In the light of evolution VIII: Darwinian thinking in the social sciences

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Darwinian thinking in the social sciences was inaugurated by Darwin himself in *The Descent of Man and Selection in Relation to Sex* (8, 9). Despite various misappropriations of the Darwinian label, true Darwinian thinking continued in the social sciences. However, with the advent of evolutionary game theory (10) there has been an explosion of Darwinian analysis in the social sciences. And it has led to reciprocal contributions from the social sciences and mathematics to biology. The theory of games had been created (11) as a theory of interaction among rational agents with a (tacit) presumption of common knowledge of rationality. Evolutionary game theory broadened the scope of game theory by removing the rationality assumption, and replacing it with an adaptive dynamics of differential reproduction. Social scientists soon saw that a whole array of other broadly adaptive dynamics of imitation, social learning, inductive reasoning with best response, and so forth, were relevant and could be analyzed with similar tools (12).

Evolutionary game theory was brought to the fore by Maynard Smith (10), but its origins go back earlier, even to Darwin himself (8, 9). The idea of an evolutionarily stable strategy of Maynard Smith and Price (13) derives from the "unbeatable strategy" that Hamilton used in his analysis of sex ratios (14). Hamilton's analysis is explicitly game theoretic. The payoff—in expected grandchildren—of a sex ratio strategy depends of the strategies of all of the rest of the population. This is a playing-the-field game in Maynard Smith's terminology. Hamilton builds on the reasoning of Fisher (15) in explaining human sex ratios. Under reasonable assumptions, differential reproduction drives the sex ratio toward that empirically observed. Fisher quotes Darwin from the second edition of the *Descent of Man* (9), where Darwin says that the problem was unsolved. However, in the first edition (8), Darwin gives essentially Fisher's argument (16). Darwin had, in a way, invented evolutionary game theory. The idea had to wait until the present to come full flower.

Evolutionary game theory was initially seen by some social scientists as just a way to provide a low rationality foundation for high rationality equilibrium concepts. A Nash equilibrium is a rest point of a large class of adaptive dynamics. If the dynamics converges to a rest point, it converges to Nash. This may not happen in all games, but it may happen in large classes of games, depending on the dynamics in question.

However, another idea from evolutionary biology shows that the dynamical point of view can be more subversive. That is the idea of population structure. Interactions are not always best modeled as random encounters in a large population. There may be correlation, positive or negative, between the strategies that interact. Hamilton (17–19) and Price (20) clearly saw that such correlations lie at the basis of evolutionary explanations of both altruism and spite. Sources of such correlation for humans are central areas of concern for social sciences: interaction on a social network, homophily or heterophily in network formation, reputation and partner choice in repeated interactions, formation and dissolution of groups for collective action, and honest and dishonest signaling. All are discussed in this colloquium.

Evolution of Social Norms

It is a commonplace in the social sciences that the values that are manifest in individual decisions may reflect norms of the society in which the individual lives. Social norms themselves evolve. They exhibit both commonalities and differences across cultures. This suggests that both biological and cultural evolution—and coevolution—play a role in their explanation.

In "Bargaining and fairness" (21) Binmore discusses the evolution of fairness norms as devices for selection between multiple equilibria. Consideration of equilibrium outcomes in repeated interactions leads one to a bargaining game. This game has an infinite number of Pareto optimal equilibria. Achieving an efficient social contract requires selection among these equilibria, and fairness norms are seen as a society's way of coordinating on one of these equilibria. This, rather than enforcement of out-of-equilibrium behavior, is seen as the function of these norms. Fairness norms, however, may involve interpersonal comparisons of utility. This is true of egalitarian norms, and of the norms of proportionality suggested by Aristotle. In Binmore's account, the standards for such interpersonal comparisons themselves evolve.

Komarova (22), in an article that could equally well be in *Social Dynamics*, discusses the speed evolution of complex phenotypes in asexual populations. Initiation of new complex phenotypes may require changes in multiple genes. Accumulation of all of the requisite mutations may require crossing a fitness valley, which could take a very long time. Various factors may affect this time. For instance, spatial interaction (as modeled by a contact process) can make a significant difference. Social interaction among cells, modeled using division-of-labor games, can also accelerate the evolution of complex phenotypes. There are applications to biofilm formation and to evolution of cancer.

