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LEARNING AND PHONOTYPICAL ADAPTATION IN THE PROCESS OF ACHIEVING EVOLUTIONARY STABLE STRATEGIES

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Abstract. This article aims at presenting the solution of the issue of reaching the stability in various populations in a manner different that the one proposed in the natural selection theory and the game theory. In the classical game theoretical approach it was difficult to solve dynamic and multi-stage situations, through which individuals gradually improve their payoffs, and thus increase the degree of their fitness both to natural and to social environment. Therefore, in this article the tools and the methodology of evolutionary game theory, that enable to trace not only the process of stabilization but also the simultaneous emergence of cooperative structures in both types of populations has been exploited as well as that readers are familiarized with the possibility of increasing fitness through the evolution on the phenotypic level, which entails, besides general genetic factors, also taking into consideration specific environmental or social features.

Keywords: evolution, evolutionary game theory, evolutionary stable strategy, phenotype, cooperation, prisoner's dilemma, dove-hawk game.

Jel: C71; C73.

1. Introduction

The game theory since its very beginning has sought to explain and predict a behavior of rational subjects in conflict situations, when a gain of one party would be necessarily equivalent to a loss of another one (Straffin 2004). A little later, along with a development of the mathematical apparatus, it began covering in its scope also cases of interactions of cooperative nature and games played not only between individuals, but also between an individual and a society, between number of societies or even between species, their representatives and the nature (Siegfiried 2006). Its obvious limitation was therefore the strong assumption about rationality of subjects taking part in a game and making choices (Akerloff, Schiller

2009). An additional factor impeding its usage was, and still remains, an excess of information, that ought to be considered for full and thus effective predictive analysis. Furthermore, in traditional formulation of the theory, game is considered to be static. All data are fixed on the preliminary step of an analysis and since that moment data are considered to be constant. This applies not only to external conditions, which enables us to believe that we are still within the same game, but also to preferences of a rational player (Robson, Samuelson 2007), who once assessed utility of feasible possibilities, would not change these preferences (Binmore 2007; Watson 2011). This would mean that a subject designates utilities in some objective manner.

Such a definition of game prevented its usage in many areas, to which it seems to be perfectly matched. An instantaneous approach made it difficult to analyze both social and biological, and in some cases even economical phenomena. A game could not therefore capture a complexity and above all constant volatility of the context, even when the number of feasible strategies is fixed (Samuelson 2002). Besides, as it was noticed quite early, many games are repetitive in their nature, and thus it is possible to learn from the previous experience and outcomes. Iterated problems, such as the prisoner's dilemma, which itself is an interesting game, when treated as repetitive become even more complex and enable the gradual development of evolutionary theory, which recognizes the variability of subjects, firstly at the species level and secondly also in relation to particular individuals (players), including games between human subjects (Smith 1978).

Learning proved to be extremely important factor enabling analysis of the development of adaptive features in the evolutionary perspective (Nahbar 1997), but at the same time taking into account that number of features acquired by individuals do not develop through modification of genotypes. The evolution of genotype is long and expensive from the perspective of species, therefore rapid changes must, of course, take their places through some other dimension. It is obvious that it might be possible thanks to the reinforcement of adaptive traits on the phenotypic level, and through proper learning strategies it possible to establish phenotypic features and transfer them to next generations.

