alternate modes of transferring the same traits to the next generation of individuals, as if the blueprints for an automobile factory or electrical generating plant could alternately be encoded in DNA. The fact is that the information used to construct these technological marvels that are the basis for our fitness cannot be primarily encoded either genetically or culturally in our minds because of both the parasitism problem and insufficient capacity. This tremendous volume of integrated information cannot be transferred from parent to child or from peer to peer in a process of enculturation, as studied in primitive societies. Instead this complex information must be encoded in specialized inert storage structures (books, microfilm, digital storage, etc.) that can be accurately and cheaply transcribed at the group level. The information is *translated* into human knowledge and functionality in a regulated and structured process (institutionalized education) similar to DNA translation that is itself directed by symbolic coding, and this leaves the primary *inheritance* function to the inert, group-level symbolic storage structures. Boyd and Richerson's models do not address the fact that symbolic coding has allowed society to move beyond the limitations of both genetic and cultural evolution to create an entirely new integrated selection vehicle based on an alternatively coded genome. Civilization is making the pivotal switch to selection of a linked, group-level genome that creates a new higher-level individual.

More recently Sober and Wilson (1998) and others have demonstrated the validity of group selection and shown how cultural mechanisms such as mutual policing can be a powerful evolutionary force favoring cooperative behaviour. Others (Michod, 1999; Frank, 1998) have investigated specific pathways and mechanisms that can lead to the selection of DNA traits for co-operative interaction among groups. Michod (1999) has used the Price equation to model evolution on two levels, but this model can still only handle the competition between individual- or group-level genes stored by an individual-level genetic structure. All these studies still see the evolution of civilization as a bottom-up process in which the primary focus is on the interaction of individuals or groups of individuals that influence individual genomes. But this bottom-up approach obscures the basic structural changes and the accompanying free energy feedback fundamentally driving the whole process. None of these studies have recognized the power and significance of symbolic coding as a completely separate, higher-level, higher capacity group information centre and the profound influence of higher-level government and economic entities that use this symbolically stored information and the expanded access to energy that it provides to impose order from the top down. The fact is that these business, social, and government organizations are the focus of current evolution and are expanding the dominance of symbolic genomes. These entities engage in cutthroat competition for space, resources, energy and people that determine their survival and results in their selection and the evolution of their symbolically encoded information. The rapid pace of discovery in this virgin universe of new energy-gathering possibilities is giving these higher-level organizations a decisive advantage over DNA-instructed organisms in the competition for resources.

Bingham (1999) identifies mutual policing (coalitional enforcement) as an important step toward a cooperative society, but he attributes the unique human ability to police a group and the subsequent rise of civilization primarily to the effective use of weapons for this policing function. However other animal species have the physical ability to gang up on a single individual to administer punishment; what they lack is not the means but the instructions on how and when to do it. The key to coalitional enforcement is a group-level genome that can store and translate adequate information for this complex task.

Trivers (1971) and others (Alexander, 1987) have looked at reciprocal altruism as an explanation of human cooperation. But it seems that they have not fully recognized either the pervasive nature of altruism in modern society or the role of higher-level information in regulating it. In fact, economic systems are an extreme expression of altruism; they rely on money to keep track of an impossibly intricate array of interwoven reciprocal exchanges (Mansbridge, 1990). These systems, in which nearly every participant spends most of his time working at a job that benefits either the group or other people, resemble most closely the nearly universal altruism of individual RNA-translated proteins in a cell that function in a network of reciprocal efforts to benefit the whole.

Nelson and Winter (1985) and others (McKelvey & Aldrich, 1983; Lambkin & Day, 1989; Levinthal, 1991; Baum & Singh, 1994; Lomi & Larson, 1998; Aldrich, 1999) have promoted the idea of economic organizations as evolutionary entities. Their work provides a detailed description of these entities and how they operate and are selected for. However, as economists, their focus is on developing regulatory models that maximize output and are for use by the organizations themselves. These studies are very much operative genes in themselves, causing a confusion over what is the genotype and what is the expression of genetic coding (Frank, 1993; Sober, 1998). They fail to distinguish clearly between translation and transmission and between transmission and selection. Consequently they fail to recognize the significance of written code (including economic models in books such as theirs) as the primary site for stored information. As with organic genetic material, written material is fixed, inert, and relatively permanent. It can be expressed in different ways or not at all. Because of its unique permanence, however, it is the dominating factor regulating systems and their evolution over the long term.

