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Volume I

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Biological Economics Volume I

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Introduction

Andrew W. Lo and Ruixun Zhang

1 Foundations

This volume brings together a collection of articles that reflect the influence of biological ideas in economics. Such an undertaking was considerably more challenging than we first thought – we discovered much to our surprise that this literature is vast, spanning the disciplines of evolutionary biology, ecology, evolutionary and social psychology, economics, finance neuroscience, and even genomics. A comprehensive survey is well beyond the scope of this book (and would require several volumes); our more modest goal is to provide a representative sampling of the many strands of research that are most relevant to this exciting and dynamic field of study.

Early connections between biologists and economists can be traced back to the 19th century. Malthus (1830, Part I Chapter 1) used a simple biological argument – the fact that populations increase at geometric rates, whereas natural resources increase at only arithmetic rates (at least in the 19th century) – to arrive at the dire economic consequences that earned the field the moniker “dismal science.” Charles R. Darwin was clearly influenced by this idea and published his famous *On the Origin of Species* (Darwin 1859) subsequently, which launched the discipline of evolutionary biology.

Joseph A. Schumpeter and Armen A. Alchian were among the first economists to formally bring evolutionary ideas into the study of economic systems. Schumpeter (1947, Part I Chapter 2) argued that capitalism should be understood as an evolutionary process of continuous innovation and “creative destruction,” a concept that has taken on much greater relevance as driverless cars are poised to upend the trucking, taxi, and livery industries. Alchian (1950, Part I Chapter 3) interpreted the economic system as an adaptive process that chooses among exploratory actions generated by the pursuit of “success” or “profits.” This was completely revolutionary at the time, and eliminated the unrealistic assumption of accurate anticipations and fixed states of knowledge.

Since then, biological ideas have been brought into the study of economic behavior and systems in many ways. Sociobiology and evolutionary psychology sparked early studies of social behavior from an evolutionary perspective. Similar ideas were adopted by economists in the late 20th century in a wide range of topics including utility theory, rationality, intelligence, firms, and financial markets. These developments, in turn, inspired a new and growing literature in neuroscience and genomics attempting to trace the origins of economic behavior to their biological roots. For example, Hirshleifer (1977, Part I Chapter 4) studied the connections between economics and sociobiology comprehensively and noted their mutual influences, and Nelson (1995, Part I Chapter 5) promoted the evolutionary theorizing of economics by studying the mechanisms and implications of economic change.

2 Sociobiology, Evolutionary Psychology, and Behavioral Ecology

The first concerted attempts to apply evolutionary principles to the study of human behavior span the disciplines of sociobiology, evolutionary and social psychology, and behavioral ecology, with many interrelated connections within each of these fields.

Sociobiology

The sociobiology literature began with the notion that evolution could be applied to social behaviors such as group selection, cooperation, and altruism. Hamilton (1964, Part I Chapter 6) was the first to put forward the great insight that individual fitness is not maximized by social evolution; inclusive fitness is. Trivers (1971, Part I Chapter 7) showed how “reciprocally altruistic” behavior can be favored by natural selection even when the recipient is only distantly related to the organism performing the altruistic act. The idea that something other than the individual organism could be the fitness-maximizing unit was completely revolutionary at the time and opened new research areas that are still being explored and debated today.

In particular, multilevel selection theory (including group selection) (Wilson and Sober 1994, Part I Chapter 9) and reciprocity (Trivers 1971, Part I Chapter 7) have been used to explain a wide range of social behaviors including altruism (Alexander 1974, Part I Chapter 8; Wilson and Wilson 2007, Part I Chapter 13) and cooperation (Henrich 2004, Part I Chapter 11; Nowak 2006, Part I Chapter 12). Gintis et al. (2003, Part I Chapter 10) showed that strong reciprocity is an “evolutionarily stable strategy” (see below) under certain conditions, and they present empirical evidence supporting strong reciprocity as a schema for predicting and understanding altruism in humans.

Evolutionary Psychology and Behavioral Ecology

These ideas from sociobiology were subsequently subsumed by the fields of behavioral ecology and evolutionary psychology. Examples in the behavioral ecology literature include the study of probability matching in fish (Behrend and Bitterman 1961, Part I Chapter 14) and pigeons (Herrnstein 1961, Part I Chapter 15), risk-sensitive foraging behavior in bumble bees (Harder and Real 1987, Part I Chapter 18), the evolution of group foraging behavior (Clark and Mangel 1986, Part I Chapter 17), and the deadly competition between sibling bacterial colonies (Be'er et al. 2009, Part I Chapter 21).