2. The evolutionary perspective

A proposal to adopt the evolutionary perspective comes from J. M. Smith (1982) who in his nowadays classic book *Evolution and the Theory of Games* (1982) noticed that the theory could easily be applied to analyze the adaptation of representatives of certain species in a particular environment. However, in contrast to most scholars, J. M. Smith (1982) wanted to focus not on genotype but on phenotype, which would mean that he recognized a profound relationship between fitness and features acquired through an interaction with the habitat, including representatives of own species. At the same time it is necessary to remember that both in classical and in evolutionary approaches there is no need to assume anything about intention of players. In the case of biologically defined subjects it is enough to assume that in the moment of achieving the equilibrium, one of its features is that certain beneficial (ex post analysis) characteristics are being maximized, but there is no necessity to assume that individuals "seek" the maximization, since they might not be aware of it. Therefore the evolutionary approach, as was stated by K. Binmore and L. Samuelson (2001), better reflects the complexity of the biological environment, but in some sense also the social environment. Although it cannot be forgotten that within the mathematical framework it is much easier to analyze states of equilibrium instead of sophisticated transition phases between them (Straffin 2004; Watson 2011). A change within the evolutionary framework might take place in two manners. Firstly, obviously, it is related to the principle of matching, where genes are responsible for transition of features to future generations. Secondly, it might be based on the learning principle and a cultural transmission taking place outside the genetic scheme.

Thus, starting from such premises J. M. Smith (1982) concludes that what in the classic theory is defined as a *strategy*, in the evolutionary one should be called *phenotype,* that is a set of answers to the question of what an entity would do in every possible situation it might find itself. Evolutionary stable strategy (ESS) is the one that once accepted by all (or a sufficiently large number) of representatives of a population will prevent this population from mutant strategies. Thus, if it is possible to learn from experience, such stable strategies ought to be tread as learning rules that enable gradual adjustment to the environment and through a series of trials (and mistakes) achieving a better outcome in the entire game, not only in particular competitions.

It is necessary, at least at the present stage of knowledge to distinguish between human and animal populations, because during an analysis of different assumptions on the character of these populations and possibilities of achieving the stability need to be adopted. Therefore analysis of these two groups will be based on different examples of repeated (iterated) games. In the context of human being it is obvious that individuals learn thanks to a transmission of information through generations, between members of a family and unrelated members of a society. However, learning and its rules are evolutionary (Axelrod 1984), which means that some are more efficient in approaching the equilibrium than others, and thus the efficient ones are to be adopted in populations.

The most important assumption made by J. M. Smith (1982) is to use only repeated games, because, as he stated, there is no possibility of learning without repetition. Each of individuals play number of games against other individuals or against the nature, and each game has at least one solution in terms of ESS. Generally speaking, an ESS is to adopt such a behavior that, in a long perspective, enables achieving a favorable outcome (Binmore 1998a). Thus the stability of a strategy depends on two features: a strategy acquired by an opponent or a group of opponents and features of the environment that is a context of a game. J. M. Smith (1982) distinguished games that are frequency dependent and independent, e.g. games against the particular opponent are frequency independent. Games against the nature also might be of both types, but from the evolutionary perspective the frequency dependent games are of more importance, since these games are responsible for the process of adaptation and acquiring fitness to the environment, and therefore such games enable analysis in terms of evolutionary stable strategies.

Thus it is possible to make a hypothesis that the relation between generations is not only genetic but also cultural, and therefore there must be an analogy between the evolution and the process of learning, i.e. transmission of information encoded in genes and information conveyed in phenotype. Only such a broad and more systematic analysis of the process of adaptation enables a full understanding of the complex phenomenon of social and biological evolution and thus better adjustment to variable conditions in which particular types of games are being played (Binmore 1998). Awareness of these determinants enables better understanding not only of a biological game but also an escalation of games such as neighborly conflicts or repeated bargaining problems. Analyzing the possibility of achieving stability in both these types of population I will further turn to analysis the possibility of the emergence of cooperation, especially in human populations.

Adaptation to changeable environmental conditions and at the same time improvement of both individual payoffs and payoffs of the whole population indicate not only the efficiency of some of learning strategies but also gradually lead to the emergence of the cooperation between particular individuals. Clearly the probability of particular strategies increases with its efficiency in delivering favorable outcomes in subsequent games.

