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ECONOMICS IS AN EVOLUTIONARY SCIENCE

Paul J. Zak and Arthur T. Denzau

INTRODUCTION

In a widely read 1898 essay published in the *Quarterly Journal of Economics*, Thorstein Veblen asked why economics had strayed from its foundation in the natural sciences. The title of Veblen's paper is "Why is economics not an evolutionary science?" In it, Veblen identifies the many advances of classical and the emerging neoclassical economics, but critiques their use of hypothetical constructs of human decision processes. The paper is an appeal to return the focus of economic analysis to human beings. With one hundred years perspective, Veblen's essay is amazingly prescient. Nevertheless, as this chapter demonstrates, this call has been largely ignored by professional economists. To the contrary, the predominant approach to economic analysis in the twentieth century was not the biology of human behavior, but a systems approach mimic-king the analysis of classical physics.

This chapter examines the mutual evolution of the biological and economic sciences, tracing their intimate relationship in the previous two centuries, their nearly complete divorce in the twentieth century, and their current gradual rapprochement. We do this by examining the individuals, many with familiar names, who forded the currents between disciplines, bringing to light the bi-directional contributions of one upon the other. By doing this, we reach the fundamental conclusion which is this chapter's title: Economics *is* an evolutionary science. This chapter does *not* argue that evolutionary biology is

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the proper metaphor for economic analysis, but that methods and findings in the biological sciences need to be incorporated *directly* into economics if the discipline is to continue to produce relevant insights into human behavior.

A HISTORICAL CHRONOLOGY OF THE FEEDBACK BETWEEN ECONOMICS AND BIOLOGY

German medical doctor Karl Burdach (1776–1847) coined the term "biology" to refer to the study of human beings. His masterwork *Physiology as a Science of Experience* advocated the deduction of the bases of human behavior by observation. The purview of biology was expanded to include botany, zoology, geology, chemistry and meteorology by Jean Baptiste Pierre Antoine de Monet Lamarck in 1812 who was convinced that the scientific methods of observation and experiment applied uniformly to the study of humans, animals, cells, and molecules. A near-contemporary of Burdach, Adam Smith, wrote repeatedly in 1759's *The Theory of Moral Sentiments* of the "oeconomy of nature," when describing human behavior, borrowing the phrase from a 1751 book with this title by the father of biological taxonomy Carolus Linnaeaus. By his 1776 *The Wealth of Nations*, Adam Smith had dispensed with biology as his overarching metaphor, and adopted Newtonian mechanics. Henceforth the schism between the evolutionary basis in biology and economics, for the most part, grew.

The lacuna between biology and economics deepened in the 19th century because of a fundamental misunderstanding of the relationship between the two by the polymath Herbert Spencer (1820–1903). Spencer published a simple version of biological evolution before Charles Darwin, and was the first to use the terms "evolution" and "survival of the fittest" to describe biological dynamics. Unfortunately, Spencer did not clearly identify the mechanisms through which evolution occurs as did Darwin, and the latter is rightfully identified as the father of modern evolutionary theory, though for many years Spencer outshined Darwin and was considered one of the world's leading biologists. Spencer went on to write important works in sociology and psychology (Spencer, 1851, 1855, 1880), and to work as an editor at the *Economist* magazine. Nevertheless, Spencer is often now overlooked because he was unwilling to accept the non-directional nature of Darwinian evolution; instead his take on evolution continued to be both Lamarckian and teleological. Spencer (1851) wrote that "Progress . . . is a part of nature" (p. 65). As a result, Spencer's later work advocated laissez-faire economics in order to promote adaptation and social progress via Lamarckian learning. Nevertheless, Spencer was the first to integrate biological evolution with social theory, and his influence – for better or worse – is still present, if only tacitly.

In this section, we examine the historical co-evolution of biology, especially evolutionary theory, and economics, by examining the major influences during the past two centuries. Note that by "evolutionary theory" we mean the modern synthetic or neo-Darwinian theory that adjoins genetics, biochemistry, paleobiology, and natural history as supporting pillars to the basic theory of natural selection developed by Darwin.

Adam Smith

Several features of classical economic analysis have strong ties to biology. Natural law was a fundamental notion of the Enlightenment, focusing on the innate basis of human behavior. A key notion of the Scottish Enlightenment is the idea of *unanticipated consequences*, which relates closely to the Darwinian approach to evolution. Also related is the classical economic model of population growth. These three elements are all expressed in the work of Adam Smith (1723–1790).

Smith was fully aware of one of the earliest unanticipated consequences arguments, that of Bernard de Mandeville. Mandeville, in *The Fable of the Bees* (1714), argued that the selfish motives of humans did not necessarily cause the results of their actions to be bad for society as a whole. We would now term this a discovery of an emergent phenomenon, and this is a very sensible interpretation of the unanticipated consequences idea in Scottish Enlightenment philosophy.

Smith's contemporary David Hume specifically designed the specie flow model to reference economic phenomena in his 1752 work *On the Balance of Trade*. Once again, an emergent phenomenon, in this case the stability of equilibrium was invoked to explain the implications of a mercantilist surplus in the balance of trade between two countries in the context of the use of specie, gold, for the settlement of international payments.[1] This example of a negative feedback mechanism supporting an equilibrium naturally leads to similar uses both of equilibrium and of stability in Smith's work.

Smith's 1759 book, *The Theory of Moral Sentiments*, is explicit in the ties with biology. In various parts, Smith attempts to argue for the implications of natural sentiments assumptions, based on his conception of human nature. These were tied to the natural law approach promulgated by Enlightenment scholars,

1. It is interesting to note that the anachronistic economic use of "specie" and the biological "species" have the same Indo-European root indicating a particular form or type.

both in Scotland, and on the continent. But these quite explicit ties seem both quaint and far less convincing to the modern reader.

Much more convincing, and tied more to the emergent properties idea are many arguments in *The Wealth of Nations*. For example, a version of the Iron Law of Wages is developed in which a model of population growth is made explicit. The optimistic choices of couples to procreate, and the environmental support of high wages enable more than the usual number of children to survive to adulthood, driving wages back toward the natural equilibrium. This negative feedback mechanism works in a similar manner to that in Hume's specie flow, but involves more time, and illustrates the strong power of market analysis presented in Smith.

The most famous emergent property argument of Smith is his notion of the Invisible Hand:

> . . . he intends only his own gain, and he is in this, as in many other cases, led by an invisible hand to promote an end which was no part of his intention. Nor is it always the worse for the society that it was no part of it. By pursuing his own interest he frequently promotes that of the society more effectually than when he really intends to promote it. I have never known much good done by those who affected to trade for the public good. It is an affectation, indeed, not very common among merchants, and very few words need be employed in dissuading them from it (Smith, 1776, p. 423).

Here the unanticipated consequences are quite explicit, and the analysis is a more rigorous study of the basic idea in Mandeville. By isolating the crucial elements, Smith generates the type of argument style that is followed for another two centuries. The emergent property feature is an element that becomes the center of many important economic works that follow.

Thomas Malthus

The Reverend Thomas Malthus (1766–1834) produced one of the first among a substantial series of studies that followed in the path of Adam Smith, in his 1798 *Essay on Population*. In this work, Malthus develops in greater detail and extent the population model already stated briefly in Smith. Malthus was responding to the radical institutional critics of the traditional order who arose during the American and French Revolutions. Much of the work is a statement of and argument for claims of unanticipated consequences of existing institutions, and thus the emergent properties in higher-level equilibria.

The extended deductive argumentation and relatively rigorous style of much of it was a departure from Smith, who was seldom far from an example to illustrate his theoretical analysis. The greater level of abstraction followed by Malthus' friend, David Ricardo, allowed the development of arguments that

could be used by fields other than economics or moral philosophy. One of the fields which benefited from these abstract arguments was biology, when Charles Darwin encountered the bewildering display of plants and animals on his round-the-world tour of duty as naturalist on the HMS *Beagle*.