Christakis and Fowler (23) investigate how the formation of human social ties is sensitive to genetic differences. Sociologists have long known that humans are more likely than chance to make friends with others who resemble them phenotypically—that the process of friendship formation is homophilic. There are various possible reasons for this: One being that there is some tendency to prefer genetically similar individuals, and that genetic similarity is correlated with phenotypic similarity, so that the phenotype serves

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Box 1. In the light of evolution. In 1973, Dobzhansky (37) penned a short commentary titled, "Nothing in biology makes sense except in the light of evolution." Most scientists agree that evolution provides the unifying framework for interpreting biological phenomena that otherwise can often seem unrelated and perhaps unintelligible. Given the central position of evolutionary thought in biology, it is sadly ironic that evolutionary perspectives outside the sciences have often been neglected, misunderstood, or purposefully misrepresented. Biodiversity—the genetic variety of life—is an exuberant product of the evolutionary past, a vast human-supportive resource (aesthetic, intellectual, and material) of the present, and a rich legacy to cherish and preserve for the future. Two challenges, as well as opportunities, for 21st-century science are to gain deeper insights into the evolutionary processes that foster biotic diversity and to translate that understanding into workable solutions for the regional and global crises that biodiversity currently faces. A grasp of evolutionary principles and processes is important in other societal arenas as well, such as education, medicine, sociology, and other applied fields including agriculture, pharmacology, and biotechnology. The ramifications of evolutionary thought extend into learned realms traditionally reserved for philosophy and religion. The central goal of the "In the Light of Evolution" (ILE) series is to promote the evolutionary sciences through state-of-the-art colloquia and their published proceedings. Each installment will explore evolutionary perspectives on a particular biological topic that is scientifically intriguing but also has special relevance to contemporary societal issues or challenges. Individually and collectively, the ILE series aims to interpret phenomena in various areas of biology through the lens of evolution, address some of the most intellectually engaging as well as pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

as an indication of genotype. The authors test this hypothesis statistically. There are possible confounding factors. For instance, individuals living in the same location may be genetically similar. Using a large dataset, the authors are able to control for these factors. They establish that, overall, humans in their study do have a tendency to prefer friends who are genetically similar. Further analysis shows that for some sets of genes, for instance those involved in immune response, the tendencies run in the opposite direction.

One way of sustaining cooperation in interactions where cooperation seems problematic—such as prisoner's dilemma or public goods provision games—emerges when the interactions are repeated. Cooperative equilibria can be sustained in repeated game contexts by rewards and punishments. Kandori and Obayashi (24) provide a detailed case study in human cooperation in a setting close to theoretical models of overlapping generations of repeated games. The case under examination is a community union, a kind of labor union unique to Japan. Individuals may join or exit at any time, so that typically there are overlapping generations of membership. Existing theory called for perfect monitoring of behavior, or alternatively, construction and dissemination of reputations, to support a cooperative equilibrium. This case study led to the formulation of an overlapping generations model and to the discovery of a new equilibrium that fits the observations.

Social Dynamics

Sometimes societies and cultures change rapidly. Sometimes they more or less behave as if they are approximately in equilibrium, just as some species continue changing, whereas others remain the same. Darwinian approaches to the social sciences need to study dynamic processes of social evolution. The explanatory significance of equilibrium depends on the underlying dynamics. Is the equilibrium a rest point of a plausibly operative dynamics? Is it a local attractor? Are there many rest points, posing an equilibrium selection problem? Is there any reason to believe that the dynamics will lead to a rest point at all, rather than cycling or exhibiting even more complicated behavior? The dynamics here range from models of genetic and cultural evolution to those of individual learning.

Cressman and Tao (25) give an overview of deterministic evolutionary dynamics, beginning with the replicator dynamics. Replicator dynamics was introduced in a biological setting as a simple model of differential reproduction, but it also has a social interpretation as a simple model of differential imitation. It was originally formulated in a large one-population setting, where fitness accrues from random interactions between pairs of individuals playing symmetric (matrix) games with a finite number of strategies. This paper also treats generalizations, extensions, and alternatives. Alternative best-response dynamics and adaptive dynamics are discussed. There is a generalization to games with a continuum of strategies. There is a generalization to population games—Maynard Smith's playing-the-field games, which include the sex ratio game of Fisher and Darwin. There is a generalization to multiplayer games. Asymmetric games are treated, including those in which players have several moves in an extensive form game.