The greater share of the particular strategy in the total sum of payoffs in the population, the faster and more likely it would be adopted by next individuals. Furthermore, the greater is the chance that it will become an evolutionary stable strategy in this population. In this way, without the assumption about advisability of action or tacit agreement, emerges the cooperation which is based not on a self-interest but on the choice of the best strategy in the context of choices of other members of the group. The strategy chosen and spread within the population is thus an expression of the phenotype, that is the set of features combining genotypic traits transferred through the natural selection as well as traits acquired thanks to the learning process in subsequent games (Damasio 2003, 2011).

3. Stability in animal populations – doves and hawks

To analyze the process of gaining the equilibrium in animal population, it would be proper to use a game designed specifically for the needs of the evolutionary game theory, namely the doves and hawks game. This game has several different modifications, but here I shall rely on the original formulation by J. M. Smith

(1982) and some modifications proposed by A. Dixit and B. J. Nalebuff (2008). First, before go any further in the analysis it must be noted that names of players in the game might be misleading. The purpose of the game is not to analyze any specific animal, but some logical types which are rather sets of features responsible for behavior of particular individuals. Although the game, was originally formulated as a tool in studies related to a competition of at least two species living in the same ecosystem, it is nowadays successfully used in studies on behavior in such fields as economics or politics. Extended analysis of these phenomena was published by R. Dawkins (1976, 2003) who has understood that phenotype is a crucial feature in the context of gaining stability within particular population.

To simplify the study, we can assume that individuals are fixed in such a manner, that always behave in the same way, i.e. they are always either hawks or doves and they do not change their strategy from particular competition to another, although theoretically, we might imagine a situation that would not be that simple in this aspect.

Let us imagine a situation, when two individuals compete for some good of a value (*V*), say 50. It may indicate that one of them gets defined territory in which there are large reserves of food or where it is possible to bear up offspring safely. The game is a non-zero sum game, which means that the loser does not have to bear loses corresponding to the gain of the winner. When it comes to a confrontation between two hawks, one of them wins, but the other suffers serious injuries (–100), thus the expected value of such a fight is: ½ (50) + ½ (–100) = –25. It means, that from the perspective of a species this kind of rivalry turns out to be unfavorable.

In a case of a confrontation between a hawk and a dove the situation is obviously different: a hawk gains the good (50) and a dove leaves with nothing, but at least without any harm (0). In the last of possible cases, two doves compete for the good. Here, we assume that they share the good, loosing 10 units each (15). Conclusions of the analysis might be shown in a simple matrix (Figure 1).

	Hawk	**Dove**
Hawk	(–25, –25)	(50, 0)
Dove	(0, 50)	(15, 15)

Fig. 1. Exemplary payoffs in the doves – hawks game (Dixit, Nalebuff 2008)

In order make such analysis helpful in the context of evolutionary games, it necessary to make some additional assumptions. First of all, at least partially, the behavior of particular individuals is being transmitted to future generations, i.e. is a subject of simple inheritance. Secondly, the ecosystem in this case consists only of these two species, and the existence of other is seen as negligible background that remains constant, although in real conditions it might be more complicated. Initially both populations are not stable, and only after series of competitions they stabilize in relation to each other and to the environment, assuming however that other environmental features would remain stable (Smith, Slatkin 1973). To achieve equilibrium it is thus necessary to find the evolutionary stable strategy which would ensure this. In this case it would be a mixed strategy defining a distribution of probabilities with which certain individuals ought to be in the environment.

We therefore obtain the following equation that allows us to determine the expected value and the solution of the game. In the hawk scenario we have the following outcomes: with the probability p a hawk meets another hawk and its result is -25. On the other hand it may, with the probability $1 - p$ meet a dove and then its result is 50. In the dove scenario, a dove meets a hawk with the probability p and thus gains nothing (0), but with the probability $1 - p$ meets another dove and thus gains a good worth 15 units.

$(-25)p + (50)(1 - p) = 0p + (15)(1 - p)$

$-25p + 50 - 50p = 15 - 15p$

$-75p + 15p = 15 - 50$

$-60p = -35$

$p = 7/12$

Thus, the evolutionary stable strategy, in the light of assumptions made about the value of payoffs, is a population in which the proportion of individuals bearing the hawks features are 7/12 and individuals bearing the dove features are 5/12. Such population is resistant to any mutations, which means that neither party is prone to change the strategy, because it would not allow to increase its payoffs.