Darwin had read Malthus' essay, and its deductive logic was the basis for his non-theistic explanation for the fit between organism and environment via differential survival of organisms with diverse traits. Indeed, Darwin identified Malthus' notion of "crowding and struggle" among human populations in his *Essay* as the germ from which he formulated natural selection as a general principle. Once again, emergent properties became a crucial element that united economics and biology in the eighteenth and nineteenth centuries.

The Neoclassical Reaction to Darwin and Darwinism

In English-language countries, Darwin's writings produced reactions of both horror and emulation. For those following naturalistic religions and the Argument from Design (William Paley, 1802), Darwin was a challenge to their praecognita for the existence of God. If one did not need to explain the remarkable fit between organisms and their environment by divine means, then religious belief was forced to defend itself only on traditional grounds, such as faith.

The reaction in the social sciences was diffuse. Some social scientists responded by incorporating evolutionary ideas into their fields of study. For instance, anthropologists applied Social Darwinism to study human groups. Different fields incorporated different interpretations of Darwin and evolution, but these fields generally attempted to make their efforts at least consistent with this bold new approach.

Economic theorists in the English-language countries responded in a very different manner. Mainstream analysis in the mode of what came to be called neoclassical economics, can be viewed as a reaction against Darwin and the ensuing revolution in biology. Instead of attempting to admix evolutionary findings into economic analysis, neoclassical economists looked instead to Newtonian physics for methodological guidance.

The fundamental organizing principle of classical physics is *equilibrium* (though this is not the case for quantum physics). This construct appealed to neoclassical economists as it enabled the derivation of rigorous predictions ("theorems") from economic models. As a result, neoclassical economists nearly always built mathematical models that had well-defined equilibria. Neoclassical economic models, based on differential calculus invented by Newton (and

Leibnitz), focused on analyzing static equilibria, with little or no concern at all for dynamics. Equilibrium relationships are powerful as they generate testable hypotheses, and are the primary reason for the ascension of economics among the social sciences. Nevertheless, a number of economists in the vanguard understood that equilibrium models are not the be-all and end-all of economic analysis.

Alfred Marshall

Alfred Marshall (1842–1924), whose 1890 *The Principles of Economics* became the basis for much of twentieth century microeconomics, initiated the marginalist revolution by utilizing differential calculus in imitation of classical physics. Thirty-five years after this fundamental work, Marshall (1925) asked post-humanists whether the more advanced problems of economics can be solved by analogies from physical dynamics. His answer is no: biology is where these answers reside.

Foreshadowing this argument, Marshall writes in Book I of *Principles* that "In this matter economists have much to learn from the recent experiences of biology: and Darwin's profound discussion of the question throws a strong light on the difficulties before us." Further, Marshall understood that economics is the study of the forces of change, and is therefore "a branch of biology, broadly interpreted." In Marshall (1925), he extends this exhortation, "Since that time biology has more than repaid her debt; and economists have in their turn owed much to the many profound analogies which have been discovered between social and especially industrial organization on the one side and the physical organization of the higher animals on the other."

Marshall was convinced that the economics of the future would be based not on classical physics, but on biology. Outside of some notions in Marshall's work on the aging of firms, and the interaction of firms in an industry, he did not live long enough to pursue this shift himself. With each step of advance, the *ceteris paribus* crutch gets further from reality. Instead, he suggested that the study of fluctuations around an equilibrium should be understood as a dynamic, evolving process. This is a very different Marshall than is usually presented in historical surveys. Even in Blaug (1985), there is almost no mention of this methodological shift advocated by the architect of the neoclassical school.

Most of the theoretical focus of the next two generations of economists solidified and added precision to the assumptions and arguments of Marshallian neoclassical analysis. This program by his followers at Cambridge University was complemented in the United States by the work of Frank Knight (1921) and John Bates Clark, increasing the rigor and extending the implications of the static analysis he fostered in his 1890 treatise. After World War II, many mathematically trained researchers, both from economics and from the physical sciences continued the effort to add precision to microeconomics. This effort expanded and formalized mathematical structures, but seemed to thrive on rigor alone. This formalization of economics has resulted in a theory that "is more explicitly mathematical than the work of theoretical physicists." Thus, the legacy of Marshall is marginal analysis using differential calculus and physical reasoning, and not on his stated hopes of basing economic theory on biological reasoning. Marshall's final statement in his 1925 article is that "The Mecca of the economist is economic biology rather than economic dynamics."

Carl Menger

A scholar with leanings similar to Marshall's is another of the founders of neoclassical economics, the Austrian Carl Menger (1840–1921). Menger combined differential calculus and the Newtonian approach to microeconomics with biological forms of analysis. His most important contribution in this area is his analysis of the origin of money. Menger posited that money arose organically as an unanticipated consequence of the inefficiencies of barter exchange. As a result, money is valued without human intervention, and therefore does not require, for example, a government to set its value. He writes that "the origin of money can truly be brought to our full understanding only by our learning to understand the social institution [money] discussed here as the unintended result, as the unplanned outcome of specifically individual efforts of members of society" (1883, p. 155). Menger's analysis showed that money evolved to act as a medium of exchange, a finding verified by modern monetary theorists (Kiyotaki & Wright, 1989, 1991; Wright, 1995).

Menger showed that coordinating on a single money allows substantial efficiencies to be achieved (1892). The approach he takes to illustrate this is explicitly evolutionary, albeit informal. But the ideas have readily been turned into simulations, as illustrated in the recent work of Luo (1999). For this methodological advance, Menger is rightfully viewed as an early evolutionary economist.

American Institutional Economics and Thorstein Veblen

In contrast to the neoclassical reaction to Darwinism is the work of American Institutional economists of the late nineteenth and early twentieth centuries. This approach to economics is less theoretical and deductive than neoclassical theory. Instead, it takes a sociological approach to economic behaviors, focuses on the institutions and organizations of the state and economy. Among the most prominent early Institutionalists were John R. Commons, Richard Ely, and Thorstein Veblen.

On balance, Institutionalists had little effect on mainstream theoretical economics in the twentieth century. Part of the reason for this is the growing professionalization and development of academic economics in the United States, beginning in the 1880s. Increasingly, those interested in economics were working at colleges and universities, and a professional journal literature gradually developed. As a result, the writing of economics was aimed at other professional economists, which increased the homogeneity of economic training and thinking. A few academic centers retained an Institutionalist bent, but most made a full transition to neoclassical analysis. The standards of theory shifted, and the Institutionalists failed to develop alternatives to the Marshallian theory of choice. Institutionalists, without a means of explaining the fundamentals of neoclassical theory – prices and transaction quantities – were largely ignored by neoclassical economists, and Institutionalist writings became viewed as a variant of sociology rather than a complement to neoclassical analysis.

Certainly the most interesting American Institutionalist for our purposes is Thorstein Veblen (1857–1929), who was well-acquainted with the works of Herbert Spencer, Charles Darwin, and the social Darwinist William Graham Sumner, and was also among the first to unite natural selection via environmental influences with the laws of Mendelian inheritance. Veblen was a harsh critic of the neoclassical reaction against Darwinism, and used caustic language about its thin psychological foundation and abandonment of social influences. For example, he characterizes neoclassical economics as using an outdated conception of man:

> The psychological and anthropological preconceptions of the economists have been those which were accepted by the psychological and social sciences some generations ago. The hedonistic conception of man is that of a lightning calculator of pleasures and pains who oscillates like a homogeneous globule of desire of happiness under the impulse of stimuli that shift him about the area, but leave him intact. He has neither antecedent nor consequent. He is an isolated definitive human datum, in stable equilibrium except for the buffets of the impinging forces that displace him in one direction or another. Self-imposed in elemental space, he spins symmetrically about his own spiritual axis until the parallelogram of forces bears down upon him, whereupon he follows the line of the resultant. When the force of the impact is spent, he comes to rest, a self-contained globule of desire as before (Veblen, 1898, p. 242).

