

Statistical Mechanics of Groups Interacting in Coevolutionary Games

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Abstract

Systems in which the success of an individual depends on the actions of others are described by game theory. A dynamic learning mechanism has been introduced to this concept by evolutionary game theory, which is based on Darwinian selection. This learning mechanism increases the individual fitness and can be understood as an optimization procedure. As the fitness depends on interactions between individuals, the object that is optimized changes during the process in these systems. Darwinian selection is based on competition. However, cooperation between individuals is often observed in nature. A number of mechanisms have been proposed to explain the evolution of cooperation. The determination of the relevant mechanisms in biological and social systems is still subject of research. In this thesis, cooperation based on similarity is discussed. A minimal model for such a mechanism is derived. If agents only cooperate with others similar to themselves, segregation is observed in spatially extended systems. In social systems this is usually not desired. We discuss mechanisms to avoid this segregation. If the tolerance towards others is systematically increased, a cyclic dominance of the strategies emerges. This cyclic dominance leads to spiral waves in spatially extended systems. In well mixed systems described by the replicator dynamics, oscillations are observed. We derive a minimal model that allows analytical insight in the dynamics of such systems. Previous models in this direction have mainly been based on computer simulations.

The cyclic nature of the abundances of the different strategies is similar to the one observed in cyclic games. In asymmetric games, these oscillations can be exploited by populations that adapt their selection rates to the current state of the system. In this way, an increased payoff is realized during the transient phase. This leads to a mechanism that increases the average payoff of one population under the influence of external noise. The mechanism works in cyclic games as well as in non-cyclic games. This is the first demonstration for an increased payoff in a game that arises from stochastic fluctuations.

Kurzfassung

Systeme, in denen der Erfolg eines Individuums von den Handlungen anderer abhängt, werden durch die Spieltheorie beschrieben. Eine Übertragung dieses Konzeptes auf die Biologie wurde mit der Evolutionären Spieltheorie eingeführt. Sie beschreibt einen dynamischen Lernprozess, der auf biologischer Selektion nach Darwin basiert. Dieser Lernmechanismus, der auch als Optimierungsprozess verstanden werden kann, führt zu einer Erhöhung der individuellen Fitness. Jeder Schritt in diesem Prozess kann zu einer Veränderung des Objektes führen, das optimiert werden soll, da die Fitness durch Interaktionen mit anderen Individuen bestimmt wird. Da biologische Selektion auf Konkurrenz beruht, stellt sich die Frage, wie Kooperation in solchen Systemen entstehen kann. Eine Reihe von Mechanismen wurde vorgeschlagen, um die Entstehung von Kooperation zu erklären. Welche dieser Mechanismen in biologischen und sozialen Systemen relevant sind, ist Gegenstand aktueller Forschung. In dieser Arbeit wird Kooperation diskutiert, die auf Ähnlichkeit basiert. Ein minimales Modell für einen solchen Mechanismus wird entwickelt. Wenn Individuen nur mit anderen kooperieren, die ihnen ähnlich sind, beobachtet man in räumlich ausgedehnten Systemen Segregation. In sozialen Systemen ist dies im Normalfall nicht erwünscht. Mechanismen, die diese Segregation überwinden, werden diskutiert. Wenn die Toleranz anderen gegenüber systematisch erhöht wird, entsteht eine zyklische Dominanz der Strategien. Die zyklische Dominanz führt zu Spiralwellen in räumlich ausgedehnten Systemen. In gemischten Systemen mit zufälligen Interaktionen, die durch die Replikator-Dynamik beschrieben werden, können Oszillationen beobachtet werden. Das hier entwickelte Minimalmodell ermöglicht ein analytisches Verständnis dieser Dynamik, die bisher vor allem mit Hilfe von Computersimulationen untersucht wurde.

Die zyklischen Schwankungen der verschiedenen Strategien werden in ähnlicher Weise in zyklischen Spielen beobachtet. In asymmetrischen Spielen können diese Oszillationen durch Populationen ausgenutzt werden, deren Selektionsraten sich adaptiv dem Zustand des Systems anpassen. Auf diese Weise wird ein erhöhter Gewinn auf Transienten erreicht. Dies führt zu einem Mechanismus, der den durchschnittlichen Gewinn einer Population unter dem Einfluss von externem Rauschen erhöht. Dieses Phänomen wird sowohl in zyklischen als auch in nicht-zyklischen Spielen beobachtet. In dieser Arbeit wird damit zum ersten Mal gezeigt, wie ein erhöhter Gewinn in Spielen erzielt werden kann, wenn stochastische Fluktuationen das System beeinflussen.