Such mixed strategy based on the frequency of given strategies in the population, i.e. particular individuals. Adaptation in this context is based on a determination of a elative abundance of species in relation to another one in a way that the balance might be achieved and than sustain in the whole population. The abundance is being shaped in a relation to the environment and only secondarily to the information encoded in the genotype. It might be assumed that animals only to limited extent recognize specific individuals with which they compete for the particular good. It means that such games have features of games against random opponents. If full recognition would be possible, particular competitions would create separate games, and thus learning would be of a limited meaning.

Even if identification of particular individuals is not possible, animal is able to recognize a species and thus classify an opponent to a proper type, which enables it to apply an optimal strategy. Of course, in a literally understood game the situation is quite obvious, due to the clear separation of the roles of predators and preys (Smith, Slatkin 1973). This is quite different in human games, when it is not only possible to fully recognize opponents but also games are being played frequently enough that separating them would lead to the information chaos and thus a paralysis in the process of deciding on strategies.

4. Stability in human population – the prisoner's dilemma

The game inflames minds of researchers for many years and is one of the most often commented paradoxes in the theory of games (Malawski *et al.* 2004). It might be even said, that it becomes an element of basic knowledge about this science. It is a many–sided problem which enables to present several aspects of human behavior and also some traps of rational thinking, unless it includes the criterion of the collective rationality, which makes it possible to make decisions favorable from the perspective of a group, but not necessarily particular individuals. Although in this case it does not mean a sacrifice of an individual due to the fact, that cooperation improves payoffs of particular players, and the attempt to change the behavior when an equilibrium has already been achieved, would lead to a deterioration of outcomes of at least one of players, which roughly corresponds to the definition of the V. Pareto optimality criterion (Camerer 2006; Samuelson 2009; Adair 2010; Porter 2010).

To make the game more comprehensive, it has been accompanied with a story about two arrested and interrogated suspects. Evidences available to the police officers are weak, and detainees will go free, unless at least one of them confesses to achieve a lenient penalty. Of course, a lenient penalty for one of them means a more severe for the other. If both confess, they both will be sentenced, although the punishment will not be as severe as in the case of a single betrayal. But what is the most interesting is that, if both solitarily stay silent, they will both go free without any consequences. The game situation has been presented on the Figure 2.

	Cooperation	**Betrayal**
Cooperation	(0, 0)	(–2, 1)
Betrayal	(1, –2)	(–1, –1)

Fig. 2. Exemplary payoffs in the Prisoner's Dilemma game (Source: Dixit, Nalebuff 2008)

The game leads to the paradox, because it contradicts one of basic assumptions of the game theory, namely the dominance criterion, which states that whenever there is a dominant strategy in a game, a rational player should use it. In this case both players have such a strategy, i.e. to betray, which however consequently accepted will lead to the worst possible outcome for both players (–1, –1). If therefore instead of this criterion, known also as the criterion of individual rationality, players were to adopt the Pareto criterion, they would achieve the best score in general terms, although each of them could improve his individual payoff but decreasing at the same time the payoff of the other player. This does not change the fact that the game has no solution either in terms of pure or mixed strategies. The mathematical apparatus remains helpless in the case of this game. But the game treated as a repeated one enables analysis of the learning process of particular competitors through number of competitions. Of course, it seems to be obvious that knowing values of outcomes players should cooperate to achieve the most favorable outcome. But it is not so and during experiments only a minor part (25–30 %) of people chooses to cooperate in the first round (Camerer 2003, 2005).