Only recently, with the invention of writing and other external coding structures, have human organizations crossed the line where neither models of sociobiology, cultural evolution, nor group selection adequately describe our civilization. We have created new higher-level genetic structures that are themselves the focus of evolution and that survive and compete with each other, with more primitive human groups, and with other species by organizing people and technology into higher-level selection vehicles for their accumulated information. In this new scheme of things we are no longer independent objects of selection, but rather objects of translated function or agents of translation of information into technological function in a spatial mechanical world of higher-level organizations. Increasingly, the information in our minds and DNA is no longer the result of inheritance at all, but rather is translated and regulated from a higher-level symbolic genome that is itself the focus of evolutionary selection.

A shift in perspective is needed if the biological significance of humans and their civilization is to be fully understood. It is necessary to move beyond models of group selection of individual genotypes, and also beyond the restricted view of culture as an auxiliary information system promoting the fitness of DNA-instructed systems on either an individual or group level. The development of writing as an alternative replicable coding structure and the technology and institutions associated with the storage and transmission of written knowledge has instead created a high-capacity, completely independent information centre capable of storing the linked integrated genomes of higher-level selection vehicles within which we are component parts. Modern political and economic organizations are fully integrated, wholly constituted biological systems operating with their own powerful new information-generating structures. This requires new genetic models that reflect the sophisticated information-gathering activities of modern political, scientific and economic institutions, and that combine political science, organizational theory, and the philosophy of science with a primarily biological focus in order to model the very different dynamics of these processes (Popper, 1972; Quinn, 1980; Campbell, 1990; Mowery, 1992; Black & Boal, 1994; Lynn, Reddy & Aram, 1996). A shift to this perspective could create a new field of biological study with not only broad scientific interest, but also possibly tremendous practical benefits to the operation of these organizations.

10. In summary

The ability of a system (instructed either by DNA or alternative symbols) to survive, expand and diversify is most directly due to its ability to gather more energy and utilize it to construct more of itself than its competitors. This ability to gather energy depends on the successful search for information on how to construct the most effectively functioning structure. The success of this information search depends on several factors, all of which pertain to the information system. These factors include the effectiveness of the search algorithms, the grouping and transmittal mode of coding, and the type of coding and the potential variability to which it is connected. A major realignment of these factors (resulting from a successful loop C investment into the search for better information structures) that allows a more complex and energy-rich technology to be connected to a higher-capacity information system is what creates a major transition. Understanding of these events is not only a matter of understanding the details of specific evolutionary pathways, but also involves understanding these structural changes in organization and information systems that create new capacities for the evolutionary search for information and energy-gathering ability. Human society has created a much more efficient, higher-capacity information system connected to a vast new universe of functional structure that can be organized on a higher level. The advantages of this better information system—connected to a new range of higher-level variability feeding through to the successful search for technological information (loop B) and to continued growth and diversification (loop A) at a higher level of organization—should lead to a major transition with a long-term evolutionary impact on a scale similar to or greater than previous transitions.

The literature on human evolution has for the most part missed this rather startling hypothesis by focusing only on specific pathways for individual or group evolution instead of examining broader trends and more fundamental changes in information structure. Maynard Smith and Szathmary (1995) made a good start on the analysis of information structure and major transitions, but they ended their review just before the current pivotal event, which is the invention of writing as an alternative coding structure to DNA. Simply put, the invention of writing triggered what is probably the most significant and far reaching evolutionary event since the appearance of DNA. Hopefully this outline will lead to a wider recognition of this event and encourage further study of civilization as a major evolutionary transition and alternative symbolic coding as the new DNA of living systems.

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References

Aldrich, H. (1999). *Organization evolving*. Thousand Oaks, CA: Sage Publications Inc.

