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The second wave of evolutionary economics in biology

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Several core issues in economics and biology overlap substantially. At the theoretical level, these include analogies and differences among rational choice, learning, genetic evolution and cultural evolution. At the empirical level, they include the structure of decision making, its neural basis and, more generally, human nature. We illustrate here the increasingly important collaboration between economics and biology with several characteristic examples, including signaling, markets, statistical reasoning, cooperation, punishment, reputation and social norms. In contrast to the mutual borrowing of ideas during the 1970s and 1980s, we now see the joint exploration of empirical and theoretical issues by biologists and economists that constitutes a second wave of interactions between the two disciplines.

Introduction

The close analogy between rational decision making and adaptation by natural selection generated the first wave of ideas flowing from the field of economics to that of biology. Optimal foraging theory, evolutionary game theory and other specialized fields in evolutionary ecology borrowed heavily from economics. This was a surprise to economists [1], who were so inspired by evolutionary game theory [2] that they then adopted it [3–6], replacing natural selection with various learning and imitation processes. Unfortunately, although biologists and economists adopted each others' abstract tools, the interdisciplinary discourse was limited. Recently, conversation across the two disciplines has increased, spurred, in part, by provocative results from experiments in economics (e.g. [7]) and with primates (e.g. [8,9]) and other animals (e.g. [10]). New interdisciplinary fields are also arising, such as neuroeconomics (e.g. [11,12]). The joint investigation of empirical and theoretical questions of mutual interest by biologists and economists constitutes a second wave and the birth of genuine interdisciplinary collaboration.

The second wave is long overdue. The 2001 Nobel Prize in economics was awarded to Akerlof, Spence and Stiglitz, who had sparked more than a quarter of a century of research on asymmetric information in markets (situations in which some participants in an interaction have difficult-to-observe qualities that are crucial to decision making by other participants). Spence's signaling

theory [13,14], published in 1973, is essentially the same as Zahavi's [15] handicap principle [16] but presented with far more rigor (Box 1). It took biologists more than 15 years to develop a similarly rigorous theory [17], although they could have adopted it immediately from Spence. Conversely, a stronger interaction with biology would have accelerated the efforts that we discuss here to ground economic theory in a more realistic view of human nature.

Markets in biology and economics revisited

Research on markets nicely illustrates opportunities for fruitful interdisciplinary discourse. The relationship between cleaner fish and their customers, for example, demonstrates the economic principle of monopolistic competition: buyers with few alternative sources of supply will have less advantageous transactions than will those who can shop around. Cleaners live in coral reefs and have customers from the immediate neighborhood and the open sea. Local customers, for whom long-distance moves are costly, are cleaned less well than are long-range travelers, who can exert partner choice [10].

Unfortunately, biologists have frequently used the 'market' metaphor without probing deeply enough into what its use entails [16]. For example, biologists have long referred to a 'mating market'. This is a two-sided market in which one side offers eggs to be fertilized and the other sperm to fertilize them. What determines the number of sperm and the number of eggs that are produced? Neoclassical economics (the dominant school of economics during most of the 20th century) would apply its conventional market model, termed 'Walrasian' after Leon Walras (1834–1910). This model invokes the law of supply and demand, which states that, in a market economy, supply and demand should equalize over time, a process called 'market clearing'.

In many species, the supply of sperm in a population is significantly larger than that needed to fertilize all the eggs. The law of supply and demand therefore does not apply, but why not? First, a neoclassical economist would expect individuals to prefer entering the market on the side with the scarce good, here, eggs. Yet, males and females appear in approximately equal numbers in most species. If biology did not already have sex ratio theory [18,19], the failure of our economist's expectation would have led biologists to develop it. Second, our economist would suggest that, when supply exceeds demand, a female would 'sell' her eggs for sperm plus additional 'commodities', such as a nuptial gift or paternal care.

Box 1. Signaling in market and non-market economies

In biology, Zahavi [15] introduced the handicap principle (i.e. the credibility of a signal depends on its cost), which was placed on a firm, mathematical footing by others, most notably Grafen [17]. Previously, however, economists had developed a mathematically rigorous signaling theory that could have been adopted by biologists.

Education as a peacock's tail

Spence's seminal model of education as a credible signal of productivity [13] is little known in biology. Although our teachers try to convince us that education gives us the skills that we need to succeed in life, Spence argued that higher levels of education can lead to higher wages even if education fails to improve a person's productivity; education is like a peacock's tail [16].