Note the explicit comparison of neoclassical choice theory to static models in physics. This approach involves no learning, and thus cannot be evolutionary.

An evolutionary approach would involve both learning and a social context. He wrote that "The individual is but a single agent in each case," and that "an evolutionary economics must be the theory of a process of cultural growth as determined by economic interest, a theory of cumulative sequence of economic institutions stated in terms of the process itself" (p. 243). These elements are still essential to building an evolutionary economics.

Clearly, Veblen wanted economics to follow psychology and anthropology along an evolutionary path, but the neoclassical approach at the dawn of the twentieth century took a tangential path. For Veblen, neoclassical economists are content with "repairing structure and doctrines and maxims resting on natural rights, utilitarianism, and administrative expediency." Instead, the modern sciences are evolutionary sciences, and he was convinced economics should join them.

Joseph Aloysius Schumpeter

While not himself a practitioner of evolutionary ideas in economics, Joseph Aloysius Schumpeter (1883–1950) developed concepts and made claims that have been investigated with evolutionary methods. In his most widely read work, *Capitalism, Socialism and Democracy* (1942), he introduced the idea of *creative destruction*, perhaps his most important insight into economic behavior. He argued that the most significant type of economic competition is not price competition. Instead, "The essential point to grasp is that in dealing with capitalism we are dealing with an evolutionary process" leading to competition between firms. Because "Capitalism, then, is by nature a form or method of economic change and not only never is but never can be stationary," a point also recognized by Marx, as change "alters the data of economic action." As a result, economic structures endogenously change, creating winners and losers via a selection process. Those who run firms, knowing this, will seek to anticipate structural changes in the struggle for economic survival. This occurs because "The fundamental impulse that sets and keeps the capitalist engine in motion comes from the new consumers' goods, the new methods of production or transportation, the new markets, the new forms of industrial organization that capitalist enterprise creates" (p. 82).

This fundamentally dynamic view of the economy clearly follows an evolutionary approach. Innovations, by their nature, are largely unpredictable, and an evolutionary model is the best way to incorporate them into economic theory. Instead of attempting to predict specific innovations, evolutionary models characterize the impact of innovation on the economy. For example, one can simulate the effects in an evolutionary system of a more diverse set of trials from which to select. The greater the diversity, the more rapid is the rate of change of the population of designs. Similarly, the more trials there are, of a given degree of diversity, the more rapid is evolutionary change. The importance of changing mutation rates and noise in the filtering process can also be studied with ease in an evolutionary simulation.

The link between computer simulations and evolutionary economics is crucial. With computer capabilities improving 25% to 50% per year, the increasing ability to model evolutionary phenomena computationally certainly exceeds the ability of researchers to acquire new mathematical techniques. Further, computational experiments often guide and suggest analytical theorems. For example, see the feedback between these approaches in Mahaffy, Zak and Joiner (1995). It is becoming clear that better behavioral models in economics are possible as computational capabilities grow. Popper in *The Self and Its Brain* (1984) wrote that

> A computer is just a glorified pencil. Einstein once said "my pencil is cleverer than I." What he meant could perhaps be put thus: armed with a pencil, we can be more than twice as clever as we are without. Armed with a computer (a typical World 3 object), we can perhaps be more than a hundred times as clever as we are without; and with improving computers there need not be an upper limit to this (p. 208).

Evolutionary simulations, following the approach of Schumpeter, are an important approach utilizing this dynamic.

Friedrich August Von Hayek

One of the more explicitly evolutionary thinkers in economics is the Austrian and 1974 Nobel laureate in economics, Friedrich Hayek (1899–1992). Hayek viewed human evolution as having prepared us to live in small groups at the hunter-gatherer stage of development. He thought there had been too little time and too few generations for much further development of the human brain by evolutionary means. Thus, economic "rationality" was often Pleistocene rationality.

In his 1989 Presidential address to the American Economics Association, he summarized his understanding of markets and the role of theory. He argued that the market is a profoundly subtle information aggregation device. The market contains more information than any one individual could. Further, the market is "a more efficient mechanism for digesting dispersed information than any that man has deliberately designed" (Hayek, 1989, p. 7). As a result, the market efficiently coordinates economic activity, and does so without needing government intervention. Hayek's focus on the informational properties of markets is a natural outcome of viewing economic activity in an evolutionary manner, as evolution is an information parsing process.

For example, Hayek argues that one cannot determine a particular equilibrium price except through markets. He further contended that social sciences and natural sciences both deal with structures of essential complexity. Human

sciences like economics study phenomena of organized complexity as opposed to the unorganized complexity in physics. As a result, we cannot replace models involving individual elements with statistical data. Instead, we must pay attention to fluctuations from equilibrium and to diversity, as these produce the evolutionary dynamics in human and non-human systems.

Hayek's thinking about economic theory is clearly based on evolutionary reasoning. He claims that while we cannot predict the outcome of set of interactions, we can make useful statements about the direction of change. In other words, while only some properties can be predicted by theory, one is still able to produce falsifiable propositions. To expect more than this results in charlatanism (p. 7): "To act on the belief that we possess the knowledge and the power which enable us to shape the processes of society entirely to our liking, knowledge which in fact we do not possess, is likely to make us do much harm." He also states that "in the social field the erroneous belief that the exercise of some power would have beneficial consequences is likely to lead to a new power to coerce other men being conferred on some authority." In an earlier paper, Hayek (1983) focused on the idea of unanticipated consequences. "We are led to do things by circumstances of which we are largely unaware" (p. 46). The mechanism he argued that produced this effect was cultural evolution at the group level instead of genetically-based Darwinian evolution. This evolutionary group selection argument concerned human institutions – groups which adopted the rules of private property, honesty and family prospered and multiplied, displacing other groups. Even though some political and religious leaders have advocated social organizations opposed to private property and the family, these institutions have survived, while those organizations opposed have seldom lasted more than a century. This is natural selection at work, albeit cultural Lamarckism. Kelm (1997) is a recent Darwinian analysis of instutitonal evolution.

Hayek used evolutionary principles throughout the body of knowledge he developed, with special focus on the information flowing through markets. Rather than simply thinking of the economy as being at a static equilibrium, he examined the evolutionary processes that move the economy between equilibria.

Paul Anthony Samuelson

Among the many scientific contributions of Paul Samuelson (1915–), perhaps his most important – at least in terms of the literature it generated – is the introduction in 1958 of the overlapping generations model. A demonstration of the impact of the overlapping generations model is the 504 page graduate textbook by Azariadis (1993) which is entirely based on this approach. The overlapping generations model originally appeared in the ecological literature in an analysis of multiple species by Leslie (1945), though Samuelson was not influenced by Leslie's work and developed the model *sui generis*. Samuelson was, however, keenly aware of the analysis of population dynamics in Alfred Lotka's *Elements of Mathematical Biology* (1956) as well as in Lotka's earlier journal articles, and maintained a correspondence with Lotka (Samuelson, 2000).

In the overlapping generations model, Samuelson showed that a primary reason for loans between individuals is that young people desire to save, while the old seek to convert their savings into consumption during retirement. Through this arrangement, Samuelson finds "a biological rate of interest equal to the rate of population growth" (p. 474). This insight brought demographics, and more generally, biology, into macroeconomics after the model was extended to include production by Peter Diamond in 1965. The primary insight that Samuelson made was that heterogeneity is fundamental for economic exchange. The notion harkens back to Adam Smith's "double coincidence of wants," but uses a scientifically rigorous method to demonstrate this claim. The biological basis for interest rates has recently been derived by Gordon Getty (1999) from a much different point of departure, showing the wide applicability of this finding.