1 Introduction

1.1 Motivation

In the past years, physicists have shown a growing interest in applying mathematical and computational methods from physics in other fields, as biology, economics or social sciences. These systems are far away from the extremes that are usually considered in physical systems: Often, very small or very large structures are considered in physics, as elementary particles or galaxies. Similarly, time scales are often extreme as femtoseconds in laser-pulses or the age of the universe. Another scale is the order of the system: There are successful descriptions of crystals which have a high degree of order and of gases which show no order. The theoretical description for an intermediate degree of order is much more challenging: Even glasses as partly ordered states or gases with interacting particles are tremendously more difficult to describe than these ideal systems. However, most natural systems are described by intermediate time scales and length scales. For example, ecological networks, insect colonies, the immune system and human communication networks are highly complex systems on human length and time scales. In many of these “complex systems”, physical methods have proven to be very fruitful even in areas that are not traditionally connected to physics (Schuster, 2002).

For example, the application of physical methods in economics lead to the new field of “Econophysics”. A famous historic example for the relationship between Physics and economics is the doctoral thesis of Louis Bachelier (1900), who described the market development with methods very similar to Brownian motion - 5 years before Einstein’s famous paper on this subject (Einstein, 1905). The parallels range from very heuristic examples that compare statistical mechanics to microeconomics and thermodynamics to macroeconomics (Saslow, 1999) to sophisticated mathematical tools, as the Black-Scholes equation for option pricing that is closely related to the diffusion equation (Deutsch, 2004). Another field of research between physics and economics are minimal models for markets. The simplest model for a market is the minority game (Challet and Zhang, 1997). The market is described as a game in which individuals interact. In this game, players choose between “buying” and “selling” in each time step. The group that is in the minority will be able to determine the price and win in that time step. The application of methods from statistical physics in this system has been very successful (Challet *et al.*, 2000).

Another example are artificial neural networks, which are well established in statistical physics. These systems are inspired by the structure of the brain, which can be viewed as a huge network neurons, which are comparable simple components. The human brain consists of about 10^{11} such neurons, which are connected to ca. 10^4 other neurons. There are different ways to characterize these neurons from a mathematical point of view. One possibility is to take as many details into account as feasible for an analytical theory. This approach leads to conductance based models as the Hodgkin-Huxley model (Hodgkin and Huxley, 1952) and similar formulations. Each neuron is described as a nonlinear dynamical system of several variables. While this approach has been successful for describing a single neuron, it is not longer feasible for the description of many neurons coupled in a network. However, it is clear that the description of the brain is only meaningful on this higher level. For example, computation is mainly parallel which prohibits a description on the single neuron level. Hence, a more abstract model is needed. The simplest way to describe such a system is the model of McCulloch and Pitts (1943). These neurons have only two states, either they fire or they do not fire. The coupling of many of these two state systems leads to an Ising model, where the complexity of the system is encoded in the couplings between spins. In biological systems, the spins correspond to neurons and the couplings to synaptic strengths. (Hebb, 1949) made a hypothesis about the way in which the synaptic strengths can be changed in order to describe a learning mechanism. The idea is that synaptic strengths between neurons which fire at the same time are increased, i.e. the information stored in the synapses are correlations in the input. This idea has been very successful in the training of artificial neural networks. Learning in these systems is intimately connected to optimization. In most cases, neural networks are trained in the same way in which an optimization procedure is carried out. However, optimization usually implies that the environment of the system is fixed. The system can adapt itself to a long-term change of the input structures, but it is not designed to respond to a changing environment. The basic question that motivated this thesis can be stated as “What happens, if a learning system learns from another learning system?” This question has been addressed in simple systems of coupled neural networks consisting of a “teacher” network and a “student” network (Metzler *et al.*, 2000). However, the learning mechanisms in neural networks remain complicated. A framework for systems in which the success of an individual depends on the actions of others is given by game theory (von Neumann and Morgenstern, 1944; Nowak and Sigmund, 2004).

1.1.1 Evolutionary Dynamics

Evolution through natural selection is often understood as a process that leads to an improvement of the population’s properties. Selection acts on a property called fitness, which measures the adaptation of an individual to the environment and hence the ability to survive.