Assume two types of workers in the population, type I with productivity 1, and type II with productivity 2, productivity being private information. Education has no impact on productivity, but the costs of education are negatively correlated with productivity, so the cost of achieving a level y of education for type I is y, and for type II it is $y/2$. Assume also an employer who believes that there is a level of education y^*, such that if $y < y^*$ then a worker's productivity is 1, and if $y \geq y^*$ then it is 2. The employer correspondingly offers the wage schedule in Figure I.

Given $1 < y^* < 2$, education level accurately signals type because workers of type I maximize their gain by choosing an education level of 0, whereas workers of type II maximize their gain by choosing an education level of y^*.

Signaling in market economies

Asymmetric information has had a dramatic impact on institutions in market economies. The chief executives of firms know more about the profitability of their firms than do stockholders, for example, and policy holders know more about their accident risk than do insurance companies. Instead of returning value as capital gains, firms pay dividends to shareholders, in spite of double taxation, as a costly but credible signal of favorable prospects, which increases share price. Insurance companies offer policies with lower premiums but higher
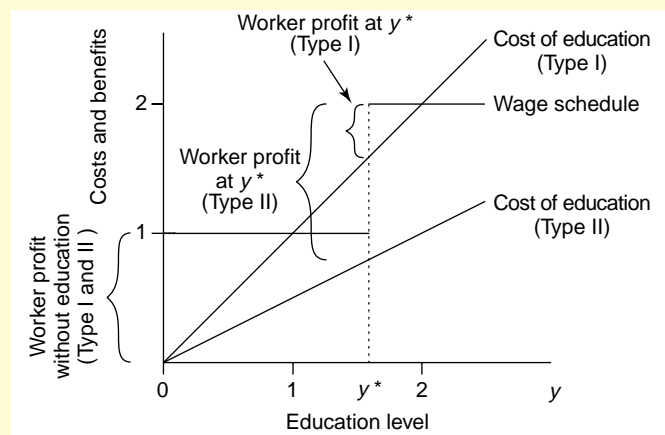

Figure I. Spence's model of education as a credible signal of productivity. Adapted, with permission, from [13].

deductibles (the amount of economic risk assumed by the policy holder) to screen policy holders into risk classes from the companies' point of view (reviewed in [53]).

Signaling in non-market economies

Signaling theory has also been invoked by human behavioral ecologists to explain institutions in non-market economies. Ironically, they were inspired, not by Spence and his colleagues in economics, but by Zahavi. The widespread distribution of valuable items, such as meat in hunter–gatherer societies, elaborately prepared food and gift items in 'big-man' societies, and potlatching (competitive feasting) by Northwest Coast Indians, has been interpreted as a credible signal of some private, but socially valuable quality of the distributor (reviewed in [54]).

However, only some species offer such commodities (e.g. male roadrunners offer lizards to females, apparently in exchange for sex). The reason is that, unlike trade in contemporary human market economies, animal trade is not subject to enforceable contracts. There are no police to arrest males that fail to pay what they promised for the eggs that they fertilize. Contrary to the expectation of 'traditional' neoclassical economics, biological markets will frequently not clear (i.e. supply and demand will not equalize).

Ironically, economists are now realizing that many human markets also do not clear. One of the reasons is again an inability to enforce contracts. In traditional economic models, this was not apparent because prices were determined without explicitly representing the interactions among traders. Unlike the biological modeling style, no account was given of who meets whom, what the traders know, and how they settle on a transaction. The new, post-Walrasian market theory, however, is different. Its assumptions include the incomplete nature of contracts (what biologists would refer to as the potential for cheating) and the limited information of traders. In recent post-Walrasian models of labor markets, credit markets and markets for goods of variable quality, market clearing does not occur [20,21]. Here, we see a convergence between biological and economic modeling approaches that lays essential groundwork for interdisciplinary collaboration in the second wave.

Behavioral economics: back to the roots

It is surprising that economics, a field devoted to understanding economic behavior, has recently founded a new subfield called 'behavioral economics' [22]. Results from this field present a challenge not only to economics, but also to evolutionary biology (Box 2). The inventors of classical economics, such as Adam Smith, were keenly interested in the psychology of economic agents. At a time when psychology did not yet exist as a discipline, these economists developed sophisticated psychological ideas about utility, including ideas that closely resemble the modern concepts of inequity and loss aversion (Boxes 2,3), that served as the foundation of their economic theories. With the rise of neoclassical theory, economics and psychology parted ways [23,24]. This was unfortunate because psychology was soon to develop powerful methods for exploring the properties of human decision making [25]. During the 1970s, psychologists brought their empirical methods to bear on the core assumptions of neoclassical economics and, in many cases, they found that these assumptions were incorrect.