Alexander, R. (1987). *The biology of moral systems*. Hawthorne, NY: Aldine de Gruyter.

Anderson, C., & McShea, D. W. (2001). Individual versus social complexity, with particular reference to ant colonies. *Biological Review*, *76*, 211–237.

Arthur, W. B. (1988). Competing technologies: An overview. In G. Dosi, C. Freeman, R. Nelson, G. Silverburg, & L. Suete (Eds.), *Technical change and economic theory* (pp. 590–607). London: Pinter Publishers.

Aunger, R. (Ed.) (2001). *Darwinizing culture: The status of memetics as a science*. Oxford: Oxford University Press.

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*, 1390–1396.

Axelrod, R. (1988). An evolutionary approach to norms. *American Political Science Review*, *80*, 1095–1111.

Barkow, J. H., Cosmides, L., & Tooby, J. (Eds.) (1992). *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press.

Baum, J., & Singh, J. V. (Eds.) (1994). *Evolutionary dynamics of organizations*. New York: Oxford University Press.

Beach, J. (1998). *Theory of self-organizing systems*. MA thesis, California State University, Fullerton. Honeywell Online: Proquest.

Berger, P., & Luckmann, T. (1966). *The social construction of reality*. New York: Doubleday.

Bingham, P. M. (1999). Human uniqueness: A general theory. *The Quarterly Review of Biology*, *74*, 171–194.

Black, J. A., & Boal, K. B. (1994). Strategic resources: Traits, configurations, and paths to sustainable competitive advantage. *Strategic Management Journal*, *15S1*, 131–148.

Boehm, C. (1992). Segmentary 'warfare' and the management of 'conflict'. Comparison of chimpanzees and patrilineal-patrilocal humans. In A. H. Harcourt, & F. B. M. DeWaal (Eds.), *Coalitions and Alliances in Humans and Other Animals* (pp. 139–173). Oxford: Oxford University Press.

Boehm, C. (1997). Egalitarian behavior and the evolution of political intelligence. In R. W. Byrne, & A. Whiten (Eds.), *Machiavellian intelligence*. Cambridge: Cambridge University Press.

Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S., & Camazine, S. (1997). Self-organization in social ants. *Trends in Ecology and Evolution*, *12*, 188–193.

Bourke, A., & Franks, N. (1995). *Social evolution in ants*. Princeton: Princeton University Press.

Boyd, R., & Richerson, P. (1985). *Culture and the evolutionary process*. Chicago: Chicago University Press.

Boyd, R., & Richerson, P. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology*, *13*, 171–195.

Brandon, R. N. (1999). The units of selection revisited: The modules of selection. *Biology and Philosophy*, *14*, 167–180.

Breden, F. J., & Wade, M. J. (1989). Selection within and between kin groups of the imported leaf beetle. *American Naturalist*, *134*, 35–50.

Bremermann, H. J., & Pickering, J. (1983). A game-theoretic model of parasite virulence. *Journal of Theoretical Biology*, *100*, 411–426.

Bresch, C., Niesert, V., & Harnasch, D. (1980). Hypercycles, parasites and packages. *Journal of Theoretical Biology*, *85*, 399–405.

Buchanan, J. M. (1954). Individual choice in voting and the market. *Journal of Political Economy*, *62*, 334–343.

Buss, L. W. (1987). *The evolution of individuality*. Princeton, NJ: Princeton University Press.

Campbell, D. T. (1990). Epistemological roles for selection theory. In N. Rescher (Ed.), *Evolution, cognition, and realism* (pp. 1–19). Lanham, MD: University Press of America.

Cavalli-Sforza, L., & Feldman, M. (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton, NJ: Princeton University Press.

Chao, L., Hanley, K. A., Burch, C. L., Dalberg, C., & Turner, P. E. (2000). Kin selection and parasite evolution: Higher and lower virulence with hard and soft selection. *The Quarterly Review of Biology*, *75*, 261–275.

Clutton-Brock, R. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature*, *373*, 209–216.

Cohen, D., & Zohari, D. (1986). The selection operating on the evolution equilibrium of the frequency of sexual reproduction in predominately asexual populations. In S. Karlin, & E. Nevo (Eds.), *Evolutionary processes and theory* (pp. 765–782). Orlando: Academic Press.