Evolutionary psychology has provided many key insights into human behavior by understanding the brain’s particular capacities and limitations (Gintis 2007, Part I Chapter 20), including the economics of overexploitation of biological resources (Clark 1973, Part I Chapter 16), and intergenerational resource transfers and wealth accumulation (Arrow and Levin 2009, Part I Chapter 22). Brennan and Lo (2011, Part I Chapter 23) proposed a single evolutionary explanation for the origin of several “irrational” behaviors that have been observed in organisms ranging from ants to human subjects. This framework suggests that these derived behaviors are primitive and nearly universal within and across species. Natural selection’s invisible hand created the structure of the human mind, and the interaction of these minds is what generates, in turn, the invisible hand of economics (Cosmides and Tooby 1994, Part I Chapter 19).

3 Economic Sciences

Applications of evolution to the economic sciences cover a wide spectrum of topics, including the biological foundation of utility functions, rationality and intelligence, the dynamics of financial markets, and the theory of firms and institutions.

The Biological Foundations of Utility

Preferences are central to economic theory, yet most economists treat them as exogenous and determined by “deep parameters” that are taken as given. In contrast to this neoclassical economic pre-determinism, evolutionary arguments can explain or “endogenize” the specific forms of utility functions. Studying the biological basis of economic behavior can help determine the leading candidates from the entire slate of standard and nonstandard models of utility (Robson 2001, Part I Chapter 27).

For example, Robson’s (1996, Part I Chapter 26) seminal paper on the evolutionary origins of utility functions derived the expected utility from fixed environments and non-expected utility from random environments. Furthermore, it can be shown that evolutionarily selected agents are less averse to idiosyncratic reproductive risks than systematic reproductive risks (Zhang et al. 2014, Part I Chapter 30). The evolutionary origin of prospect theory preferences has also been considered in a model of risk-sensitive optimal foraging theory (McDermott et al. 2008, Part I Chapter 28).

Hansson and Stuart (1990, Part I Chapter 24) focused on intergenerational saving and consumption-leisure choice and concluded that preferences with maximum biological fitness given resource constraints are selected. Following this approach, Rogers (1994, Part I Chapter 25) concluded that the long-term real interest rate should equal $\ln(2)$ per generation, and that young adults should discount the future more rapidly than their elders (which is supported by casual observation of typical teenage behavior). Robson and Samuelson (2009, Part I Chapter 29) argued that aggregate uncertainty leads to higher discount rates and can push agents away from exponential discounting in an evolutionary framework.

Rationality and Intelligence

Traditional economic models almost always assume perfect knowledge of the relevant environment and a well-defined and stable system of preferences. Simon (1955, Part I Chapter 31) was the first to propose the notion of “bounded rationality,” which was meant to replace the hyper-rationality of *Homo economicus* by a more realistic *Homo sapiens* constrained by limited access to information and finite computational capacity. From an evolutionary perspective, Brennan and Lo (2012, Part I Chapter 37) and Lo (2013, Part I Chapter 38) argued that bounds on rationality and intelligence are determined by physiological and environmental constraints, and provided a simple binary choice model that illustrates how such bounds can arise.

Evolutionary arguments have also been used to explain a wide range of systematic deviations from rationality, including foraging in ants and herding in financial markets (Kirman 1993, Part I Chapter 33), overestimation by males (Waldman 1994, Part I Chapter 34), and cooperation and group selection (Bergstrom 2002, Part I Chapter 35). Burnham (2013, Part I Chapter 39)

proposed a biological foundation for several anomalies of behavioral economics by separating proximate and ultimate causation.

Maynard Smith (1984, Part I Chapter 32) summarizes important work on evolutionary game theory that was developed in the 1970s, including the concept of an “evolutionarily stable strategy” (ESS). An ESS is an equilibrium refinement of the Nash equilibrium that is stable from an evolutionary perspective: once adopted by a population, it cannot be invaded by any alternative strategy that is initially rare. Evolutionary game theory complements general equilibrium theory and, in cases of multiple equilibria, provides support for which equilibrium we might expect to see (Samuelson 2002, Part I Chapter 36).

Financial Markets

Biological ideas have also played an important role in the study of financial markets. As an alternative to the Efficient Markets Hypothesis, financial markets can be viewed within an evolutionary framework in which instruments, institutions, and investors interact and evolve dynamically according to the “law” of economic selection (Farmer and Lo 1999 Part II Chapter 2). Under this view, financial agents are highly interconnected and engaged in complex behaviors, and can therefore pose systemic risks (May et al. 2008). They compete and adapt, but do not necessarily do so in an optimal fashion. The Adaptive Markets Hypothesis (Lo 2004, Part II Chapter 6; 2012, Part II Chapter 11; 2017) reconciles economic theories based on the Efficient Markets Hypothesis with behavioral economics: the neoclassical models of rational behavior can coexist with behavioral models, and what are often cited as counterexamples to rationality – loss aversion, overconfidence, overreaction, and other behavioral biases – are, in fact, consistent with natural selection shaping human behavior over many generations and across a variety of environments.