Behavioral economics aims to return economics to its roots by grounding economic theory in rich and empirically well supported models of human psychology. It shares with the above-mentioned post-Walrasian market approach an interest in the theoretical implications of real economic agents. One of the most important aspects of

In the ultimatum game, a proposer offers a responder a fraction *s* of a fixed amount of real money put up by the experimenter. If the responder accepts *s*, the proposer gets to keep the remainder. If the responder rejects *s*, each gets 0. A rational, profit-maximizing responder would accept any *s*, no matter how small. However, in one-shot experiments with complete anonymity conducted in numerous cultures, proposers routinely offer more than 0 and, in a few societies, many responders reject even relatively generous offers [55,56].

One proximate theory explains this discrepancy by retaining the rationality assumption, but replacing the profit-maximizing utility function with a function where, for a player's given monetary payoff, their utility is maximized when inequity is minimized [57]. If $x = (x_1,...,x_n)$ is the vector of monetary payoffs, the 'inequity aversion' utility function of player $i \in \{1,...,n\}$ is given by Equation I:

$$U_i(x) = x_i - \alpha_i \frac{1}{n-1} \sum_{j \neq i} \max\{x_j - x_i, 0\} - \beta_i \frac{1}{n-1} \sum_{j \neq i} \max\{x_i - x_j, 0\}$$

[Eqn I]

where $\beta_i \leq \alpha_i$ and $0 \leq \beta_i < 1$. The second term is the utility loss from disadvantageous inequality (weighted by α_i), and the third term the loss from advantageous inequality (weighted by β_i). Given a monetary payoff x_i, player *i*'s utility is maximized at $x_j = x_i$. After empirically calibrating α_i and β_i, this function can account for players' performance in the ultimatum and similar games (but see [58]).

Genetic group selection could explain the evolution of cooperative, 'other regarding' utility functions, but even small amounts of migration hinder group selection by increasing genetic variability within-groups and reducing it between-groups. Genetic data suggest high migration rates for prehistoric women, similar to many contemporary small-scale societies [59], making genetic group selection a weak evolutionary force.

Cultural group selection, where social norms, rather than genes, are selected, is a more plausible explanation. Within-group norm variation is kept low by a naturally selected conformist tendency: immigrants abandon nonconforming norms, adopting the norms of their new group (e.g. [60,61]). Between-group competition selects for groups with norms, such as inequity aversion, that enhance group performance even at individual cost.

Another explanation for the experimental results is that ancestral humans never interacted anonymously, so we cannot have evolved to act as though reputations did not matter. Humans' 'bounded' rationality then causes many anonymous players to act as though their reputations would suffer from offering or accepting stingy offers. Fehr *et al.* [35], who favor group-selection models, respond that players react differently in games with and without anonymity, so rationality is not overly bounded. In our view, the substantial variation in game play, even within cultures, implies that there is no single explanation for the ultimatum game results. This variation might be a consequence of the lack of explicit framing (contextualization) in the experimental design of many of these games.

decision making studied by behavioral economists is probability judgments (e.g. [26]). Tversky and Kahneman [27], for example, identified what they termed the 'law of small numbers': people overestimate how probable it is that a small sample resembles the population from which it is drawn. Rabin [28] developed a simple model reflecting this error that could explain many of the curiosities seen in economic behavior. In his model, a person observes a sequence of binary signals of some underlying quality, such as a sequence of good and bad investments by a stock-fund manager that signals his competence. The signals are independent and drawn from the same distribution. This is equivalent to drawing from an urn with an infinite number of signals whose proportion corresponds to the manager's competence. In Rabin's model, the person believes, however,

that signals are randomly drawn without replacement from a finite urn of size N. This means that the person believes that the proportion of signals must balance out to the population rate by the time N signals are observed.

The gambler's fallacy, that getting heads on a flip of a coin decreases the probability of heads on subsequent flips, follows trivially from this model. More importantly, successive runs of heads are less likely if the urn is finite. This will cause the gambler to overestimate the rate of heads generated by this coin. Similarly, the competence of the stock-fund manager will be overestimated if he has a 'hot hand' and is successful two years in a row.

There is an aspect of this model that is more relevant to evolutionary biologists than is improving their finances. If this model does explain the empirical law of small numbers, what might the evolutionary explanation be? Perhaps gamblers and investors are using decision-making machinery that evolved to estimate returns from depleting patches of resources, or to estimate the probability of finding a hidden item during a search. If you hear a bird in some bushes, and you confirm that it is not in the first bush, then the probability increases that it is in the second.