The next two papers deal with dynamics of individual learning. Erev and Roth (26) argue that human learning dynamics provides a good explanation of many of the experimental findings of behavioral economics. Subjects who learn by reinforcement will, in some kinds of games, rapidly learn to play a Nash equilibrium. However, in other kinds of games, including the infamous ultimatum-bargaining game, learning to play Nash may be difficult. Experiments are in accord with these theoretical predictions. Learning from experience tends to underweight rare events because there is less experience with them. This is in contrast to learning by description, which tends to overweight rare events. One large loss early on may keep subjects from exploring alternatives sufficiently to discover optimal actions. In general, it is easy to learn the optimal action when it gives the best payoff both on average and most of the time. These principles are applied to mechanism design, such that the desired behavior is easily and quickly learnable. Empirical case studies are given.

Fudenberg and Levine (27) also discuss learning dynamics. In contrast with the previous paper (26), this is a theoretical investigation whose focus is on the long run. Psychological studies show that in learning, recent trials count more than older ones. One model of such recency bias has recursive discounting of the past. The distant past is always there, but with small weight. A different kind of model postulates a limited memory capacity. More recent experience is more likely to be found in memory. The authors consider a model of each kind, and show how they are related. In certain conditions, for instance with a long enough limited memory, the models give related asymptotic results. This includes a kind of universal consistency, which generalizes that used in their previous work. Convergence to strict Nash equilibrium, provided that there is such in the game, is proved.

The next paper returns to evolutionary dynamics, but looks at the interplay of multiple dynamics. Creanza and Feldman (28) present a dynamical model of cultural niche construction. There are three traits: a focal trait, a trait that can alter the selection pressure on the focal trait, and a trait that affects assortative mating. Extensive simulations are used to sweep the parameter space. The model is found to be capable of exhibiting complex dynamical behavior. This includes cycles, stable polymorphisms, and simultaneous stability of oscillation and fixation. A number of applications of the model are discussed. These range from education and contraception to agriculture and animal domestication.

Levin (29) focuses on problems of collective action that are common to all social species, from humans to bacteria. Central concerns are (*i*) the creation of a public good through individual contributions and (*ii*) collective prudent management of common pool resources. These are really two sides of the same coin. Some species have solved these problems, but humans are still struggling with them on a global scale. The paper focuses on three central issues. The first is the nature of discounting the future. The second is prosociality—the extent to which individuals value the welfare of others. The final one is the nature of collective decision making. The discussion is complex. Some of the factors that make evolution of prosociality possible, such as local interaction in space and repeated interaction in time, can also make possible the evolution of spite. For humans, evolution of social norms is seen as playing a critical role.

Special Sciences

Various sciences are, of course, represented throughout this colloquium. This section includes papers with special interdisciplinary perspectives: biodemography, evolutionary political science, bioeconomics, and neuropsychology.

Wachter et al. (30) discuss evolutionary factors that shape demographic schedules. They review three main approaches, which have proceeded more or less independently. Mutation accumulation theory postulates a steady stream of mutations with age-specific effects on mortality. In a mutation-selection equilibrium, there will be more deleterious alleles that act at a later age. Stochastic vitality theory postulates a heterogeneous population impacted by stochastic shocks. Robustness to shocks changes over life history. Optimal life history theory studies the balance between factors that influence reproductive success over a lifetime. The authors prove a theorem about mutation accumulations that raises an explanatory challenge for biodemography, and discuss possible approaches for addressing it. They close by considering the prospects for combining the three different approaches.

O'Neill (31) gives a case study in cultural evolution based on policy folklists. These are lists of supposed facts that appear to be relevant to social policies. They are picked up by media, and copied, sometimes modified, and recopied over generations. Often these lists have no true foundation in reality, but have features that enhance their reproductive success as memes. He discusses both similarities to genetic evolution and relevant differences. Phenotypic plasticity, self-repair, speciation, and predation all come under consideration.