It is not surprising that Paul Samuelson integrated biology and economics. He has contributed to the theory of population biology (Samuelson, 1974, 1978, 1983; Samuelson & Yellin, 1977; Yellin & Samuelson, 1974), and has advocated the use of biological methods in economics (1993, 1985). In particular, Samuelson has sought to re-incorporate demography into economic models, writing that "Population analysis is at the intersection of social science and biology. Once upon a time, throughout the heyday of classical economics, demography belonged to political economy" (1985, p. 166). He laments that neoclassical economics has "removed population as a variable" subject to analysis, and that economists are far from a "satisfactory state of knowledge in these between-discipline domains" (p. 167–168). Samuelson fully understands that the development of the biological foundations in economics will be impeded by those wedded to traditional methods. Ultimately, Samuelson drolly observed, knowledge advances "funeral by funeral."

Influences from Economics to Biology

One of the fundamental principles in biology is scarcity. Michael Ghiselin (1974), following Linneaus (1751), calls this "the economy of nature." Because of scarcity, the natural economy is competitive. This is the essence of natural selection – the more efficient species in a given environment survive. Just as recessions have a "cleansing" effect on the economy by causing inefficient firms to go extinct, environmental changes lead some species into extinction and others to ascendancy. It is in this sense that heterogeneity has an adaptive advantage. Just-in-time production processes and the wild boar are presumably both adapted to their particular niches. A change in the economic environment may cause a variant of a production "species" to have a differential survival advantage. Entrepreneurship is precisely niche-seeking.

Technically, both economics and biology are concerned with optimization (e.g. of fitness, or profits, or utility) under environmental constraints (e.g. predators, or crowding, or budgets, or a given market structure). In addition, biological entities from genes to species behave strategically, opening up biological modeling to game-theoretic methods. For example, Ridley (1995) documents male chimpanzees preferentially hunting for large game and sharing it with other members of their troop after the successful hunter first eats his fill. Subsequently, while the other males are eating, the successful hunter seeks to have sexual liaisons with the female partners of the other males. Female chimpanzees acquiesce to these liaisons since hunting prowess is a strong signal of desirable qualities in a mate, viz., the ability to provide resources, which makes the successful hunter a valued mate. This example also illustrates a division of labor in the natural economy. The division of labor occurs within organisms, among organisms, and within societies.

The chimpanzee behavior described above is explicitly strategic, and therefore can be described in game-theoretic terms. The first application of game theory to biology was Lewontin (1961), with subsequent important work by Maynard Smith (1972, 1982) who introduced the notion of an Evolutionarily Stable Strategy (ESS). An ESS is behavior among competing organisms that maximizes fitness in a given environment – even as other organisms adopt competing strategies. Robert Axelrod (1984) showed that a tit-for-tat strategy in a round-robin competition can support cooperative outcomes by purely selfish players. In a more general model, Hirshleifer and Martinez Coll (1988) show that tit-for-tat is less successful at maintaining cooperation in more general environments, though strategies that include punishment do sustain cooperation for a proportion of agents. This result was recently extended by Segal and Sobel (1999). The theory of kin selection developed by William Hamilton (1964) implicitly has organisms (or genes) comparing marginal benefits and costs when determining when to reciprocate cooperative behavior, just as human agents do in the cited game-theoretic models.

Robert Trivers (1972) and Trivers and Willard (1973) use explicit marginal cost-marginal benefit analysis to characterize, respectively, intrasex mate competition driven by differential parental investments in offspring, and variations in organic sex ratios as environmental resources change. These fundamental papers in sexual selection apply "economic" reasoning to explain observed animal behaviors. Such reasoning quite nicely describes the effect of selection pressures on species, organisms, and genes. At each level of biological analysis, evolution induces a constrained optimization problem representing the grand compromise of nature. Trivers (1985) also develops this line of reasoning. Nevertheless, species are designed to be attracted to not the average attributes in a mate, but the extraordinary, in order to raise the reproductive advantage of one's offspring. One indicator of this behavior is exaggerated features that indicate a mate's reproductive value, for example, extra-bright or large plumage on birds, larger wings on butterflies, and surgically enhanced breasts in human females. When mating, species of all types seek to optimize, resulting in a "red queen" effect in mate preference: each sex must evolve just to keep from falling behind.

Paul Krugman (1996) notes the close methodological correspondence between evolutionary biology and economics, writing that

> To read the real thing in evolution – to read, say, John Maynard Smith's *Evolution and the Theory of Games*, or William Hamilton's new book of collected papers, *Narrow Roads in Gene Land*, is a startling experience to someone whose previous idea of evolution comes from magazine articles and popular books. The field does not look at all like the stories. What it does look like, to a remarkable degree, is – dare I say it? – neoclassical economics.

A partial list of open issues in biology that economic theory can fruitfully be used to examine include the analysis of multi-species communities, biodiversity and ecology, a fundamental theory of the gene as an informational unit, niche-seeking as entrepreneurship driven by competition for resources, social institution formation among non-human species, and better models of population genetics and dynamics. Much of this list comes from an editorial by economist Janet Tai Landa and zoologist Michael Ghiselin (1999), co-editors of the *Journal of Bioeconomics* which debuted in 1999. This journal seeks to promote the synthesis between economics and biology by providing a forum for the bi-directional transfer of ideas. Landa and Ghiselin's stated goal is "extending and integrating economics and biology" (p. 10). This is an important step toward the fusion that is now occurring between these two fields. An early example of this synthesis is Gordon Tullock's (1971) analysis of foraging by the coal tit. In the next two sections, the morphology of this emerging synthesis will become clear.

EPISTEMOLOGY AND METHODOLOGY

What is the methodology that we are advocating? Thomas Kuhn (1962) suggested an approach to understanding science using the concept of paradigms.

In the battle between conflicting paradigms, he argued that a judgment between them cannot be made on the basis of each paradigm's standards alone, as each competing paradigm will certainly be a better fit with the evaluative features of that paradigm. Judgment must be on some other basis. In postmodern times, we have some who question the existence of objective reality, and interpret Kuhn's ideas to imply that all scientific knowledge is a social construct, and therefore relativistic. Quite simply there is no difference in this view between scientific knowledge and knowledge in nonscientific areas, such as music or art.

Other approaches to understanding knowledge lead to similar reinterpretations of the status of scientific knowledge. In the hermeneutic approach to knowledge, understanding is embodied in language communities, and meaning is only shared within that community. The idea of external, objective referents is outside this view of knowledge. In the deconstruction movement, meaning is in the mind of the reader of a "text," and there is again no relevance for external, objective references of the sort required for a science. In these approaches to the meaning of truth and knowledge, the difference between science and non-science is not a sharp qualitative divide, as argued by Popper (1959), as constituting statements that are potentially falsifiable by observation of an external reality. The existence of external reality is in fact either denied, or at least a contentious idea in these newer philosophical schools.

This raises the issue of the basis of knowledge in economics. Evolutionary analysis provides an answer to this fundamental question. Epistemological logic is the foundation upon which one can assert that a claim is true. *Evolutionary epistemology* – based in substantial part on the work of Karl Popper – developed over the past forty years to provide serious answers to this question; answers that underpin economic analysis. Popper posited that every organism has inborn reactions or responses, which are often, though not always, appropriate to expected situations. For these reactions to have survived, they must have been advantageous more often than not. "One of the most important of these expectations is the expectation of finding a regularity" (1959). This argues for two claims, linking evolutionary biology and epistemology. First, surviving organisms will come to embody models of the external reality that reflect important regularities of the environment. There would be no basis for these models without such an external reality, and some degree of regularity in it. Second, there is an inborn propensity to find regularities in the environment, and it is likely that our approach to learning reflects this expectation.

On 15 November, 1960, Popper presented what is known as the three worlds approach, the three worlds being the external world of reality, the world of sensations, and the internal world of mental models. He linked this approach to biology, providing support for Hegel's theory of the objective mind (Radnitzky, 1987, p. 18–20). Popper (1984) wrote that

> The main task of the theory of knowledge is to understand it as continuous with animal knowledge; and to understand also its discontinuity – if any – from animal knowledge.