Behavioral economics: new challenges to evolutionary biology

The behavioral economists who have reached out most to biology are those who study cooperation. Their findings challenge the standard view in evolutionary biology that cooperation among non-kin can be explained in terms of individual interest (Box 2). One of the best examples is the public goods game. A public good is a resource that can be freely used by everyone, such as water from the town well. Rational choice theoreticians have long wondered why public goods are produced in the first place, because free riders can benefit from them without contributing to their production and maintenance. This 'tragedy of the commons' has been observed in economics experiments. In Fehr and Gächter's public goods game [29], four anonymous participants simultaneously contribute real money, in an amount of their choosing, to a 'group project.' The experimenter then multiplies the total amount contributed, creating the public good. This good is divided equally among all players, regardless of the amount that they contributed. Subsequently, the experimenter informs participants of others' contributions. Fehr and Gächter ran this game by forming six groups of four from a pool of 24 students. After playing one round, participants were organized into new groups that played the same game. No two individuals were ever in the same group more than once. Thus, although participants acquired experience with the game in a population, they could not form individual reputations.

If fully rational participants aimed to maximize their individual monetary gain, they should contribute nothing to the group project. Yet, the mean contribution in the first round was about half of the maximum possible contribution. There were some low contributors (free riders), however, and mean contributions decreased steadily from round to round. These results are consistent with the view [30] that many participants begin the sequence of six games in a cooperative mood but continually lower their

Box 3. Behavioral and neuroeconomics

Under classical economic assumptions, stocks should yield an 'equity premium' of ~1% over government bonds because stocks are a riskier investment, requiring a premium to induce investors to hold them. Yet over the past 100 years, the premium has been closer to 7%, a discrepancy that has been termed the 'equity premium puzzle' [62,63]. Here, we discuss one of several proposed resolutions of the puzzle.

In the standard theory, utility comes from consumption, rather than money, which merely aids transactions of valued goods. Drawing upon results in psychology [64], Barberis *et al.* [65] have modified those assumptions: wealth itself, not only consumption, has utility; investors are more sensitive to losses than to gains (loss aversion); and this sensitivity is modulated by prior outcomes. Prior losses increase loss aversion, driving down stock prices, whereas prior gains decrease loss aversion, driving up stock prices. This increased stock volatility increases the stock premium charged by loss-averse investors, who value not only consumption, but also wealth itself.

Barberis *et al.*'s assumptions have received a boost from several neural imaging studies revealing that monetary gains activate brain regions that largely overlap with the 'reward' regions that are activated by pleasant tactile stimuli, cocaine and morphine (see references in [66]). One such experiment [66] reveals the importance of prior expectancies to the experience of internal 'reward' from monetary gains. Here, subjects first viewed the effects of a set of three different monetary amounts (the 'prospect') on one of three simplified roulette wheels. A spinning arrow eventually stopped on one value (the 'outcome'), which was awarded to the subject. Subjects played on good, intermediate, and bad wheels, in which US$0 was the minimum, intermediate, maximum outcome, respectively.

Neural responses to the anticipation and experience of monetary gains and losses were monitored in several projection fields of the ventral tegmental, dopaminergic neurons, including the orbitofrontal cortex, nucleus accumbens (NAc), amygdala, sublenticular extended amygdala (SLEA) of the basal forebrain, and hypothalamus. An extensive electrophysiological literature relates cell firing in such dopaminergic terminal fields to the expectation and experience of positive outcomes and, in some cases, to negative outcomes (see references in [66]).

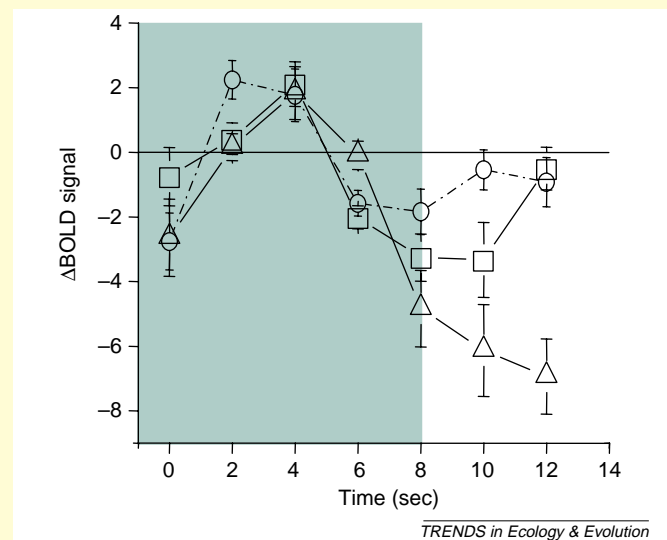Responses in the SLEA and orbital gyrus tracked the expected values