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.

Dennett, Daniel C. (1995). *Darwin's dangerous idea*. New York: Simon & Schuster.

Dugatkin, L. A. (1997). *Cooperation among animals: An evolutionary perspective*. New York: Oxford University Press.

Durham, W. H. (1991). *Coevolution: Genes, culture and human diversity*. Stanford, CA: Stanford University Press.

Eigen, M., & Schuster, P. (1977). The hypercycle. A principle of natural self-organization. Part A: Emergence of the hypercycle. *Naturwissenschaften*, *64*, 541–565.

Findlay, C. S. (1992). Phenotypic evolution under gene-culture transmission in structured populations. *Journal of Theoretical Biology*, *156*, 387–400.

Fisher, H. E. (1992). *Anatomy of love: The natural history of monogamy, adultery, and divorce*. New York: W.W. Norton.

Frank, R. H. (1988). *Passions within reason: The strategic role of the emotions*. New York: W.W. Norton.

Frank, R. H. (1993). Does studying economics inhibit cooperation? *Journal of Economic Perspectives*, *7*, 159–171.

Frank, S. A. (1991). Spatial variation in coevolutionary dynamics. *Evolutionary Ecology*, *5*, 193–217.

Frank, S. A. (1992). A kin selection model for the evolution of virulence. *Proceedings of the Royal Society of London*, *B25*, 195–197.

Frank, S. A. (1994). Genetics of mutualism: The evolution of altruism between species. *Journal of Theoretical Biology*, *170*, 393–400.

Frank, S. A. (1995a). The origin of synergistic symbiosis. *Journal of Theoretical Biology*, *176*, 403–410.

Frank, S. A. (1995b). Mutual policing and repression of competition in the evolution of cooperative groups. *Nature*, *377*, 520–522.

Frank, S. A. (1996). Host control of symbiont transmission: The separation of symbionts into germ and soma. *The American Naturalist*, *148*, 1113–1124.

Frank, S. A. (1997a). Models of symbiosis. *The American Naturalist*, *150*, S80–S99.

Frank, S. A. (1997b). The design of adaptive systems: Optimal parameters for variation and selection in learning and development. *Journal of Theoretical Biology*, *184*, 31–39.

Frank, S. A. (1998). *The foundations of social evolution*. Princeton, NJ: Princeton University Press.

Gachter, S., & Fehr, E. (1997). Social norms as a social exchange. *Swiss Journal of Economics and Statistics*, *133*, 275–292.

Gibbard, A. (1990). *Wise choices, apt feelings*. Cambridge, MA: Harvard University Press.

Goodnight, C. J., & Stevens, L. (1997). Experimental studies of group selection: What they tell us about group selection in nature. *American Naturalist*, *150*, S59–S79.

Grafen, A. (1984). Natural selection, kin selection, and group selection. In J. Krebs, & N. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (pp. 62–84). Oxford: Blackwell Scientific Publications.

Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, *7*, 1–16.

Hannan, M. T., Carroll, G. R., Dundon, E. A., & Torres, J. C. (1995). Organizational volution in a multinational context: Entries of automobile manufacturers in Belgium, Britain, France, Germany and Italy. *American Sociological Review*, *60*, 509–528.

Haveman, H. A. (1993). Ghosts of managers past: Managerial succession and organizational mortality. *Academy of Management Journal*, *36*, 864–881.

Hegel, G. W. F. (1807). *The phenomenology of mind* (Trans. J. B. Baillie). New York: Harper & Rowe 1967.

Herre, E. A. (1993). Population structure and the evolution of virulence in nematode parasites of fig wasps. *Science*, *259*, 1442–1446.

Holland, J. H. (1975). *Adaptation in natural and artificial systems*. Ann Arbor: University of Michigan Press.

Hull, D. L. (1980). Individuality and selection. *Annual Review of Ecology and Systematics*, *11*, 311–332.