This was a break from his earlier *Logic of Scientific Discovery* (1959), which defined scientific knowledge with the demarcation criterion: a statement is scientific if it is, at least in principle, falsifiable. All other statements are non-scientific.

Popper proceeded to argue that scientific knowledge and prehuman knowledge are the best means to underpin epistemology. Both scientific knowledge and the biologically based cognitive structures of animals can be viewed as products of evolution. He argued that both are produced by the same Darwinian mechanism: they are both the product of blind variation and selective retention, also known as trial and error. This same process governs the biological emergence of knowledge and the growth of knowledge in science. Instead of focusing on the subjective interior experience of the individuals – beliefs and perceptions – Popper focused on the objective products of the cognition. He contended that truth lies in the outcome of tests of conjectures. "We do not know: we can only guess" (1984) This process of discovering truth must be controlled by a method involving systematic tests of external reality.

This is the basis of evolutionary epistemology, an approach to the philosophical question of the source of knowledge that employs a scientifically based answer.

The Basic Evolutionary Model of Selective Retention

The basic model in evolutionary epistemology and evolutionary economics applies a three step learning algorithm. Consider an evolving population, whether of living things, or of ideas, in which:

(1) Variation exists – a large number of "experiments" or trials take place – this may be due to random variation, or a more directed process based on mental models;
(2) Selection by a filter occurs in which designs judged to be "better" survive at a higher rate than other designs; and
(3) Retention by reproduction or memory of those selected by the filter (e.g. written records, digital bits, or tasks repeated in a work system).

This is known as the model of *selective retention*, and is the basis of any evolutionary model. It is the heart of the neo-Darwinian approach to biological evolution, and was present in the original work published by Darwin in 1859.

Is there support for this simple evolutionary approach to understanding the creation of knowledge? If all three of the factors above are not included in the process, little knowledge is learned over time due what is known as a *combinatorial explosion* (Campbell, p. 105). We illustrate this using the *British Museum algorithm*. Kurt Lasswitz (1958) wrote a science fiction story, "The Universal Library," describing how all of knowledge was being produced and codified by a collection of monkeys punching keys on typewriters. The improbability of this story is due to the way that possibilities explode with each new choice of a letter. At each step, one of 26 keys could be typed, and in the course of typing ten letters, there are $26^{10} = 1.4 \times 10^{14}$ possible combinations that could be produced by random permutations. Clearly, this number rises as one types more than ten keys. Consider the standard English sentence used in typing classes: "Now is the time for all good men to come to the aid of their country." which has 71 characters, including spaces and punctuation. Typing at random among the 37 letter and punctuation keys gives us $37^{71} = 2.2 \times 10^{111}$ possible lines of 71 characters. A simple calculation demonstrates the near impossibility of arriving at the desired sentence this way. Suppose every atom in the universe operated as a computer capable of deciding if a particular set of 71 characters were the desired sentence. Even working with maximum speed, making decisions in the time it takes a light photon to cross the nucleus of a hydrogen atom, it would, on average, take more time to find this sentence than the current age of the universe. This is an obviously futile approach to producing a Shakespeare play!

This example demonstrates that random variation alone – that is, trial and error without memory and retention of successes – cannot be the basis of knowledge, or of biological life. The process by which knowledge grows requires cumulation and maintenance of successes, if not memory of failures. Popper (1969) writes that "our knowledge grows only through the correcting of our mistakes" (p. i).

Evolution solves the problem of combinatorial explosion by solving a long sequence of small steps, rather than a global, one-shot trial such as monkeys seeking to type a Shakespeare play. Each step of the evolutionary sequence is tested by a selection filter, and the more successful trials are retained. Further, the process takes advantage of parallelism. The number of trials can be enormous, and it may only take one successful trial to avoid a large number of failed pathways.

Once a small improvement occurs, it is selected for and retained in the population. Further improvements build on this foundation. Such a sequence of small steps gradually and continually improves the fit of the selection unit – whether ideas or organisms – to a particular environment. Instead of succeeding in one large leap, the process continually climbs up the hill toward a maximum. The model of selective retention is even more important when the environment itself is changing. In this case there is no global optimum, only a constrained best approximation to the optimum. Isaac Newton (1675) understood this when he wrote in a letter to his rival Robert Hooke, "If I have seen further [than you and Descartes], it was only because I stood on the shoulders of giants."

Equilibrium or Kaizen?

One of the first explicit uses of an evolutionary approach to economic analysis is the remarkable paper by the Armen Alchian (1950). Alchian proposed a completely new class of economic models. He began by removing the unrealistic assumption of perfect competition typically used in standard economic analysis. Then, he included incomplete information, and uncertain forecasts of the future. Most radically, he dispensed with optimizing choices based on profit maximization, "where foresight is uncertain, 'profit maximization' is *meaningless* as a guide to specifiable action" (p. 211). Instead he modeled environmental adaptation through imitative and trial-and-error schemes by firms in pursuit of positive profits.

In this way, Alchian built a model of variation and (Schumpeterian) selection by the marketplace. The firms in his model seek maximum profits, but do not know the best way to achieve this. This model humbly admits that the ability to measure the implications of choices on costs and profits is imperfect, and in the face of true Knightian uncertainty (1921), models of choice under risk are vacuous. This follows because such models assume that decisions are based on a complete menu of possible actions and their related outcomes. Obviously, this is not true – innovation is the discovery of new choices not previously imagined, and the menu of alternatives is continually changing.

The standard economic model of firm choice is similar to Frederick Taylor's approach to industrial engineering. Taylor (1911) advocated engineering studies that include time and motion measurements in order to determine the unique best method of production. The job of the worker was merely to follow instructions in implementing the best method as specified by the industrial engineer. This approach to mass production delivered major benefits to American and European industry in the first half of the twentieth century, but then a better approach appeared – the Toyota Production System. This system, a set of adaptations to bank-required restructuring and inventory reductions (see Shingo, 1981, for a discussion of the system and its history) is in nearly complete opposition to Taylor's approach. Every production worker in the Toyota system has the power to change the way they work, in order to increase quality and

productivity. Instead of assuming there is a unique, identifiable maximum, the Toyota view is evolutionary: improvements in terms of the selection filter always exist, and can be found by allowing trials to occur. Each production worker trying a new approach is another trial, to be selected for its value. Instead of a few industrial engineers determining the static equilibrium production process, thousands of production workers with a wide variety of ideas are harnessed in the dynamic process of improving productivity and quality. This method is called *kaizen* in Japan. A basic result from the selective retention model is that the more diverse and numerous the trials in the first stage (the greater the variation in the initial population), the faster the process evolves.

This approach is also the basis of a method of maximizing functions without uniformly signed second-order conditions – the *genetic algorithm*. It is clear that wanting to maximize and knowing how to maximize are not the same thing, but neoclassical economics treats them identically. The difference between them is the basic difference between the usual equilibrium modeling of the firm, and an evolutionary model. Improvements must be discovered in an evolutionary model, and are not simply the result of satisfying specific marginal conditions.

In fact, if we take the problem of second-order conditions seriously, instead of assuming them away as is normally done, all the standard optimization method can guarantee is that a local optimum has been found. Optima with higher utility or profits may be attainable, but undiscoverable except through trial and error. The genetic algorithm accepts this challenge, and produces a sequence of local optima, though there is no guarantee that any of these is the global optimum even if one can prove that such a global optimum exists. Existence proofs are not necessarily constructive, while the genetic algorithm explicitly constructs local optima in a practical way. This method also applies to econometric optimization. Dorsey and Mayer (1995) show that several published nonlinear econometric models fail to find the global maxima of their respective likelihood functions. In most cases, a genetic algorithm produces quite different parameter estimates.