In some experiments it has been proven that the most efficient strategy, i.e. allowing to obtain the highest score in sufficiently large number of repetitions, is the strategy called t*it for tat*, based on the initial trust: in the first round always cooperate, and than copy a behavior of an opponent from the previous stage (Samuelson 2005). We can already see, that this rather intuitive strategy is not the most common one among typical players. Thus, if we meet only once with each of opponents, the optimal strategy would be to betray (about 70 – 75 % of examinees), which would prevent the emergence of cooperation. What is more, even in experimental conditions people rarely cooperate, because of the lack of the basis to believe that the other side wants to cooperate.

The assumption that stands behind the result achieved by R. D. Axelrod and A. Rapoport (Axelrod 1984) is the iterated game with the same opponent, and at the same time large enough number of repetition (and frequency), which enables to use an evolutionary stable learning rules that lead to desired equilibrium. Unfortunately, in the case of human population, subsequent games rarely take place between the same opponents, and the adjustment of strategies in terms of classic evolutionary approach, based on genotype, would take more time than only one generation. Such an analysis would than be useless due to the too broad time perspective as well as too large amount of data that ought to be consider. Learning through genetics might be very costly, because it means serious and long–lasting changes in the organism that might prove to be too slow to satisfy the need for rapid response to changes in the structure of environment (Binmore, Samuelson 2006).

5. The emergence of cooperation

Yet it is undeniable that there is cooperation in human (and not only) populations. Among human population it is possible to learn on the basis of repeated interactions between the same opponent. But even when games with similar characteristics take place between different players, but is repeated sufficiently often, individuals may draw a conclusions and thus adjust their behavior to mutable conditions on the basis of this restricted in some aspects experience. This is how they can learn through analogies and how they make typologies of actual and potential opponents (Crips *et al.* 2008). Moreover, interfacing frequently enough, they will be able to draw conclusions on the frequency of particular types of individuals in the population, and thus adjust their behavior to requirement of the particular game. It is obvious here that individuals are not treated here as fixed in their types and even if we try to translate the hawk – dove game into human categories, it would not necessarily be associated with a rigid assignment of particular types to particular individuals. Of course, this makes the whole analysis much more difficult, but obviously better reflects the actual games. In such cases strategies become rather heuristics that lead to desired positive outcome not with the certainty but only with some probability.

It is worth noting that favorable from the evolutionary perspective strategies will spread in the population, because the probability of its occurrence is equal to the sum of payoffs gained thanks to the strategy in relation to the general sum of all payoffs in the population. Thus the greater share of the strategy in generating the benefits of the whole population, the more frequent it will be applied by its particular members. Of course, there are numbers of games testing the tendency to cooperate, which aims at showing how fragile is cooperation based on such a learning process. One of such games is the dictator game, which, when repeated fixed number of times, leads to a betrayal in the last competition. But if so, the second player should predict the betrayal of the opponent and betray in the previous one, etc. Thus the cooperation would never emerge, but contrary to this rational analysis it functions, although in some restricted extend, in the population and breaks down only in about seven – eight round. Notwithstanding this, R. D. Axelrod (1984) has described properties of a good ES strategy, namely it should be clear, polite, provocable and forgiving. Just as his own strategy, the tit for tat.

Such a strategy is the best answer in the situation of repeated interactions among both cooperating and non–cooperative individuals. It enables increasing gradually the sum of own payoffs together with effective acquisition of certain skills through the learning process. In this way, regardless intentions of players emerges the cooperation, which is not intentional in its characteristics. It is likely that the basic mistake is an attempt to exploit artificially defined concept of cooperation in the analysis of real games. The cooperation might be secondary to the maximization of own payoffs, however it does not undermine its value (Axelrod 1981, Binmore 1998).

Thus, through learning and the gradual acquisition of new skills it is possible to stabilize the population and then, as a consequence the emergence of cooperative behavior, however these two features might be consider as two aspects of the same phenomenon. A choice of a strategy in the initial phase of the population forming is difficult, because it is impossible to predict with certainty, which of strategies will be the most effective one. However, when the evolutionary method, which assumes that games are being repeated, is being used, then gathering of information fosters not only the choice of most favorable options but also the increasing uniformity these choices in the whole population. And this uniformity, according to accepted definitions and without any semantic misuse might be called the cooperation.