Figure I. Functional magnetic resonance imaging of the blood oxygenation level-dependent (BOLD) signal in the SLEA region of the brain. Increases in the BOLD signal are thought to correspond to increased cell firing. The first eight seconds of SLEA response (green region) were used to zero the outcome data. The white region represents the time window used to analyse outcome responses. Responses to receiving US$0 on the good wheel (triangles) decline, whereas responses to receiving US$0 on the bad wheel (squares) remain flat or increase. (Circles indicate responses to receiving US$0 on the intermediate wheel). These results illustrate the impact of prior expectancies. Reproduced, with permission, from [66].

of the prospects (Figure I), showing that prospects modulate responses to outcomes. In addition, responses to outcomes on the good wheel increased monotonically with monetary value in the NAc, SLEA and hypothalamus, lending support to the idea that, in part, utility is a function of wealth itself.

expectations about others' contributions, correspondingly reducing their own. It seems that the assumption of either rationality or a desire to maximize individual monetary gain, or both, is incorrect (Box 2).

Fehr and Gächter's experiment also had a punishment condition. In this condition, after participants are informed about the others' investments, they can each impose a cost on individuals of their choice at a lesser cost to themselves. All punishment decisions are made simultaneously. Punishment occurs frequently, with >80% punishing at least once, and approximately one third punishing more than five times during the six periods. Approximately three quarters of punishment acts were imposed by above-average contributors on below-average contributors. In this version of the game, contributions start out even higher and then increase from round to round. This is a wonderful demonstration of the role that punishment can have in inducing and stabilizing cooperation. As Boyd and Richerson pointed out [31], unlike defection in an *N*-player prisoner's dilemma, where a few defectors cause the entire group to stop cooperating, punishment can be targeted at individual defectors.

Punishing behavior correlates with the activation of brain regions associated with subjective rewards: punishing feels good [32]. These findings are an example of how the new field of neuroeconomics brings biology and economics together in the second wave (Box 3).

Two evolutionary problems arise from the observation of punishment. One is the second-order free rider problem. Whereas the first-order free rider does not cooperate, the second-order free rider cooperates but avoids the cost of punishing. In evolutionary models, second-order free riders are as deadly to cooperation as are first-order free riders. The other evolutionary problem is why, in the public goods game and other games studied by Fehr and colleagues [33], individuals punish public-good free riders in situations where they are most likely to never see them again. Any correctional effect on the free riders would be to the benefit of others, so that, in this sense, one can speak of altruistic punishment (see Box 4 for another example). Altruistic punishment and its converse, altruistic reward (also observed experimentally), have been dubbed 'strong reciprocity' [34,35].

Many people are frequently willing to both help and punish others with little regard for their personal benefit. The puzzle is how the psychological mechanisms producing this behavior evolved. Biologists must now respond to a solution proposed by economists (Box 2).

Evolutionary economics in economics

There are several strands of evolutionary thought within economics. The one that actually calls itself 'evolutionary economics' [36–38], with a journal of the same name, is inspired by the early work of Schumpeter on the role of innovation in economic change over time [39]. Schumpeter

Box 4. Altruistic punishment in indirect reciprocity

The logic of repeated games was enthusiastically adopted from economics by biologists over 30 years ago (e.g. reciprocal altruism and tit-for-tat), but, except in humans and contrary to textbook wisdom, biologists have found little evidence of it in nature [67–69]. This might be due to the complexity of the cognitive machinery necessary to implement individual recognition, book-keeping and correct attribution of 'moves' of social partners as cooperative or non-cooperative.

Indirect reciprocity (helping those who help others) is a related concept that also requires complex cognitive machinery. Following a suggestion by Alexander [70], Novak and Sigmund [71,72] showed that, under special and perhaps unrealistic circumstances, cooperation could evolve by a reputation mechanism that they called 'image scoring'. In their model, an individual's image score increases every time he/she aids an individual in need, and decreases every time he/she fails to aid an individual in need. Interactions occur in groups of moderate size so that image scores are common knowledge. Aid is costly to the donor and beneficial to the recipient. In their simplest model, the authors find that the strategy 'help those with an image score above a critical value (good reputation) and do not help those with an image score below this value (bad reputation)' occurs frequently in a long evolutionary run of a very small population.

