

GAME THEORY AND EVOLUTION
AN OVERVIEW

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ABSTRACT: The history of application of game theory in evolution is briefly reviewed. The concepts of equilibrium point, evolutionary stable strategies and stable points are compared. The meaning of utility theory in evolutionary models is examined and compared to classical game models.

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This conference examines two great metaphors. The first, Darwin's nineteenth century concept that species originate and change due to a process of differential survival analogous to the artificial selection used to breed domestic animals. This selective process is due to nature, that is to the effects of the inorganic and organic environment and it may operate either on the individual or upon the group, family grouping, genetic population or on a larger taxonomic grouping. This metaphor of the process of change in living things, is also examined, in terms of its validity in social change, and finally, of course, in the ways in which man's artifacts, have changed under a social and a physical environment.

The other grand metaphor that we will be examining is the theory of games. A game consists of two or more players who may make a series of moves by chance or rule. A strategy is the complete set of moves made by a player or the rule for choosing these moves. An information set governs the available moves at any stage of the game. The possible outcomes of the game have associated payoffs to each player. A solution to the game for each player is to decide on the best strategy, given the set of payoffs, and some assumptions about how the other players will behave. Game theory was introduced by Borel in 1921 (Frechet and Von Neumann 1953) and generalized by Von Neumann (1928, 1937). In these early papers the concept of a solution to a parlour game played by rational players, involved the idea that the best strategy to follow is found by looking at the lowest pay-offs to be gained from each strategy and choosing the largest of these lowest pay-offs. This minimax, or maximin, strategy was proven to be optimal in certain cases, but is not so in general. Borel made a few special cases and Von Neumann extended this for the two-person game in which winnings equal losses, that is the zero-sum game. The work of Borel and Von Neumann led on to a vast activity in this century. The metaphor was extended in two different directions. In one direction it became statistical decision theory from Wald (1939), and in the other direction, it

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culminated just at the end of the second world war, in the work of Von Neumann and Morganstern (1944, 1947) on the theory of games.

The philosophy underlying the relationship of these two great metaphors is as follows: At the level of the individual and of the population the dominant influences on genotype and phenotype are stochastic variables, that is random sequences of mating, segregation, crossing over, and gene fixation under the influences of the environment. When this entire system includes selection it becomes a learning process in the broad sense. The successful phenotypes are easily classified into "evolutionary strategies". When enough generations are considered, these stochastic processes lead to results which converge towards "optimal strategies". The methods of game theory give a short hand form of arriving at these equilibria.

In the 1950s, game theorists were searching for ways of finding the equilibrium points (Brown and Van Neumann 1950, Brown 1951, Robinson 1951, Bellman 1953). They discovered that if for instance a computer program reinvested its winnings in those strategies with which it had won, in proportion to the amount of their winnings, then the program would iterate towards the equilibrium point over many successive games. This is a direct analogy of the iterative learning process of evolution, particularly under K selection conditions. A formal proof of this is given in Hansell and Marchi (1975).

Conceptually each individual in a biological population will produce offspring in accordance with the availability of food, its efficiency in utilizing the food and its natural fecundity. If competition is free - with no spoilage of food or other negative interactions, the amount of food gained by each individual will be in proportion to the effort it exerts in obtaining it. This effort will in general be proportional to the amount of food it could utilize under unlimited supply conditions. So the number in one generation for individuals with a particular phenotype will depend upon their previous number and their fecundity as modified by food available. From any given starting density the individuals with phenotypes superior under competition conditions will grow in proportion. Thus in the case of competition between species each species will experience a gradual selection of its members towards a strategy which maximizes the number of individuals bearing superior phenotypes. This occurs in the face of the competition from other species expressing a gradual selection for those phenotypes which effectively minimize the available resource to the former species. It has been demonstrated (Hansell and Marchi 1974) that the outcome of this selection is effectively predicted by taking the maximin solution of a payoff matrix which incorporates the concept of relative value of the various biological parameters of the phenotype of each species compared to all other competitive combinations.

A new and creative concept of the solution of an evolutionary game played within a biological population was developed by John Maynard Smith (1972) and by Smith and Price (1973). Solutions based on Minimax strategies in evolutionary games are dependent upon the 'constant sum' assumption that what one player loses another wins, and indeed this may be the case at the level of entire ecosystems (Van Valen 1973) and of local K selective competition, it is patently not the case for interference competition and in many conflict situations in animal behaviour. Maynard Smith pointed out that in evolutionary terms, stability of a strategy has to do with its stability under introgression by mutant strategies. The evolutionary stable strategy (E.S.S.) does at least as well as an invading strategy in terms of competitive outcome, and when it in turn is the invader, it must out-perform the numerically dominant strategies. Specifically an organism using the strategy must do as well or better against itself than the invading strategy does against it and it must do better against the invading strategy than that strategy does against itself.

The evolutionary stable strategy has been compared to the Equilibrium point for n-person games. Nash (1951a) generalized the concept of the maximin or saddle point equilibrium of 2 person games to an n-tuple of strategies by which one player cannot increase his payoff by changing his strategy choice if other players do not change theirs. If the players are restricted to pure strategies, then such an equilibrium point need not exist, however, it was shown by Nash that if mixed strategies (that is randomizing the frequency with which different strategies are played) are permitted, then every finite game has at least one equilibrium point (Luce and Raiffa 1957). This concept has been used (Lewontin 1961) and extended in biological games (Marchi and Hansell 1973a, 1973b, 1975), but it is clearly not the same as the E.S.S. Maynard Smith (1976) points out that his definition applies only to two person encounters but the payoff to the individual depends upon the frequency with which the strategy is played in the entire population. Two points are of interest here, first, the E.S.S. conditions can certainly be reformulated to apply to an n-person non constant sum game which is equivalent to the Maynard Smith game, and secondly, if the individual can play a mixed strategy, then a Nash equilibrium point exists. If the individuals are restricted genetically to playing only a pure strategy, then the Nash equilibrium may not exist, and a direct equivalence with the E.S.S. is not possible.