6. Conclusions

The evolutionary game theory might be a scheme of thinking about the evolution on the phenotypic level, where the fitness of individuals depends on the frequency of occurrence of particular phenotypes within the population. The phenotype is therefore nothing more than a certain evolutionary strategy including features acquired through the contacts with other members of the population and with the environment. Features acquired in this manner do not necessarily be all passed to future generations, but thanks to the socialization and the learning process it is possible to acquire them from more experienced individuals through the observations or direct instructions.

By considering these factors, and specifically thanks to the ability of constant learning, i.e. adjusting own behavior to mutable conditions, it is possible to achieve and sustain evolutionary stable strategies (ESS), because in large enough number of trials it is more and more probable that individuals will apply the strategy that maximizes possible payoffs. The more frequent the strategy is, the lower is the susceptibility to mutations from non–cooperative strategies. Of course in modern societies there is a range of restrictive measures applicable in a case of a non–cooperative behavior and diminishing its attractiveness (Binmore 1998). In some sense, where the evolution on the phenotypic level could not manage to achieve the full cooperation, it has been forced by other methods, also developed in a cooperative manner, although on another level. The equilibrium achieved thanks to such reasoning is not based on trust nor it assumes the trust, but is based on long–lasting relation between particular members of the population.

Together with the knowledge acquired from the experience, the genotype allows for the assessment of the behavior of certain rivals. Their cultural, social and environmental ballast is a serious issue, which should be taken into account during the analysis of probable actions of such a player, because some of seemingly feasible strategies might be excluded by this context, while other might become even more probable. During the learning period, which could be called socialization, inexperienced individuals make some mistakes, but the payoffs obtained after this period are sufficiently high to offset initial losses, and thus effectively lead to co-operation, and therefore to increasing the frequency of the evolutionary stable strategy.

Through the trial period, the individual gains necessary knowledge about the strength and resources of the opponent but also about his motivations and, perhaps most importantly, learns how to make typologies i assess relative frequency of particular types of individuals in the population. Due to the fact that learning is possible, it is also possible to transfer information that is not encoded in the genotype through generations. It might be said that phenotype is an environmental enclosure of genes, that enables faster and more flexible response to mutations of environmental conditions, and thus limits the losses in own population. Adaptation through learning increases of success whenever achieving the fitness necessary for the survival or the evolutionary success would take time longer than one generation and thus might earlier lead to it destruction.

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MOKYMOSI IR FONOTIPINĖ ADAPTACIJA SIEKIANT EVOLIUCIŠKAI STABILIŲ STRATEGIJŲ

M. Adamus

Santrauka

Straipsnyje nagrinėjama įvairių populiacijų stabilumo problematika. Dinamiškas ir daugiaetapes situacijas, kurių metu asmenys laipsniškai gerina savo atlyginimus ir tokiu būdu didėjant jų tinkamumo tiek natūralioje, tiek ir socialinėje aplinkose laipsniui, sunku spręsti taikant klasikinio žaidimo teorijas. Todėl šiame straipsnyje buvo panaudoti tie žaidimų teorijos įrankiai ir metodologija, kuri leido ištirti ne tik stabilizacijos procesą, bet ir sinchroninį bendradarbiavimo struktūrų atsiradimą abiejuose populiacijų tipuose. Taip pat apibūdinama tinkamumo padidinimo per fenotipo lygio evoliuciją galimybė, kuri, be bendrųjų genetinių veiksnių, reiškia, jog taip pat atsižvelgiama į specifinius aplinkosaugos ar socialinius požymius.

Reikšminiai žodžiai: evoliucija, evoliucijos žaidimų teorija, evoliuciškai stabili strategija, fenotipas, bendradarbiavimas, kalinio dilema, dove–hawk žaidimas.

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