Leimar and Hammerstein [73] pointed out that this type of 'indirect reciprocity' strategy includes an element of altruistic punishment because individuals who refuse aid to those with bad reputations nonetheless suffer a decrease in their own reputation. Thus, punishing uncooperative people involves a cost in a population playing Nowak and Sigmund's image scoring strategy. In simulations of a large population with multiple groups and some migration, all of the strategies discussed by Nowak and Sigmund fared poorly.

The economist Sugden [74] suggested a more plausible strategy for indirect reciprocity where failing to aid individuals with bad reputations does not decrease one's own reputation. In Leimar and Hammerstein's population scenario, this strategy does well and is evolutionarily stable [73].

Experiments by Milinski and colleagues investigating indirect reciprocity leave us with a puzzle similar to that raised by public goods games. Consistent with Nowak and Sigmund's evolutionarily unrealistic model, subjects' reputations suffered even when they only refused aid to those with bad reputations [75]. In this sense, they paid a price for punishing non-cooperators, with no compensating benefit.

challenged a price-centered view of economic competition with one in which innovation is brought into the picture as a major force for economic change. One of his influential arguments is that the innovative technology of a firm creates profit until competitors imitate it. The loss of profit motivates firms to innovate. This dynamic underlying economic evolution is fundamentally different from biological evolution where, for example, organisms do not have research and development departments. The modern Schumpeterian branch of evolutionary economic theory is relevant to economics but remote from biology.

A second strand incorporates behavioral ecology into economics, seeking to root human preferences and beliefs in human evolutionary history. Examples include the nature of utility and discounting the future [40], kin-related behavior and family life [41], strategies across the life course [42,43], attitudes towards risk [44] and bounded rationality [45,46]. The Nobel Prize-winning experimental economist, Vernon Smith, and colleagues have recently looked to evolutionary psychology for inspiration [47,48]. This strand involves productive interactions between biologists, economists and other social scientists.

Of particular importance to biology is the field of research in economics that explores models that relate to the replicator dynamics (a standard phenotypic model for describing Darwinian selection). In these models, players choose strategies via learning or imitation processes. The replicator equation can then be interpreted either as reinforcement learning or learning by imitation [49–51]. Thus, although there are important exceptions [52], rational choice, evolution by natural selection, and learning often arrive at the same result. This is the strongest conceptual link between economics and biology.

Concluding remarks

Recent empirical research on human behavior has uncovered facts, such as altruistic punishment (Boxes 2,4), that challenge the theoretical paradigms of economics and biology. In response to these challenges, some economists have largely retained their assumption of rationality while expanding their notion of utility to include, for instance, a desire for prosocial outcomes that value the welfare of others. Inequity aversion and fairness (Box 2), as well as loss aversion (Box 3) are examples of such expanded utility. Others have explored models of decision making that invoke bounded rationality and simple heuristics [45]. Evolutionary biologists, however, have tended to invoke a type of 'ecological rationality' that emphasizes the adaptedness of decision making in ancestral human environments. One of the fruits of the genuine interdisciplinary collaboration between economists and biologists that we call the 'second wave' will be the synthesis of these three approaches. Here, we see an important role for neurobiology in understanding the brain mechanisms that underlie decision making (Box 3). We also believe that the missed opportunities of the first wave to capitalize on economic insights, as happened with the reinvention of signaling theory (Box 1), are less likely to occur in the second wave.

Economists' renewed interest in the detailed empirical properties of individual agents has brought their style of theorizing closer to that of biologists and represents an important step towards a unified theory of animal and human behavior.

References

1 Kuhn, W. *et al*. (1995) The work of John F. Nash Jr. in game theory: Nobel Seminar, 8. *Duke Math. J.* 81, 1–29
2 Maynard Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge University Press
3 Weibull, J.W. (1995) *Evolutionary Game Theory*, MIT Press
4 Vega-Redondo, F. (1996) *Evolution, Games, and Economic Behaviour*, Oxford University Press
5 Samuelson, L. (1997) *Evolutionary Games and Equilibrium Selection*, MIT Press
6 Gintis, H. (2000) *Game Theory Evolving: A Problem-Centered Introduction to Modeling Strategic Behavior*, Princeton University Press
7 Hammerstein, P., ed. (2003) *Genetic and Cultural Evolution of Cooperation*, MIT Press
8 Hauser, M.D. *et al*. (2003) Give unto others: genetically unrelated cotton–top tamarin monkeys preferentially give food to those who give food back. *Proc. R. Soc. London B Biol. Sci.* 270, 2363–2370