For example, fitness can be measured by the number of offspring an individual produces. A heritable trait that is connected with a higher fitness will spread within the population. An increase of the average fitness of the population is therefore expected. This is often pictured as a steady ascent on a so-called fitness landscape, which assigns a fitness value to the individual's properties. In general, these properties can be discrete or continuous and constitute a high dimensional space. For example, consider a genome of length Λ . Genomes are arranged in a sequence space in such a way that nearest neighbors differ in one base only. As there are four choices for each gene representing the four bases (adenine, guanine, cytosine, thymine), this reasoning leads to a Λ -dimensional discrete lattice with four possible choices in each dimension. The fitness landscape assigns a number to each of these 4^Λ values and can be viewed as a high-dimensional mountain range. The landscape metaphor suggests a movement of the population over such a space to higher fitness values driven by natural selection, see Fig. 1.1.

The proper technique for describing uphill motion on such a steady space is optimization theory. Optimization usually tackles problems that have a solution that might not be accessible to analytical solutions due to their nonlinear character. A possible solution is chosen and improved until a further optimization cannot longer improve the solution. Examples would be the determination of a car body with minimal aerodynamic resistance or the wave function of a Hamiltonian with minimal energy. Various computational methods to tackle these problems exist: Simple steepest descent (or ascent) methods start from an initial value and change the parameters into the direction that yields the highest improvement until a local optimum is reached. Simulated annealing (Kirkpatrick *et al.*, 1983) allows to make steps into directions that do not improve the solution with a probability decreasing over time (Schuster, 2002). The goal of this procedure is to avoid local optima and to increase the probability to find the best possible solution. Genetic algorithms consider an ensemble of solutions with very different initial parameters. The best solutions are combined and modified in a random way motivated by biological systems. Point mutations are considered as well as crossovers between two solutions. This improves the solutions in the ensemble until they are concentrated around the optimal solution (Holland, 1975; Mitchell, 1996).

However, the idea of a fixed fitness landscape neglects the co-evolutionary character of the evolutionary mechanism: Although the environment selects the adaptations, these adaptations can shape the environment again. By moving across a fitness landscape, populations can change that landscape. This is particularly clear if several populations interact, because each population is a part of the fitness landscape of the other: If a prey population evolves such that it can escape from predators faster, this will increase the selection pressure on predators. This leads to a different selection pressure for the prey population in the long run. If the camouflage of a species improves by natural selection, predators will be selected for abilities that can identify the species anyway. But even within a single population, the

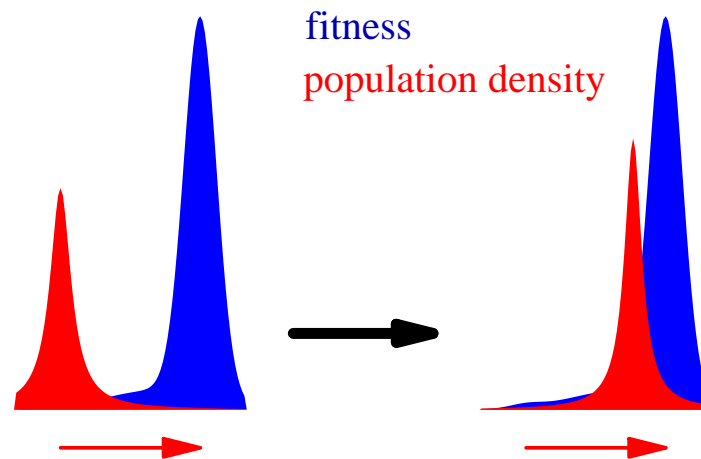


Figure 1.1: Evolution with a fixed fitness landscape. The population distribution (red) moves in the fitness landscape (blue) from lower to higher fitness values. In general, the fitness landscape is defined in a high-dimensional discrete or continuous space.

fitness of a trait often depends on the prevalence of that trait: The selective advantage of a given tree height, for example, depends on the heights of neighboring trees. Similarly, the success of a given sex ratio depends on the overall sex ratio in the population. Therefore, the fitness landscape is shaped by the phenotypic distributions of the involved populations. As the population moves through the fitness landscape, new peaks and valleys form, channeling its further motion, see Fig. 1.2. This viewpoint affects not only the intuition of evolutionary biologists but also their theoretical tools. For these problems, optimization theory is not longer the appropriate tool as the fitness landscape is not longer fixed.