Alchian (1950, p. 213) uses a selection filter based on ex post realized profits, not ex ante expected profits. He assumed that firms with positive profits survive, and those with losses perish. Variations in production processes result both from chance and from explicit attempts to adapt to the environment. For either source of variation, the most important aspect of the model is the filtering and retention of successes. This occurs during interactions with the population of other firms, including competitors, suppliers and buyers. The environmental filter shapes the characteristics of the population of surviving firms. Put differently, the agents in this system attempt to solve a signal extraction problem. The environment is sending signals regarding production processes that improve profits, but the signals are noisy. No individual firm is able to solve this problem due to its complexity, but, over time, the population of firms gradually improves the ability to do so.

Is there an equilibrium to such a system? Alchian (p. 215) argues that individuals choosing actions randomly may produce outcomes that are consistent with models of perfect foresight. That is, the results generated by a genetic algorithm are often observationally equivalent to choices by agents with complete knowledge of the environmental parameters. This suggests that evolutionary models may produce outcomes identical to those predicted by standard economic models, though this is by no means certain. Blaug (1980, p. 117) calls this the Alchian thesis, "the notion that all motivational assumptions in microeconomics may be construed as as-if statements." Friedman (1953, p. 22–23) follows this path and interprets the long-run characteristics of the surviving population of firms as exactly that described by an equilibrium model of microeconomics. This is fundamentally at odds with the notion of *kaizen* and the methodological approach of much of the work employing evolutionary ideas. Nevertheless, as the next section shows, evolutionary economics has value independent of the veracity of the Alchian thesis.

THE STATE OF THE ART AND PROSPECTS FOR THE FUTURE

Let us return to Thorstein Veblen to ask where economics is headed. In his 1898 essay he states that

> The process of change in the point of view, or in the terms of definitive formulation of knowledge, is a gradual one; and all the sciences have shared, though in an unequal degree, in the change that is going forward. Economics is not an exception to the rule, but it still shows too many reminiscences of the "natural" and the "normal," of "verities" and "tendencies," of "controlling principles" and "disturbing causes" to be classified as an evolutionary science . . . it is precisely in this use of figurative terms for the formulation of theory that the classical normality still lives its attenuated life in modern economics; and it is this facile recourse to inscrutable figures of speech as the ultimate terms of theory that has saved the economists from being dragooned into the ranks of modern science.

The error in this mode of analysis lies in viewing humans as simply hedonistic calculating machines, separate from their biology. Veblen also observed that

> In all the received formulations of economic theory, whether at the hands of English economists or those of the Continent, the human material with which the inquiry is concerned is conceived in hedonistic terms; that is to say, in terms of a passive and substantially inert and immutably given human nature.

He proposes a method through which economics will be an evolutionary science,

> The later psychology, re-enforced by modern anthropological research, gives a different conception of human nature . . . [T]n the view of the science, they are elements of the existing frame of mind of the agent, and are the outcome of his antecedents and his life up to the point at which he stands. They are the products of his hereditary traits and his past experience, cumulatively wrought out under a given body of traditions, conventionalities, and material circumstances; and they afford the point of departure for the next step in the process.

The significance of Veblen's tract is his exhortation that economists return to the primary method used in biology: methodical observation of the creature under analysis, both in the laboratory and in the field. This requires that economists read the literatures in evolutionary biology, psychology, behavioral genetics, and natural history, and integrate these findings and methods into their analysis. Economists have generally preferred to behave like philosophers, sitting in towers without windows and believing that their ruminations accurately reflect the world, rather than verifying that this is so. Popper (1985) called this approach to science "the world is my dream."

Let us be clear here, the method we are advocating is a difficult and time-consuming task, especially as the literature in the natural sciences is becoming more difficult to comprehend (Hayes, 1992). It is at the same time vital to the health and continued relevance of the field of economics. As E. O. Wilson eloquently argues in his 1998 book *Consilience: The Unity of Knowledge*, there is not an economic methodology and a biological methodology, but simply a scientific methodology which embraces findings in any field that improves a theory's ability to characterize and predict behavior. The disciplinary wall between evolutionary biology and economics is entirely false. As it crumbles, both fields benefit.

A typical criticism of biologically based theories of behavior, beginning with the reaction to E. O. Wilson's book *Sociobiology* (1975), is that they are deterministic – all behaviors are evolutionarily hardwired. Wilson was subject to intense criticism, including on several occasions being pelted with tomatoes when he spoke, for seeking to demonstrate that biological factors, along with environmental cues, affect behavior. The efforts to refute Wilson's findings were led by Wilson's Harvard colleagues Stephen Jay Gould and Richard Lewontin. Their views are perfectly captured by the title of a 1984 book by Lewontin (with Steven Rose and Leon J. Kamin), *Not in our genes*. This counter-assault was more an effort to support a philosophical viewpoint, than good science. Research in the last half-century provides copious support for the biological basis of behavior – clearly not in a deterministic manner, but in the sense of a built-in repertoire of possible actions, some of which are individually idiosyncratic. If the study of the human genome has taught us anything, it is the vital importance of individual diversity. This essential Darwinian insight into human behavior has largely been ignored by economists.

A small but growing group of economists has begun to develop the modern biological basis for decision-making, including Gary Becker (1976), Jack Hirshleifer (1977), and Gordon Tullock (1979). Becker (1976) builds a model of genetic fitness and altruism in the vein of Hamilton's (1964) theory of kin selection to explain the evolutionary advantage of economic altruism. Hirshleifer (1977) use the four basic evolutionary operators, variation, inheritance, competition, and selection, to explain firm lifecycles, altruistic behavior, and the emergence of economic institutions. In introducing the basic analytical aspects of evolutionary biology, Hirshleifer advocated a return to Marshall's view of economics as a branch of biology. More generally, he states that "the social sciences can fruitfully be regarded as the sociobiology of the human species" (p. 51). All three of these trailblazers have continued since the 1970s to utilize evolutionary biology in their analysis, with Hirshleifer the most strongly committed to this approach, especially in models of conflict (e.g. Hirshleifer, 1998; Durham, Hirshleifer & Smith, 1998). Hirshleifer's objective is "to make bioeconomics a household word" (Hirshleifer, 2000). Becker continues to study human capital, fertility, and the evolution of preferences with "innate components" (Becker, 1993; Becker & Mulligan, 1997), while Tullock (1994) has contributed to evolutionary biology itself.

Another early pioneer who has used insights from evolutionary biology in economics is Vernon Smith who began the field of experimental economics when he performed his first laboratory experiments in 1956. Prominently, Smith has found significant deviations from noncooperative Nash equilibrium in experiments where participants play sequential prisoner's dilemma games with cash payoffs. Indeed, more than half of first-players in these experiments signal that they want to cooperate and share a larger payoff. After such a signal, nearly three-quarters of second-players cooperate, rather than defect and take a larger payoff but leaving the first-mover with nothing (Smith, 1997). Cooperation is not the predicted Nash equilibrium.

In related work, Smith has found deviations from theory in the "ultimatum" game where the first player has N dollars to split with player two, and player two either accepts or rejects. If the split is accepted, the proposed payment is made; if rejected, both players receive nothing. The Nash equilibrium is to offer player two $1, since player two is better off with $1 than with nothing. In the laboratory, offers less than 40% of N are almost always rejected. That is, individuals choose to punish the other player at the cost of hurting themselves (see also Fehr & Schmidt, 1999; and Fehr & Gachter, 1998). Smith and

colleagues attribute both the high levels of cooperation in sequential prisoner's dilemma games, and the desire to punish those who don't "play nice" in the ultimatum game as evidence of evolutionary imprinting (Landa, 1999). Humans are social animals because there is a survival advantage to living and cooperating in social groups. Maintenance of social order and cooperation were therefore essential to survival, and the genes that code for such activities were preferentially selected for, explaining these "irrational" behaviors. Evolutionary psychologists hypothesize that this type of "social accounting" is the reason humans evolved large frontal cortexes, including a specialized brain module to detect cheating (Cosmides & Tooby, 1995).