9 Brosnan, S.F. and de Waal, F.B.M. (2003) Monkeys reject unequal pay. *Nature* 425, 297–299

10 Bshary, R. and Noë, R. (2003) Biological markets: the ubiquitous influence of partner choice on the dynamics of cleaner fish – client reef fish interactions. In *Genetic and Cultural Evolution* (Hammerstein, P., ed.), pp. 167–184, MIT Press

11 Glimcher, P.W. (2002) *Decisions, Uncertainty, and the Brain: The Science of Neuroeconomics*, MIT Press

12 Camerer, C. *et al.* (in press) Neuroeconomics: how neuroscience can inform economics. *J. Econ. Lit.*

13 Spence, M. (1973) Job market signaling. *Q. J. Econ.* 87, 355–374

14 Spence, M. (1974) *Market Signaling*, Harvard University Press

15 Zahavi, A. (1975) Mate selection – a selection for a handicap. *J. Theor. Biol.* 53, 205–214

16 Bowles, S. and Hammerstein, P. (2003) Does market theory apply to biology? In *Genetic and Cultural Evolution* (Hammerstein, P., ed.), pp. 153–165, MIT Press

17 Grafen, A. (1990) Biological signals as handicaps. *J. Theor. Biol.* 144, 517–546

18 Düsing, K. (1883) Die Factoren, welche die Sexualität entscheiden. *Jen. Zeitschr. Naturwissen.* 16, 428–464

19 Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press

20 Stiglitz, J. (1987) The causes and consequences of the dependence of quality on price. *J. Econ. Lit.* 25, 1–48

21 Bowles, S. (2004) Microeconomics: Behavior, Institutions, and Evolution, Princeton University Press

22 Camerer, C.F. et al., eds (2004) Advances in Behavioral Economics, Princeton University Press

23 Camerer, C. (1999) Behavioral economics: reunifying psychology and economics. *Proc. Natl. Acad. Sci. U. S. A.* 96, 10575–10577

24 Camerer, C.F. and Loewenstein, G. (2004) Behavioral economics: past, present, and future. In *Advances in Behavioral Economics* (Camerer, C.F. *et al.*, eds), pp. 3–51, Russell Sage Foundation

25 Gardner, H. (1987) *The Mind's New Science: A History of the Cognitive Revolution*, Basic Books

26 Tversky, A. and Kahneman, D. (1974) Judgment under uncertainty: heuristics and biases. *Science* 185, 1124–1131

27 Tversky, A. and Kahneman, D. (1981) The framing of decisions and the psychology of choice. *Science* 211, 453–458

28 Rabin, M. (2002) Inference by believers in the law of small numbers. *Q. J. Econ.* 117, 775–816

29 Fehr, E. and Gächter, S. (2002) Altruistic punishment in humans. *Nature* 415, 137–140

30 Fehr, E. and Fischbacher, U. (2003) The nature of human altruism. *Nature* 425, 785–791

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

32 de Quervain, D.J. *et al.* (2004) The neural basis of altruistic punishment. *Science* 305, 1254–1258

33 Fehr, E. and Fischbacher, U. (2004) Third–party punishment and social norms. *Evol. Human Behav.* 25, 63–87

34 Gintis, H. (2000) Strong reciprocity and human sociality. *J. Theor. Biol.* 206, 169–179

35 Fehr, E. *et al.* (2002) Strong reciprocity, human cooperation, and the enforcement of social norms. *Human Nat.* 13, 1–25

36 Nelson, R.R. and Winter, S.G. (1982) *An Evolutionary Theory of Economic Change*, Belknap Press

37 Nelson, R.R. and Winter, S.G. (2002) Evolutionary theorizing in economics. *J. Econ. Perspect.* 16, 23–46

38 Witt, U. (1993) *Evolutionary Economics*, Aldershot

39 Schumpeter, J.A. (1934) *The Theory of Economic Development*, Harvard University Press

40 Robson, A.J. (2002) Evolution and human nature. *J. Econ. Perspect.* 16, 89–106

41 Bergstrom, C.T. and Bergstrom, T.C. (1999) Does mother nature punish rotten kids? *J. Bioecon.* 1, 47–72

42 Kaplan, H. *et al.* (2000) A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* 9, 156–185

43 Hagen, E.H. and Hammerstein, P. (2005) Evolutionary biology and the strategic view of ontogeny: genetic strategies provide robustness and flexibility in the life course. *Res. Human Dev.* 2, 87–101

44 Robson, A.J. (1996) The evolution of attitudes to risk: lottery tickets and relative wealth. *Games Econ. Behav.* 14, 190–207

