From Myopic Self-interest to Cooperative Behavior

The Calculus of Selfishness. By Karl Sigmund, Princeton University Press, Princeton, New Jersey, 2010, 192 pages, \$35.00.

A new form of game theory is quietly emerging. Pioneered by biologists William D. Hamilton and John Maynard Smith in a series of papers written during the 1960s, it was originally intended to explain the evolutionary spread of cooperative behavior in animals, such as parental investment in offspring and/ or strategic combat avoidance. In the New Year 2000 edition of *Science*, the editors listed "the evolution of cooperation" as one of the ten most challenging

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problems of the new century. Sometimes described as "game theory without rationality," evolutionary game theory replaces heretofore standard assumptions regarding competitors' ability and/or inclination to "pursue their objectives in a rational manner" with hypotheses to the effect that observed strategic behavior will persist in particular populations.

When von Neumann and Oskar Mor-genstern first formulated their groundbreaking theory, they had in mind chess, checkers, poker, and other parlor games that—like most military and economic conflicts—come equipped with clearly specified rules and objectives. They were able to demonstrate that these rules, either alone or in combination with seem-

ingly innocuous rationality assumptions, make it possible to identify highly effective (though seldom precisely optimal) strategies for all participants. Yet early attempts to apply their theory to competition in the wild—among or within species of plants and animals—were frustrated by the fact that neither the rules governing such competition nor the relevant payoff functions seem at all obvious. As a result, "game theory without specific rules and objective functions" might be a more accurate description of the new theory.

Robert Axelrod conducted some of the earliest experiments in evolutionary game theory during the late 1970s. One of them was meant to mimic biological evolution in a region populated by frequently interacting members of a single species. Each interaction took the form of a single play—or series of plays—in prisoner's dilemma, that most famous of two-person non-zero-sum games. In it, the players must decide independently whether to cooperate with one another. If both choose to cooperate, each receives a medium-sized reward *M*. If neither cooperates, each receives a smaller reward S < M. The only way to earn a large reward L > M is to effect a successful double-cross: first leading (or at least allowing) the "co-player" to expect cooperation, then failing to deliver it. The victim, in that event, receives the null reward 0 < S < M < L.

It is well established that iterative prisoner's dilemma (IPD) differs markedly from ordinary PD in that players of the iterative version accumulate experience on which to predicate decisions. For obvious reasons, strategies that do this are called "history-dependent." Tit for tat (T4T) is a particularly successful history-dependent strategy for playing IPD, having won not one but two of Axelrod's original tournaments. T4T cooperates in the first of a sequence of games; for each subsequent game it chooses whatever strategy the opponent chose in the previous game. Once play has begun, it rewards previous cooperation and punishes (promptly though not harshly) subsequent failure to cooperate. Other successful IPD strategies seem to resemble T4T in several respects, of which reciprocity and "niceness" seem to be the most important. A player using a "nice" strategy never fails to cooperate without provocation.

Rather than allowing contestants—each of whom was assigned an initial history-dependent strategy—to wander about testing those strategies against randomly chosen opponents, Axelrod required the subjects in his experiment to compete in a sequence of round-robin tournaments (meant to represent generations in a species) in which every subject interacted with every other a fixed number of times. To simulate "survival of the fittest," he arranged that the fraction of players using a given strategy in one round of a tournament would be proportional to the fraction of total reward points earned by that strategy in the previous round. He found that, after the first five rounds, one group of strategies (presumably weak ones) had lost about half its initial popularity, and another (presumably stronger) group had roughly retained its initial popularity, while a third (the high-scoring elite) was clearly gaining adherents. After 50 rounds, those trends continued. The first group was in virtual disuse and the second in visible decline, while the third seemed well on its way to eventual dominance.

For some twenty years, Karl Sigmund of the University of Vienna and others have conducted purely mathematical studies of the diffusion of successful strategies throughout a population. To that end, he and his co-workers employ systems of ordinary differential equations, known as "replicator equations," of the form

$$\dot{x}_{i}(t) = F_{i}(x(t)) = \sum_{i} F_{ii}(x(t)).$$
(1)

Here, $x_i(t) \ge 0$ denotes the fraction of the given population using strategy *i* at time *t*, $x(t) = (x_1(t), x_2(t), \dots, x_n(t))$, and $F_{ij}(x(t))$ denotes the rate at which individuals currently switch from strategy *j* to strategy *i*. The latter is positive if and only if adherence to strategy *i* is currently more profitable than adherence to strategy *j*. Obviously, the sign of $F_{ij}(x(t))$ can vary with x(t). Finally, $F_1(x) + \ldots + F_n(x) = 0$, and $F_i(x)$ is positive whenever x_i vanishes, so that x(t) may never escape from the *n*-simplex of non-negative quantities x_i such that $x_1 + \ldots + x_n = 1$. Sigmund describes several methods for constructing suitable functions $F_{ij}(x)$ from the payoff matrix *A* of a symmetric *n*-player game.

If a solution x(t), $t \ge 0$, of (1) tends to a limit x^* , then x^* is a Nash equilibrium in which a fixed non-negative fraction x_i^* of the population adheres permanently to strategy *i*, because no individual can gain by switching unilaterally to a different strategy. It is of course easy to construct arrays of functions ($F_{ij}(x)$) that cause the solutions of (1) to cycle endlessly, without approaching a fixed limit. But Sigmund finds many situations of interest in which one or more stable limits can indeed be identified. By studying the latter, he is able to propose mechanisms whereby once-exceptional animal and human behavior can become standard practice.

Early researchers in the field tended to use PD or IPD as their model for individual interactions. More recent studies employ other games in which cooperation is advantageous, yet difficult to establish. In Snowdrift, one such game, two players receive equal endowments from a benefactor, on condition that together they pay back a stipulated fraction of the benefactor's initial investment. If the required fraction is less than half the total, it pays either one of the players to assume the entire burden of repayment, should the other refuse to contribute in any way. In the laboratory, human players often refuse to assume that burden, foregoing an immediate cash reward to preserve self-respect. Replicator methods demonstrate that, if

enough individuals in the population are initially willing to make such sacrifices, cooperative behavior can overcome myopic self-interest and become commonplace if not ubiquitous.

Ultimatum, Trust, Donation, and Dictator are other two-person non-zero-sum games whose evolutionary effects are currently under investigation, both theoretically and in the lab. Sigmund describes these and related games, before launching his exposition of replicator equations, and the role of payoff matrices in their construction. Among the virtues of evolutionary game theory, at least in the eyes of its practitioners, is the ease with which theoretical results can be compared with experimental data. Sigmund's carefully annotated little volume—which includes 13 pages of references—seems an ideal introduction to this burgeoning field of (partially) mathematical research.

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