Karniol, R. (1982). Settings, scripts, and self-schemata: A cognitive analysis of the development of prosocial behavior. In N. Eisenberg (Ed.), *The development of prosocial behavior* (pp. 251–278). New York: Academic Press.

Kitcher, P. (1993). The evolution of human altruism. *Journal of Philosophy*, *110*, 497–516.

Kondrashov, A. S. (1988). Deleterious mutations and the evolution of sexual reproduction. *Nature*, *336*, 435–440.

Lambkin, M., & Day, G. (1989). Evolutionary processes in competitive markets. *Journal of Marketing*, *53*, 4–20.

Lawrence, P. A. (1992). *The making of a fly*. Oxford: Blackwell.

Levinthal, D. (1991). Organizational adaptation and environmental selection—interrelated processes of change. *Organizational Science*, *2*, 140–145.

Lewis, D. H. (1991). Mutualistic symbiosis in the origin and evolution of land plants. In L. Margulis, & R. Fester (Eds.), *Symbiosis as a source of evolutionary innovation* (pp. 288–300). Cambridge (MA): MIT Press.

Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics*, *1*, 1–18.

Lloyd, E. A. (2000). Groups on groups: Some dynamics and possible resolution of the units of selection debates in evolutionary biology. *Biology and Philosophy*, *15*, 389–401.

Lomi, A., & Larson, E. R. (1998). Density delay and organizational survival: Computational models and empirical comparisons. *Computational & Mathematical Organization Theory*, *3*, 219–247.

Lumsden, C. J., & Wilson, E. O. (1981). *Genes, mind and culture*. Cambridge, MA: Harvard University Press.

Luyet, B. J. (1940). The case against cell theory. *Science*, *91*, 252–255.

Lynn, L. H., Reddy, N. M., & Aram, J. D. (1996). Linking technology and institutions: The innovative community framework. *Research Policy*, *25*, 91–106.

Mansbridge, J. J. (1990). *Beyond self-interest*. Chicago: University of Chicago Press.

Margulis, L. (1970). *Origin of the eukaryotic cells*. New Haven, CN: Yale University Press.

Margulis, L. (1993). *Symbiosis in cell evolution* (2nd ed). New York: W.H. Freeman.

Margulis, L., Dolan, M. F., & Chapman, M. J. (2000). Centrioles and kinetisomes: form, function, and evolution. *The Quarterly Review of Biology*, *75*, 409–429.

Martin, G. W. (1957). Concerning the 'cellularity' and acellularity of the protozoa. *Science*, *123*, 125.

May, R. M., & Anderson, R. M. (1982). Coevolution of hosts and parasites. *Parasitology*, *85*, 411–426.

Maynard Smith, J. (1964). Group selection and kin selection. *Nature*, *201*, 1145–1147.

Maynard Smith, J., & Szathmary, E. (1993). The origin of chromosomes. I. Selection for linkage. *Journal of Theoretical Biology*, *164*, 437–446.

Maynard Smith, J., & Szathmary, E. (1995). *The major transitions in evolution*. Oxford: Oxford University Press.

Maynard Smith, J. (2000). The concept of information in biology. *Philosophy of Science*, *67*, 177–194.

McKelvy, B. (1982). *Organizational systematics*. Berkeley, CA: University of California Press.

Mckelvy, C., & Aldrich, H. (1983). Population, natural selection, and applied organizational science. *Administrative Science Quarterly*, *28*, 101–128.

Meyer, J. W., & Scott, R. S. (Eds.) (1983). *Organizational environments: Ritual and rationality*. Beverly Hills, CA: Sage.

Michod, R. (1983). Population biology in the first replicators: The origin of genotype, phenotype, and organism. *American Zoologist*, *23*, 5–14.

Michod, R. (1999). *Darwinian dynamics*. Princeton, NJ: Princeton University Press.

Mitchell, M. (1996). *An introduction to genetic algorithms*. Cambridge, MA: MIT Press.

Mowery, D. (1992). The U. S. national innovation system. *Research Policy*, *21*, 125–144.