45 Gigerenzer, G. and Selten, R. (2001) *Bounded Rationality: The Adaptive Toolbox*, MIT Press

46 Hutchinson, J.M.C. and Gigerenzer, G. (2005) Simple heuristics and rules of thumb: where psychologists and behavioural biologists might meet. *Behav. Proc.* 69, 97–124

47 Hoffman, E. *et al.* (1998) Behavioral foundations of reciprocity: experimental economics and evolutionary psychology. *Econ. Inq.* 36, 335–352

48 McCabe, K.A. *et al.* (2000) Intentionality detection and 'mindreading': why does game form matter? *Proc. Natl. Acad. Sci. U. S. A.* 97, 4404–4409

49 Weibull, J.W. (1997) *Evolutionary Game Theory*, MIT Press

50 Hofbauer, J. and Sigmund, K. (1998) *Evolutionary Games and Population Dynamics*, Cambridge University Press

51 Samuelson, L. (2002) Evolution and game theory. *J. Econ. Perspect.* 16, 47–66

52 Hammerstein, P. (2001) Games and markets: economic behaviour in humans and other animals. In *Economics in Nature: Social Dilemmas, Mate Choice, and Biological Markets* (Noë, R. *et al.*, eds), pp. 1–19, Cambridge University Press

53 Riley, J.G. (2001) Silver signals: twenty-five years of screening and signaling. *J. Econ. Lit.* 39, 432–478

54 Bliege-Bird, R. and Smith, E.A. (2005) Signaling theory, strategic interaction, and symbolic capital. *Curr. Anthropol.* 46, 221–248

55 Güth, W. *et al.* (1982) An experimental analysis of ultimatum bargaining. *J. Econ. Behav. Org.*, 367–388

56 Henrich, J. *et al.*, eds (2004) *Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies*, Oxford University Press

57 Fehr, E. and Schmidt, K.M. (1999) A theory of fairness, competition, and cooperation. *Q. J. Econ.* 114, 817–868

58 Fehr, E. and Gächter, S. (2005) Human behaviour: egalitarian motive and altruistic punishment (reply). *Nature* 433, E1–E2

59 Seielstad, M.T. *et al.* (1998) Genetic evidence for a higher female migration rate in humans. *Nat. Genet.* 20, 278–280

60 Richerson, P.J. and Boyd, R. (2005) *Not by Genes Alone: How Culture Transformed Human Evolution*, University of Chicago Press

61 Rosser, J.B., ed. (2004) Evolution and altruism. *J. Econ. Behav. Organ.* 53, 1–143

62 Mehra, R. and Prescott, E.C. (1985) The equity premium: a puzzle. *J. Monet. Econ.* 15, 145–161

63 Mehra, R. (2003) The equity premium: why is it a puzzle? *Finan. Analysts J.* Jan/Feb, 54–69

64 Kahneman, D. and Tversky, A. (1979) Prospect theory: an analysis of decision under risk. *Econometrica* 47, 263–292

65 Barberis, N. *et al.* (2001) Prospect theory and asset prices. *Q. J. Econ.* 116, 1–53

66 Breiter, H.C. *et al.* (2001) Functional imaging of neural responses to expectancy and experience of monetary gains and losses. *Neuron* 30, 619–639

67 Hammerstein, P. (2003) Why is reciprocity so rare in social animals? A Protestant appeal. In *Genetic and Cultural Evolution* (Hammerstein, P., ed.), pp. 83–93, MIT Press

68 Stevens, J.R. and Hauser, M.D. (2004) Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* 8, 60–65

69 Stevens, J.R. and Hauser, M.D. Cooperative brains: psychological constraints on the evolution of altruism. In *From Monkey Brain to Human Brain* (Dehaene, S. *et al.*, eds), MIT Press (in press)

70 Alexander, R.D. (1987) *The Biology of Moral Systems*, Aldine de Gruyter

71 Nowak, M.A. and Sigmund, K. (1998) Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577

72 Nowak, M.A. and Sigmund, K. (1998) The dynamics of indirect reciprocity. *J. Theor. Biol.* 194, 561–574

73 Leimar, O. and Hammerstein, P. (2001) Evolution of cooperation through indirect reciprocity. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 745–753

74 Sugden, R. (1986) *The Economics of Rights, Cooperation and Welfare*, Blackwell

75 Milinski, M. *et al.* (2001) Cooperation through indirect reciprocity: image scoring or standing strategy? *Proc. R. Soc. London B Biol. Sci.* 268, 2495–2501