More specifically, evolutionary principles have been used to explain the survival of the “fittest” investment strategies and traders, and their impact on market dynamics. Blume and Easley (1992, Part II Chapter 1) studied wealth flows between investors and found that fit rules need not be rational and rational rules need not be fit. In the context of trading with market orders, Farmer (2002, Part II Chapter 3) found that value investing and trend following can generate boom–bust cycles, excess and temporally correlated volatility, and fat tails in price fluctuations all of which slows the progression to efficiency. He went so far as to argue that the timescale for efficiency is years to decades. Brock et al. (2005, Part II Chapter 8) modeled the dynamical behavior of heterogeneous markets with many trader types. Kogan et al. (2006, Part II Chapter 7) showed that survival and price impact are two independent concepts, and irrational traders can have a significant impact on asset prices even when their wealth becomes negligible. Hommes and Wagener (2009) calibrated a model of complex evolutionary systems to real financial market data and laboratory experiments with human subjects. Sugihara et al. (2012, Part II Chapter 10) studied causal networks in complex ecosystems including financial markets.

Psychological and physiological effects in financial traders and stock markets have also been documented. Through links between seasonal affective disorder and depression and between depression and risk aversion, seasonal variation in length of day can translate into seasonal variation in equity returns (Kamstra et al. 2003, Part II Chapter 4). By examining daily market index returns across 26 countries, Hirshleifer and Shumway (2003, Part II Chapter 5) found that sunshine is significantly positively correlated with stock returns, which is difficult to

reconcile with fully rational price setting. In live trading sessions, fear, greed, and other emotional responses to price fluctuations cause financially ruinous biases, and it has been documented that even the most seasoned trader exhibits significant emotional response, and that successful trading behavior and emotional reactivity are negatively correlated (Lo et al. 2005, Part II Chapter 9).

Evolution of Firms and Institutions

Biological analogies in the theory of the firm can be traced back to Alchian (1950, Part I Chapter 3). Winter (1964, Part II Chapter 12) examined systematically the implications of the natural selection mechanism in firms and argued that it only supports the profit-maximization assumption under special circumstances and for a restricted range of applications. Luo (1995, Part II Chapter 14) showed that the industry converges to the same perfectly competitive equilibrium as profit maximization, even if firms behave irrationally. More recently, Darwinian ideas such as group selection have also been used to understand institutional change in history (Herrmann-Pillath 1991, Part II Chapter 13), and the selection of organizational routines and structures, social norms, and public policy (van den Bergh and Gowdy 2009, Part II Chapter 15).

4 Neuroscience, Hormones, and Genomics

Human genomics determines the structure of our brain, and the brain controls human behavior, which includes economic behavior; hence, the emerging field of behavioral genomics. In the past two decades, an enormous amount of research in biology, neuroscience, and human genomics has, in turn, been stimulated by developments in the study of economic behavior.

Neuroscience and Neuroeconomics

Progress in functional magnetic resonance imaging (fMRI) technology has made possible a series of studies on the neural basis of decision making, giving rise to the new field of “neuroeconomics.” Examples of this burgeoning literature include the anticipation and experience of monetary gains and losses (Breiter et al. 2001, Part II Chapter 16), deviations from rationality including risk-seeking and risk-aversion mistakes (Kuhnen and Knutson 2005, Part II Chapter 18), framing effects (De Martino et al. 2006, Part II Chapter 19), loss aversion (Tom et al. 2007, Part II Chapter 21), and altruistic, fair, and trusting behaviors (Fehr and Camerer 2007, Part II Chapter 20). These studies suggest that distinct neural circuits promote specific types of financial choices (Kuhnen and Knutson 2005, Part II Chapter 18), and highlight the importance of incorporating emotional processes within models of human choice (Lo and Repin 2002, Part II Chapter 17; De Martino et al. 2006, Part II Chapter 19).

These rapid developments in neuroscience provide an understanding of human decision making from a completely new perspective. Gold and Shadlen (2007) reviewed the formal, mathematical prescriptions for how to make a decision, and then identified neural substrates of decision making from experimental results. Fehr and Rangel (2011, Part II Chapter 23) described computational models of two choice problems as well as the neuroeconomic

experiments that distinguish among the different components of the model. Neural activity causally determines economic choices (Fehr and Rangel 2011, Part II Chapter 23), and emotions play a crucial supporting role even if they may not always be balanced appropriately (Bosschaerts 2009, Part II Chapter 22). This view is shared by Lo (2013, Part II Chapter 24), who pointed out that by exploring the neuroscientific basis of cognition and behavior, including fear and greed, we may be able to identify more fundamental drivers of financial crises and improve our methods of dealing with them.