Nelson, R., & Winter, S. (1982). *An evolutionary theory of economic change*. Cambridge, MA: Harvard University Press.

von Neumann, J. (1966). *Theory of self-reproducing automata*. Ed. A. W. Burks. Urbana, IL: University of Illinois Press

Parsons, T., & Shils, E. (Eds.) (1952). *Towards a general theory of action*. Cambridge, MA: Harvard University Press.

Pattee, H. H. (1973). *Hierarchy theory*. New York: George Braziller, Inc.

Popper, K. R. (1972). *Objective knowledge: An evolutionary approach*. Oxford: Clarendon Press.

Quinn, J. B. (1980). *Strategies for change: Logical incrementalism*. Homewood, IL: Irwin.

Ratnieks, F. L. (1988). Reproductive harmony via mutual policing by workers in eusocial hymenoptera. *American Naturalist*, *132*, 217–236.

Ridley, M. (1993). *The red queen: Sex and the evolution of human nature*. New York: Penguin Books.

Rushton, J. D., Fulker, D., Neale, M., Nias, D., & Eysenek, H. (1986). Altruism and aggression: The heretibility of individual differences. *Journal of Personality and Social Psychology*, *50*, 1192–1198.

Schmidt-Nielsen, K. (1984). *Scaling: Why is animal size so important?* Cambridge: Cambridge University Press.

Schumpeter, J. A. (1934). *The theory of economic development*. Cambridge, MA: Harvard University Press.

Simon, H. A. (1990). A mechanism for social selection and successful altruism. *Science*, *250*, 1665–1668.

Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Cambridge, MA: Blackwell Publishers.

Sober, E. (1981). Holism, individualism, and the units of selection. *PSA 1980* (Vol. 2, pp. 9–121). East Lansing, MI: Philosophy of Science.

Sober, E. (1998). Three differences between deliberation and evolution. In P. Danielson (Ed.), *Modeling rationality, morality, and evolution* (pp. 408–422). Oxford: Oxford University Press.

Sober, E., & Lewontin, R. C. (1982). Artifact, cause and genic selection. *Philosophy of Science*, *47*, 157–180.

Sober, E., & Wilson, D. (1998). *Unto others*. Cambridge, MA: Harvard University Press.

Swaminathan, A. (1996). Environmental conditions at founding and organizational mortality: A trial by fire model. *Academy of Management Journal*, *39*, 1350–1377.

Szathmary, E. (1993). Coding coenzyme handles: a hypothesis for the origin of the genetic code. *Proceedings of the National Academy of Sciences, USA*, *90*, 9916–9920.

Szathmary, E. (1999). The first replicators. In L. Keller (Ed.), *Levels of selection in evolution* (pp. 31–52). Princeton, NJ: Princeton University Press.

Szathmary, E., & Demeter, L. (1987). Group selection of early replicators and the origin of life. *Journal of Theoretical Biology*, *128*, 463–486.

Taylor, C. E., & Mcguire, M. T. (1988). Reciprocal altruism: 15 years later. *Ethology and Sociobiology*, *9*, 67–72.

Theraulaz, G., & Bonabeau, E. (1995). Coordination in distributed building. *Science*, *269*, 686–688.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35–57.

Tucker, D. J., Singh, J. V., & Meinhard, A. (1990). Organizational form, population dynamics, and institutional change: The founding pattern of voluntary organizations. *Academy of Management Journal*, *33*, 151–178.

Turner, P. E., Cooper, V. S., & Lenski, R. E. (1998). Tradeoff between horizontal and vertical modes of transmission in bacterial plasmids. *Evolution*, *52*, 315–329.

Wade, M. J. (1985). Soft selection, hard selection, kin selection and group selection. *American Naturalist*, *125*, 61–73.

Wilson, E. O. (1978). *On human nature*. Cambridge, MA: Harvard University Press.

Wimsatt, W. (1980). Reductionist research strategies and their biases in the units of selection controversy. In T. Nickles (Ed.), *Scientific discovery: Case studies*. Dordrecht: Reidel.

Wimsatt, W. C. (1999). Genes, memes and cultural heredity. *Biology and Philosophy*, *14*, 279–302.

Wolpert, L. (1991). *The triumph of the embryo*. Oxford: Oxford University Press.