A genetically programmed bias to cooperate notwithstanding, the context ("environment") of exchange matters. Smith reports that in face-to-face exchanges, nearly 100% of players cooperate (Smith, 1999). Conversely, cooperation breaks down, though not completely, when payoffs increase from tens to hundreds of dollars. Inside and outside the laboratory, changing the social, institutional, and economic environments causes variations in measured levels of trust, showing that the evolutionary basis for cooperation is highly context-dependent (Zak & Knack, 2001). Adam Gifford Jr. (1999) identifies the role of evolution in forming cultural institutions that reduce cognitive costs by specifying rules for personal exchanges. Smith and Kevin McCabe are currently examining the evolutionary basis for decision-making by imaging subjects' brains while they form and execute strategies, a field they have dubbed "neuroeconomics." The goal of these functional magnetic resonance imaging studies is to develop a cognitive theory of exchange that integrates rational choice, specialized brain functions, and natural selection.

Herbert Simon, the 1978 Nobel laureate in Economics, has done related work. Simon began integrating findings from psychology to develop cognitive theories of bounded rationality based on the difficulty of making decisions in uncertain environments (see his collected works in Simon, 1997). One of the primary insights that Simon's work revealed is that individuals seldom maximize, rather they seek to "satisfice" (Simon, 1955, 1959). When satisficing, individuals seek to reach a point at which they are sufficiently happy with an outcome when using a rule of thumb to make choices. If rules of thumb are insufficient to reach a desired outcome, then Simon showed that people typically revise their expectations and therefore satisfice at an achievable outcome. Simon writes (1959, p. 263)

> Models of satisficing behavior are richer than models of maximizing behavior, because they treat not only equilibrium, but the method of reach it as well . . . (a) When performance falls short of the level of aspiration, search behavior . . . is induced. (b) At the same time, the level of aspiration begins to adjust itself downward until goals reach levels that are

practically attainable. (c) If the two mechanisms just listed operate too slowly to adapt aspiration to performance, emotional behavior – apathy or aggression, for example – will replace rational adaptive behavior.

Having a repertoire of rules of thumb for a variety of circumstances is consistent with psychological studies of behavior. For example, Cosmides & Tooby (1995) present results regarding relatively simple mathematical puzzles that most subjects had trouble calculating in the abstract, but most had no trouble with when translated into a question about social behavior. This reveals the contextual nature of decision-making rules. Context- and heredity-dependent rules of thumb are called "epigenesis" by biologists, and permit rapid solutions to commonly arising problems, preserving scarce neuro-resources for other activities.

Psychologists Daniel Kahnemann and Amos Tversky also contributed influential work integrating psychology into economic choices. In a 1979 paper in *Econometrica*, Kahnemann and Tversky introduced "prospect theory." Based on extensive laboratory studies they had done, Kahnemann and Tversky developed a substantial extension to expected utility theory where individuals value and weight various outcomes subjectively. Specifically, they found that individuals systematically overweight small probabilities and underweight moderate to high probabilities. In addition, the value of alternative outcomes depends on a reference point such that for losses, value (their analog of utility) is convex and relatively steep, while for gains it is concave and less steep. This theory predicts that people are risk-loving over losses, and risk averse over gains as the reference point shifts – as suggested by their data. Reference points are shown to shift due to diminishing sensitivity in which marginal valuations close to one's reference point are larger than marginal values far from a reference point. Models of reference point dynamics predate Kahnemann and Tversky (e.g. work by economists Harl Ryder & Geoffrey Heal, 1973; and James Dusenberry, 1949), but a fully developed theory of transmutating preferences dates to Kahnemann and Tversky (1979).

While prospect theory generated great enthusiasm and follow-up research in the 1980s, by the 1990s, little of the results have entered standard economic analysis. Rabin (1998) writes

> Over the years, economists have proffered many reasons for downplaying the relevance of behavioral research challenging our habitual assumptions . . . As the aggressive uncuriosity shown in the past toward behavioral research continues to diminish, we can look forward to focusing entirely on its substance.

Associated theories of mind have been developed recently by Matthew Rabin and coauthors (O'Donoghue & Rabin 1999a, b; Bowman, Minehart & Rabin, 1999; Rabin & Schrag, 1999; Rabin, 1993, 1994), Arthur Denzau and Douglass North (1994), Timur Kuran (1991), and Bentley MacLeod (1999). This work incorporates observed psychological findings into economic decisions, in particular, by modifying the model of the decision-making process. Specifically, Rabin uses psychological findings to include "reference levels" for consumption, loss aversion, and adaptation to new environments. Preferences such as these permit economic models to replicate experimental findings, including the endowment effect (once a good is owned, its value increases relative to the value when unowned), framing effects (when an option is presented relative to other outcomes, choices vary), and valued social goals (e.g. cooperation in public goods experiments). Denzau and North bring the psychological notion of "mind reading" or mental models (forecasting what others will do) into economics. They argue that decisions are based on perceived subjective values, not objective ones. These perceived values come from mental models built to understand the world. Such models may, if repeated feedback is available, be good approximations to objective reality, but need not be. In cases where feedback is unavailable, such mental models may have only a casual relation to reality. Kuran presents a theory of individual preference formation that depends on choices made by one's social group, with both individual and group choices jointly evolving. This construct permits errors to compound over time, producing lasting aggregate effects. MacLeod (1999) uses an evolutionarily based model of cognition as the foundation for a model of learning in noisy environments.

Psychological findings have had a significant influence on some game theorists, financial economists, and experimentalists. For example, loss aversion and reference points affect people's determination of what is "fair" in common contribution analyses (Richard Thaler, 1985; Kahnemann, Knetsch & Thaler, 1986; Rabin, 1993). Psychological factors also explain deviations from the standard theory's prediction of consumption smoothing by building in imperfect self-control (Thaler & Hersh Shefrin, 1981). Thaler, as well as financial economists such as Robert Shiller, have used biases in judgment to explain volatility in financial markets. Overconfidence, or "the law of small numbers" (Tversky & Kahnemann, 1971), indicates that individuals too heavily weight recent events, especially those from small samples, and overweight their own ability relative to others. This behavior can explain speculative booms and busts in financial markets (Thaler, 1993; Shiller, 2000). The results of evolutionary psychology have had little impact in equilibrium theory, and especially dynamic macroeconomic models upon which policy prescriptions are based (for a macroeconomic perspective, see Sargent, 1993; Day, 1987, 1989a, b).

The most promising area of strategic analysis that utilizes Darwinian principles is the field known as evolutionary game theory. Evolutionary games differ from standard pure strategy or mixed strategy approaches in that a player's success at playing the game determines his or her fitness. Evolutionary games are explicitly dynamic, and include experimentation in strategies via replicator dynamics (i.e. reproduction). In these strategy choices, a Nash equilibrium is equivalent to a learned behavior, with players occasionally choosing strategies at random (Kreps, 1990; Weibull, 1995). Some evolutionary game theorists have used fitness strategies to develop a theory of preference formation as a foundation for utility theory (Güth & Yaari, 1992; Hanson & Stuart, 1990). Explicitly biological theories of preference formation have also been developed by Roger (1994) and Rubin and Paul (1979).