If the adaptive steps imply changes in the environment, eventually necessitating new adaptations, then game theory is the appropriate framework. This theory has first been developed to reach a deeper understanding of simple two player zero-sum games, where one player wins and the other one loses. However, game theory turned out to be much more general in order to describe economic and social problems involving interdependencies among several agents. Evolutionary biologists soon understood its potential and started applying it to evolutionary problems, starting from the seminal paper of Maynard Smith and Price (1973). The success of a strategy in a game depends on the co-player's strategy, much as the fitness of a phenotype depends on the composition of the population. Game theory is the mathematical toolbox for methodological individualism, the systematic attempt to found social theory on the actions and needs of individual agents. For outcomes determined by selfish genes (Dawkins, 1976) or by the selfish homo economicus Gintis (2000), this is the proper instrument.

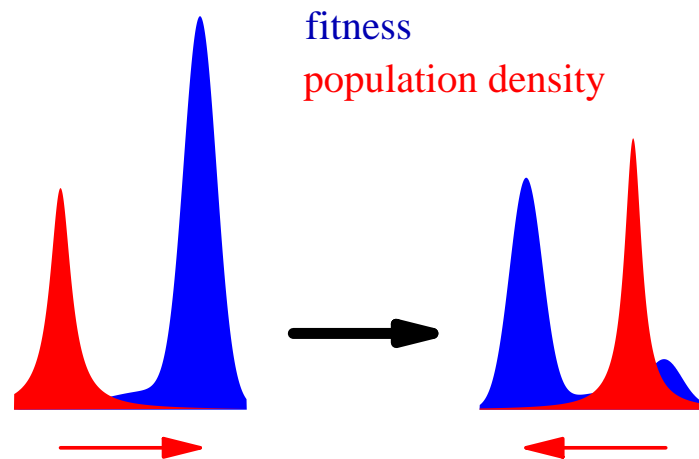


Figure 1.2: Evolution with a changing fitness landscape. While the population distribution (red) moves in the fitness landscape to the fitness maximum at the right (blue), the height of this maximum is reduced and a new fitness maximum to the left appears. In the next time step, the population distribution would evolve to the left again.

1.1.2 Biological games

At first, the idea to apply game theoretic arguments to biology seems to be weird: Animals do not play games. However, they do not choose between strategies, as humans usually do in interactions. Instead, they are equipped with a strategy and their survival (or their potential to produce offspring) depends on this strategy. Examples for such strategies are a tree's height, a parent's sex ratio, a parasite's virulence, a female's choosiness, or a male's ornament. The applications of game theory in biology are as diverse as these examples for strategies (Nowak and Sigmund, 2004). Evolutions of root structure or tree height are problems of resource allocation. Conflicts concerning mate choice, sibling rivalry, and parent-offspring antagonism provide motivation for game-theoretic models. The arms races between predators and prey, or between parasites and their hosts, offer many examples of games between distinct populations. Communication in its widest sense, including alarm calls, threat displays, or sexual advertisement, lead to game-theoretic problems concerning false and honest signaling. Acquisition and performance of human language in a heterogeneous population can be studied as an evolutionary game. Increasingly, evolutionary game theory is used in economic and social sciences and applied to experimental games with human subjects. Even genes, bacteria, organelles, and viruses can be engaged in games of cooperation and conflict. The evolution of virulence of infectious agents is another vast field that makes use of game-theoretic arguments. The classical understanding, based on constant selection, is that

parasites evolve to maximize their basic reproductive ratio. Frequency-dependent selection arises when several parasite strains superinfect the same host or when rapid evolution generates many different parasite mutants in any one infected individual. Lack of cooperation among parasites can lead to shortsighted, maladapted levels of excessive virulence harming both host and parasite.

The growth in the range of applications demanded an extension of classical game theory, away from the static doctrine dominated by the equilibrium notion of John Nash. Evolutionary game theory introduced a learning mechanism to these systems (Maynard Smith, 1982), leading to a dynamic theory.

The concepts of unbeatable strategy and evolutionary stability implicitly assume some underlying population dynamics describing the potential success of invading mutants. An exact formulation of these population dynamics depends on various details: First, the structure of the population can have an important influence (Nowak and May, 1992). The dynamics can be totally different if randomly chosen individuals or only nearest neighbor interactions in a spatially extended system interact. In addition, the mechanisms for the transmission of the relevant traits can be different, as evolutionary game theory can describe genetic inheritance as well as cultural learning. For both scenarios, a wealth of different mechanisms is possible. Finally, the time scale underlying the evolutionary and ecological processes can be of importance.