Hormones

In addition to brain activity, a variety of hormones have also been associated with economic behaviors. Testosterone is known to be involved in males seeking dominance in a wide range of species, and a series of studies found that testosterone is also related to human decision making. In the context of the “ultimatum game,” men who rejected low offers had significantly higher testosterone levels than those who accepted (Burnham 2007, Part II Chapter 26), which is difficult to reconcile with the standard view of economic rationality where any positive offer should be preferred over the prospect of receiving nothing. In an investment game with potential for real monetary payoffs, risk-taking behavior correlated positively with salivary testosterone levels (Apicella et al. 2008, Part II Chapter 27). Under real working conditions on a London trading floor, a trader’s morning testosterone level predicted his day’s profitability, and his cortisol level rose with both the variance of his trading results and the volatility of the market (Coates and Herbert 2008, Part II Chapter 28). In a study of 98 young subjects on the Harvard campus, salivary testosterone levels were significantly correlated with Zuckerman’s sensation-seeking scale (Campbell et al. 2010, Part II Chapter 29).

Other hormones that correlate with economic behavior include oxytocin and dopamine. In the context of a “trust game,” higher oxytocin levels were associated with trustworthy behavior, and perceptions of intentions of trust affected levels of circulating oxytocin (Zak et al. 2005, Part II Chapter 25). Among serious tournament bridge players, the dopamine system played an important role in both advantageous and disadvantageous risk-taking behavior among men, in the context of both bridge and financial gambles (Dreber et al. 2011, Part II Chapter 30). However, no relationship was found among their female subjects.

Genomics

Nature versus nurture: it has long been a hotly debated topic as to which determines behavior, including economic behavior. Benjamin et al. (2012, Part II Chapter 35) provided an excellent review of the existing research at the intersection of genetics and economics. Twin studies suggest that economic outcomes and preferences, once corrected for measurement error, appear to be about as heritable as many medical conditions and personality traits (Benjamin et al. 2012, Part II Chapter 35). This view is supported by Barnea et al. (2010, Part II Chapter 32) and Cesarini et al. (2010, Part II Chapter 33), who found that genetic variation explains between a fifth and a third of the variance in stock market participation and asset allocation among identical and fraternal twins. Furthermore, in a game with real monetary payoffs, men with the 7-repeat allele (7R+) in the dopamine receptor *D4* gene were significantly more risk loving than 7R– men. This is consistent with previous evolutionary explanations that selection for

this allele was linked to behaviors associated with migration and male competition, both of which entail an element of risk (Dreber et al. 2009, Part II Chapter 31).

Genetic variation has also been used to explain behavioral anomalies and biases. Survey-based evidence from more than 11,000 Swedish twins demonstrated that a number of anomalies such as the conjunction fallacy, the default bias, and loss aversion are moderately heritable (Cesarini et al. 2012, Part II Chapter 34). Up to 45 percent of the variation in several investment biases including the lack of diversification, excessive trading, and the disposition effect can be explained by genetic differences after controlling for individual characteristics (Cronqvist and Siegel 2014, Part II Chapter 36). These studies suggest that the heritable variation in behavioral anomalies is partly mediated by genetic variation in cognitive ability (Cesarini et al. 2012, Part II Chapter 34), and that investment behaviors are manifestations of innate and evolutionarily ancient features of human behavior (Cronqvist and Siegel 2014, Part II Chapter 36).

5 Conclusion

Upon deeper reflection and introspection, the close connections between biology and economics should come as no surprise to anyone. After all, economics is simply the study of how one particular animal species has adapted to its environment. The opposable thumb is no more a product of natural selection than fiat money, property rights, and derivative securities. Moreover, economies are populated with people, not automatons, hence biology is inextricably linked to economic activity.

In fact, the biggest barrier between the fields of biology and economics is the “physics envy” that still pervades the economics profession (Lo and Mueller 2010). The elegant axiomatic derivations of expected utility theory, general equilibrium theory, and rational expectations models are irresistible to economists who aspire to explain 99 percent of all observable phenomenon with three laws, as physicists do. Unfortunately, biology is more complex than physics, especially human biology. As the great physicist Richard Feynman explained succinctly, “imagine how much harder physics would be if electrons had feelings.”

Our hope in putting together this volume is to stimulate greater collaboration between biology and economics – both fields will be the richer from such engagement. Biology is messier and not nearly as mathematically precise as physics, but it is a much closer cousin of economics and has a logic and aesthetic of its own. To paraphrase Dobzhansky, nothing in economics makes sense except in the light of human biology.

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