In "On the evolution of hoarding, risk-taking, and wealth distribution in nonhuman and human populations" (32) Bergstrom analyzes optimal strategies for savings in an environment with stochastic payoffs. This is a problem for both humans and some animals., Bergstrom uses squirrels stocking nuts to survive winter as his focal example. However, storing additional nuts exposes the squirrels to an additional predation risk, therefore one should not stock too many nuts. However, because winters may be long or short, the squirrels have to take their chances. The optimal gene may be one that plays a mixed strategy, producing more or less conservative phenotypes. The optimal strategy is analyzed first for long and short winters, and then for variable length winters. Finally it is shown how the analysis is impacted by the presence of a redistribution mechanism.

Morgenstern et al. (33) approach empirical phenomena of color constancy and color contrast, which are instances of the inverse problem in optics. The perceiver makes inferences to the physical state of the world based on stimuli reaching the retina that underdetermine, and sometimes seem to misrepresent, the physical state. Somehow the nervous system has evolved to use contextual information to compensate for this misinterpretation, at least in cases impacting reproductive fitness. Color constancy is a case in point. Colors originating from the same physical surfaces appear the same under different illumination even though the stimuli reaching the retina are different. The authors see this as an evolutionary adaptation. They investigate it via the dynamics of artificial neural networks. Simulated evolution leads their model neural networks to display color constancy and color contrast. A double-opponent system, similar to that found in humans and some animals, evolves.

Applications

We may have applications of general theory to a specific theoretical problem, or applications of theory to empirical phenomena, or a discussion of empirical phenomena calling for theoretical analysis. We have seen examples of all of these already in this colloquium. Here we have application of a number of dynamics of evolution and learning to signaling, application of learning with a finite level of experimentation to spread of innovation through a social network, and application of online experimentation to cultural differences in a coordination game.

Huttegger et al. (34) discuss the dynamics of signaling games. They consider replicator dynamics, replicator–mutator dynamics for large populations, finite population dynamics in the rare mutation limit, and individual reinforcement learning. These are applied to games of common interest and opposed interest and games where interests can be aligned by costly signaling. Throughout it is shown that to predict the outcome of play, it is not sufficient to rely on classical equilibrium concepts. In signaling games where perfect signaling is the unique evolutionarily stable strategy and the unique strict Nash equilibrium, equilibrium may or may not evolve and may or may not be generated by reinforcement learning. In games where no-information-transfer is the unique Nash equilibrium, replicator dynamics may never reach equilibrium, but instead result in chaotic dynamics, where signals always bear some information. In finite populations, the population may spend a substantial proportion of the time signaling, even if signaling is not a Nash equilibrium at all.

Kreindler and Young (35) study spread of innovations through social networks. Individuals play a 2×2 coordination game with neighbors on the network. There are two equilibria: Both play status quo and both play innovation. The innovation is assumed to be risk dominant. Players change, one at a time, by smoothed best response [e.g., logistic best response, softmax] to the play of their neighbors. Previous results in the literature have focused on the effect of different network topologies on the speed of diffusion. This paper derives topology-free results providing that errors (or experiments) have a large enough finite rate, and the payoff gain from innovation is large enough. Upper bounds for expected waiting times are derived, first for regular networks and then for general networks. The model is then reinterpreted as one where there is a strict best response, but the payoffs are subject to random shocks.

Jackson and Xing (36) present a comparative study across two cultures, India and United States. The experiment is conducted online using Amazon's Mechanical Turk. The game used was a coordination game—a battle-of-the-sexes game augmented by an additional strategy. There are two asymmetric pure equilibria from the battle-of-the-sexes component: Player 1 gets a lot and player 2 a little, or conversely, player 2 gets a lot whereas play 1 a little. If players coordinate on the additional strategy, they both get equal payoffs, less than a lot and more than a little. Average total winnings in most of the games were US$1; some experiments were run with higher payoffs with similar results. Overall, the majority of players chose the strategy that led to equal payoffs. However, in India a greater proportion of players than in the United States chose strategies that led, in equilibrium, to asymmetric payoffs. Strategies were presented to players as different colors. The effect of subtly suggesting strategies to players, by telling them that they are in a room corresponding to a particular strategy, is investigated.

The essays collected here cross many disciplinary lines, both between evolutionary theory and the social sciences, and between individual social sciences. They represent demography, economics, evolutionary biology, mathematics, medicine, neuropsychology, political science, sociology, and philosophy—with many of the papers being the result of collaboration of authors from different disciplines. These papers give us a representative picture of the ongoing Darwinian thinking in the social sciences.

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