An extension of the concept of the equilibrium point is found in Marchi and Hansell 1973a. Considering the evolutionary game in which speciation occurs, each new species is under competition from the original species in the community, other populations speciating from the same parental species, and other new species. It is clear that the phenotype similarities between the sister populations having the same parental population are constrained by gene flow but subject to the 'law' of limiting similarity. In other words there is a permissible subrange of stra-

tegies open to each population which is determined by the composed actions of the other players. In the case of unrelated populations, the information transferred between populations is through the environment (e.g. by food shortage etc.), rather than by direct gene flow, and the action of any one population is not directly determined by the others, but is limited, so that again there is a permissible subset of strategies available to each population. This gives rise to a generalized game which has a pi-equilibrium point.

In considering the 'parsimony' models of evolution another concept of solution to a game is applied (Marchi and Hansell 1973b). If the competition is between populations in a community, then some species will be indifferent to the outcome of local competition between others. These neutral species can be viewed as an "indifference coalition" of players, and the resulting game model can be solved for 'stable points' of undominated strategy sets (see Luce and Raiffa 1957) and for "quasi static simple" stable points (Marchi and Hansell 1973b). The idea of a coalition of species is also central to Van Valens (1973) concept of the special two person constant sum game. In the Red Queens hypothesis, Van Valen postulates that each species must evolve rapidly to maintain its relative competitive advantage. Competition is for resources which are in short supply and between each species and what may be called its 'antagonist coalition'. This game may also possess 'stable point' solutions.

Bargaining games have not been applied in biology, however in commensalism and other mutualistic evolutionary situations, they may be appropriate. It is worthwhile to examine Nash's (1951b) assumptions for his solution to the bargaining problem in order to point out the differences in the evolutionary situation. The Nash axioms are (Owen 1968):

1. Individual rationality: each player tries to maximize its utility subject to the actions of the other players.
2. Feasibility: the optimal payoffs with their associated strategies must be in the set of available payoffs and strategies.
3. Pareto optimality: all players cannot do jointly better by using other strategies.
4. Independence of irrelevant alternatives: if the feasible set of payoffs is enlarged the solution will be either the same as the old solution or else one of the new payoffs.
5. Independence of linear transformation of the utilities: essentially any measure of the payoff is as good as any other.

6. Symmetry of payoffs: if the players reverse strategies they will get the opposite payoffs.

At least three of these assumptions are seriously modified in the evolutionary case: Individual Rationality becomes equivalent to the requirement that the strategy "chosen" for play will be either a previously successful strategy or a standard genetic modification of such strategies (such as a heterozygote) or rarely a mutant strategy. When the player is a biological population 'rationality' becomes the somewhat stronger condition that strategies will be played in proportion to their previous successes.

Pareto optimality is limited in a local sense to a zone of perturbation of moves. The players cannot jointly do better within the limits of escape from local maxima. These limits will be determined by chance variations in environment or by mutation of strategy. This phenomenon is typical of many hill climbing optimization problems in which there may be many local 'hills' or 'adaptive peaks' which prevent a move to a 'global optimum'.

Symmetry of payoff is not generally applicable to games in which the individual plays against the remainder of the population (Owen 1968), indeed many games in biology are asymmetric in strategy sets, and hence the axiom does not apply (see for example, Maynard Smith and G. A. Parker 1976).

Slobodkin (1964, 1968), has pointed out that games are always played on boards or the equivalent space, while the payoffs represent winnings in an external value system. He points out that there is no such external value in biological systems, other than the ability to continue the game. However, games such as poker in which the chips have a value within the game give a good approximation to biological games. Technically the theory needs an objectively described measure of the current condition of the game in order to decide on the optimal strategy of play. This remains a prime requirement of any particular biological model: the development of a sound theory of the utility or value of the outcomes at any stage of the game. Taking an analogy from chess which is a finite two person zero sum game: aside from the expensive task of working out every possible combination of moves throughout every game, there is no general theory of how to play the next few moves. Clearly the need for a measure of value of the position to each player at any moment in the game represents a close analogy to the biological game.

The problem of assigning value to outcomes is a major problem in economics and psychology, and in this sense the evolutionist has an advantage: the problems of biology are relatively objective, survival and probability of survival are relatively tangible conditions. It is only in behavioural games, and particularly in human socio-political behaviour, that utility theory is in real difficulty due to an innate instability. The problem has been well expressed in Peter McNaughton-Smith's unpublished ob-

servation that behavioural games resemble theatrical performances more than parlour games. There is a dichotomy between the players as performers and the players as audience. The audience enters with a set of values for measuring the performance, but the actor is at liberty to induce the audience to change its values, to appreciate a new style, to set new standards. This instability of utility theory is missing from evolutionary models, in which the economics of survival set the ultimate values. Biological utilities involve individual genetic fitness, in the Maynard Smith games (1972, 1976), and the sex ratio games of Fisher (1930), Hamilton (1967, 1971) and resource allocation games Oster (197). In the Slobodkin-Rapoport games (1974), the payoff consists in survival itself. In other models (Rapoport 1956, Van Valen 1973, Marchi and Hansell 1973a, b, 1975) the payoff is in terms of the more difficult concept of population fitness.

As behavioural games are more difficult than genetic games, so evolutionary models of human cultural development are more difficult than biological evolutionary models. Indeed even the unit of information transferal in cultural development is in doubt. A first approach to this problem is given in Dawkins (1976) with the concept of the "meme". Actual game models of this process of cultural evolution remain to be developed.

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