Related to theories of cognition is the way that humans commit to a particular choice among alternatives. An important advance in this area blends neuroscience, psychology and economics into a coherent theory of decision execution that identifies the emotions as, in Hirshleifer's (1987) memorable phrase, "the guarantors of threats and promises." Frank (1988) develops this notion into a general theory where emotions are directly tied to choices, especially in a social context which extends the study of the emotions by Darwin (1872). For example, Frank argues that blushing upon telling a lie may be adaptive in that it constrains short-run non-cooperative behavior by signaling intentions to others. Thus, what appears to be irrational behavior at a point in time can be understood as adaptive since life itself is a repeated game. Natural selection has placed survival within a social setting as a primary adaptive mechanism affecting economic exchange. Moreover, Frank's evolutionary explanation contextualizes Herbert Simon's (1959) claim that emotions are maladaptive when making choices, i.e. at times they may be, but they are also critical to choice execution as well, especially in repeated interactions. The role of emotions as motivators for decisions is supported by findings in evolutionary psychology (Cosmides & Tooby, 2000), and among brain-damaged individuals who lack emotion and as a result cannot execute choices (Bechara, Damasio, Tranel & Damasio, 1997; Damasio, 1994).

An emerging methodology that fruitfully integrates evolution, neuroscience, and economics is known as Alife, for Artificial Life, or ACE, for Agent-based Computational Economics. Alife models have their foundation in von Neumann machines. In the 1940s, mathematician extraordinaire John von Neumann conjectured that a machine could be built that could replicate itself, complete with a full instruction book. Just as DNA is a digital code (Ridley, 2000), von Neumann understood that information is the basis for life – actual or artificial. By the 1960s, John Horton Conway was experimenting with cellular automata that simulated life and death in the celebrated Game of Life (Berlekamp, Conway & Guy, 1982). This game was essentially a checkerboard grid in which under- or over-exposure to other automata lead to death. Conway's innovation was that von Neumann machines can be profitably designed as software agents. This is

currently a very active area of research that permits researchers to observe evolutionary selection and organization in environments with high degrees of heterogeneity, i.e. more heterogeneity than can be handled analytically. The primary mode of analysis utilizes the complex adaptive systems paradigm developed by John Holland (1992), using a bottom up approach (Epstein & Axtell, 1996). The method of analysis designs a computational laboratory where alternative agent-based and institutional structures can be examined.

There are several fundamental issues that have been discovered in Alife modeling. The first is the emergence of economies as self-organizing systems without top-down control – Adam Smith's "invisible hand," Hayek's "economic order," and Schelling's (1978) macrobehavior are shown to emerge spontaneously under very general conditions. Bak (1996) identifies evolution as the fundamental organizing principle leading to spontaneous organization. Second, Axelrod (1997, 1984), Hirshleifer (1999) and many others have shown that cooperation occurs in social exchange, supported by a variety of strategies, even when mutants who always defect enter the system, as long as their number is small. Third, institutional arrangements evolve with the environment as argued would occur by Schumpeter, Alchian, and as discussed in Nelson (1995). Fourth, learning via genetic algorithms (GA) (Holland, 1975; Dawid, 1996) exploits the creation of new approaches via recombination, linkage, mutation, and selection for fitness. GA has been used to explore areas ranging from auctions (Dawid, 1999), networks (Montesinos, Garcia-Guzman & Ayuso, 1999), trading rules (Allen & Karjalainen, 1999; Dorsey, Johnson & Van Boening, 1994), and economic stagnation and growth (Arifovic, Bullard & Duffy, 1997).

Fifth, herding behavior and path dependence is shown to occur in asset markets with costly information acquisition in the work of W. Brian Arthur and coauthors at the Santa Fe Institute, a hot-bed for complexity studies that intentionally cross disciplinary boundaries with much success (Arthur, Durlauf, & Lane, 1997; Arthur, 1995, 1994, 1993, 1991). Sixth, explicit models of the distribution of genetic material over generations characterizing human population genetics reveal the impact of institutions such as marriage and divorce, and technologies such as genetic engineering on output growth (Zak, 2000; Zak, Feng & Kugler, 2000; Zak & Park, 2000a, b). In these models, biology enters explicitly, for example, impacting mate choice by including the innate evolutionarily based evaluation of a potential spouse's physical attributes and economic resources, and constraining attainable human capital via the genetic endowment from one's parents and the nurturing parents give children. Related biologically based models of fertility have been developed by zoologist Alan Grafen (1998, 2000).

The Alife literature has shown that in the limit, agents behave like *homo economicus*, but in finite samples exhibit a richer set of behaviors (Vriend, 1996). A related area of research is artificial neural networks that seek to model the distributed processing of the human brain. This work is, to date, rather speculative, but very provocative nonetheless (Arbib, 1995; Fausett, 1994). Reviews of the Alife literature can be found in special issues of *Journal of Economic Dynamics and Control* and *Computational Economics*, with introductions by LeBaron (2000), and Leigh Tesfatsion (2000a, b). Also see the often updated ACE website maintained by Leigh Tesfatsion at http://www.econ.iastate.edu/tesfatsi/ace.htm. On the power of this method, Tesfatsion (2000b) concludes that "... agent based computational modeling should one day join analytical modeling, econometrics, field study, and human subject laboratory study as a standard tool in every economist's toolkit."

CONCLUSION

Economics is an evolutionary science, only most economists have not discovered this – to their detriment. Until they do, the economics of "what if" will predominate over the economics of "is." Darwinian evolution is not an analogy or metaphor for economic analysis as argued by Hodgson (1993) and Witt (1999). Rather, economics is fundamentally concerned with human decision-making that is at its core a process dictated by the interaction of evolution and environment. What this chapter has documented is that while the adoption of this approach has waxed, waned, and is again ascending (Day, 1995), there is no reason to separate biological evolution from economic analysis – they are one and the same. Hirshleifer (1977) writes "The ... social processes studied by economics ... are not mere analogs but are rather instances of sociobiological mechanisms" (p. 17). As findings from the natural sciences enter into the purview of economists, the grounding in economic analysis in the evolution of the human species will both deepen and broaden economics to include theories of mind that lead to theories of action. That is, to do economics properly requires, in many instances, that Darwinian evolution enter explicitly into the analysis. Metaphor is simply not enough.

This viewpoint is seen as radical by most "mainstream" economists. But let us appeal one last time to Veblen who ends his 1898 essay with a similar call to action. Veblen is convinced that economists who continue to ignore advances in the natural sciences risk working with speculations rather than facts. Indeed, over one hundred years ago Veblen was convinced that

> The social and political sciences must follow the drift, for they are already caught in it.

Because the quiddity of economic analysis is human decision-making, the nascent evolutionary approach to economics recognizes, to paraphrase Theodosius Dobzhansky, that nothing in economics makes sense except in light of evolution.

Postscript: Related Graduate Programs

The research program outlined in this chapter has yet to be fully realized. One of the primary stumbling blocks is the interdisciplinary (read: interdepartmental) nature of this endeavor. There are a number of programs worth noting that explicitly combine evolutionary biology and economics in one way or another. The leading program to date is the University of Michigan's Program on Complexity which combines social science, behavioral science and computation. The new graduate program in economic system design at the Interdisciplinary Center for Economic Science at the University of Arizona combines experimental economics, operations research, computer science, and neuroeconomics. Iowa State University is currently designing a graduate program with an emphasis in complex adaptive systems that looks promising. The Santa Fe Institute, while it does not grant degrees, holds summer courses for graduate students and post-doctoral fellows in complex systems and in computational economics. UCLA is spearheading a Southern California center for Social Informatics which commences in 2001 that unites the biological and social sciences under the banner of computation, though experimental methods and field work will also be encouraged (the authors of this chapter are contributing members). The Rand Graduate School (Santa Monica, CA) teaches courses on complex adaptive systems, but does not have a complete program in this area.

There are several good programs in bioinformatics, notably at Stanford University, though these are rather far from economics as it stands today. Carnegie Mellon University's Graduate School of Industrial Administration has a flexible, rigorous program that can be designed to include interdisciplinary coursework, especially from the program in Algorithms, Combinatorics, and Optimization, as well as biology and psychology. Similarly the Center for Complex Systems Research at The University of Illinois at Champaign, Urbana has operated since 1986 and has a solid reputation. We caution, though, that these programs are focused primarily on computation rather than on human decision processes.

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