Of particular interest are cyclic games (variants of “rock-paper-scissors”) where the long-term outcome is not a static Nash equilibrium but endless regular or irregular oscillations. Even in very simple systems, Hamiltonian chaos has been found (Sato *et al.*, 2002). Hence, the static approach is in principle unable to provide a full analysis.

The most common approach for such a dynamic theory is to consider the deterministic limit of infinite populations, which results in the replicator dynamics or related formulations (Hofbauer and Sigmund, 1998; Weibull, 1995). Within this framework, coevolutionary dynamics can be analyzed directly.

In evolutionary game theory, usually a single population evolves under the influence of interactions defined by a game. If groups of individuals interact, the first problem is the definition of the own group. If a group aims to outwit others, it has to create some kind of group identity. Such an identity is in the simplest case given by a common trait that is directly visible. After a brief introduction to the field of evolutionary game theory, this thesis analyzes such kind of models in spatially extended systems with local interactions as well as in mixed populations. If the effect of neutral mutations is included by introducing a drift term, cyclic dominance emerges.

In the next step, asymmetric conflicts are analyzed. In this setting, two (or more) populations interact with different goals and ambitions. It is shown that a simple extension of the usually applied coupled replicator dynamics with adaptive learning rates can lead to an

increased payoff on average. In addition, we show that this learning mechanism can exploit external fluctuations in a resonance like fashion. In the conclusions, we discuss the next steps motivated by the questions that were raised in this thesis.

1.2 Game Theory

1.2.1 Classical Game Theory

Classical Game theory is a branch of mathematics that studies interactions with formalized incentive structures. The success of an individual in these interactions does not only depend on the own action, but also on the actions of others. Starting as a branch of pure mathematics, game theory has become a more applied subject with a variety of applications, including evolutionary biology, economics, and political science. John von Neumann and Oskar Morgenstern first formalized the subject in 1944 in their book “Theory of Games and Economic Behavior” (von Neumann and Morgenstern, 1944). This work included the method for finding optimal solutions for two-person zero-sum games. John Nash (1950) generalized this result to multi-player games. The equilibrium he defined is now well known as Nash equilibrium (Holt and Roth, 2004). If every interaction partner uses the strategy of the Nash equilibrium, no one will be better off switching his strategy.

This thesis focuses on the theory of non-cooperative games, where players optimize their actions only according to their own interests. There are two nearly equivalent ways to formalize non-cooperative games. An extensive form game (Gintis, 2000; Fudenberg and Tirole, 1998) consists of a number of players, a game tree, and a set of payoffs. Extensive form games are very general, any finite number of players can interact in an arbitrary sequence. This thesis, however, focuses on the theory of normal-form games (also called strategic form games) with two players only.

A normal form game consists of a set of players, which we take to be the finite set $1, 2, \dots, I$, the pure-strategy space S_i for each player i , and the payoff function u_i . The pure strategy set consists of all possible actions of the corresponding player. A strategy profile is given by $\mathbf{s} = (s_1, s_2, \dots, s_I)$, where s_i is the strategy of player i . The payoff function assigns a payoff u_i to each player that depends on the strategy profile \mathbf{s} . Normal forms for finite two-player games are usually depicted with the help of payoff matrices. As an example, we consider the game

	L	M	R	
U	(2, 1)	(3, 2)	(0, 1)	(1.1)
D	(1, 2)	(4, 5)	(0, 2)	

The column and the row player have three and two strategies, respectively. The first entry is the payoff of the row player for the corresponding strategy profile and the second entry is the column player’s payoff. For example, if the row player chooses **U** and the column player chooses **M** we have $\mathbf{s} = (\mathbf{U}, \mathbf{M})$ and the payoffs are $u_1 = 3$ and $u_2 = 2$. A mixed strategy of a player i can be defined as a probability distribution x_i over the pure strategies S_i . In a two-player

game, the payoff of the column player choosing strategy j can be computed from

$$u_j = \sum_k u_k(s_k)y_k, \quad (1.2)$$

where y_k is the probability that the row player chooses the strategy k . A mixed strategy \mathbf{x} is a best reply to itself if no other strategy \mathbf{x}' leads to a higher payoff, i.e. $u_i(\mathbf{x}) > u_i(\mathbf{x}')$. A Nash equilibrium is a point in which every player uses a strategy that is a best reply to the strategies of the other players. If only pure strategies are involved in the equilibrium, it is called pure-strategy Nash equilibrium, otherwise mixed-strategy Nash equilibrium. Nash (1950) showed that every finite normal-form game has at least one Nash equilibrium.

Players are expected to play according to a Nash equilibrium if they have full information on the payoff matrix and if they are hyperrational, i.e. if they include in their reasoning that the others will choose their strategy assuming that every player acts rationally. However, this is not even the case in humans. Consider a game in which every player chooses an integer number between 1 and 100. The player which is closest to half of the average wins. Although it is obvious that the rational choice is 1, humans tend to choose significantly higher numbers (Nagel, 1995).

Although the existence of the Nash equilibrium is proven in classical game theory, no statement on the learning dynamics in games is given due to the static character of classical game theory. Such a learning dynamics is given by evolutionary game theory.

1.2.2 From classical game theory to evolutionary game theory

The first approach to transfer game theoretical ideas explicitly to biology has been made by Lewontin (Lewontin, 1961). His approach was to describe a species playing a game against nature in order to minimize the probability of extinction. In 1973, Maynard Smith and Price introduced an elegant way in which game theory can be applied to animal contests (Maynard Smith and Price, 1973). The idea of applying game theory to animals seems to be strange at first, as game theory was first developed with respect to hyperrational players, as discussed above. This kind of rationality can hardly be expected from simple animals or even bacteria. Three critical shifts have been made in order to transfer game theoretic ideas to biology (Gintis, 2000).

Strategy

In classical game theory, players choose from a set of strategies. In biology, a species consists of strategy sets (phenotypic variants). Each individual inherits a variant, which it uses in its interactions. In this way, individuals do not choose their strategy, but the population dynamics within the species eliminates less successful strategies. This allows to transfer

game theoretic concepts even to simple bacteria. In biology, the payoff from classical game theory is identified with the fitness of an individual¹. The fitness is then identified with the number of offsprings of an individual. In this way, the idea of hyperrationality is replaced by Darwin's "survival of the fittest". Individuals that do not use the rational strategy simply extinct.

Equilibrium

In Maynard Smith and Price (1973), the concept of "Evolutionary Stable Strategies" was introduced, which is closely related to the Nash equilibrium of classical game theory. A strategy is evolutionary stable if a population using that strategy cannot be invaded by a small group of mutants using a different strategy. The original definition of evolutionary stability is only valid for infinite populations. Recently, alternative definitions for finite populations have been made (Schaffer, 1988; Gintis, 2000; Nowak *et al.*, 2004). Every "Evolutionary Stable Strategy" is a Nash equilibrium, but the reverse holds only for strict Nash equilibria.

Player interactions

In classical game theory players meet only once or they interact repeatedly with the same opponent. In evolutionary game theory, individuals are randomly paired and use strategies determined by their phenotype (Maynard Smith, 1982; Gintis, 2000). Although the game is repeated, a basic assumption is that individuals do not meet the same opponent twice. This avoids the concept of an individual memory. However, the species still has some kind of abstract memory due to the distribution of phenotypes, which is determined by previous interactions.

More recently, the requirement of random interactions has been relaxed. Evolutionary games on lattices (Nowak and May, 1992; Lindgren and Nordahl, 1994) and on network structures have been considered (Abramson and Kuperman, 2001; Ebel *et al.*, 2002; Lieberman *et al.*, 2005)

1.2.3 Social dilemmas

Probably the best known game-theoretic example is the famous Prisoner's Dilemma (Trivers, 1971; Axelrod and Hamilton, 1981; Axelrod, 1984), which belongs to the class of social dilemma games. In these games, individual advantage and collective benefit contradict each other. In physical terms, this can be compared to a frustrated interaction, since global and local optimizations are not possible simultaneously.

¹Usually, interactions have a relative influence on the fitness only. Other influences on the fitness of individuals can often be described by a background fitness (Nowak *et al.*, 2004).

In the Prisoner's Dilemma, two players decide simultaneously whether they cooperate or defect with the co-player. The payoff matrix of the Prisoner's Dilemma is

$$P = \begin{pmatrix} R & S \\ T & P \end{pmatrix}. \quad (1.3)$$

If both players cooperate, they receive a reward R . However, if a player suspects that the opponent will cooperate he is tempted to defect. This leads to an increased payoff T for himself, while it decreases the payoff of his opponent to the sucker's payoff S . If he suspects his player to defect, he should also do the same, as the payoff for mutual defection P is higher than the sucker's payoff S . Hence, the best decision for every player is to defect, no matter what the opponent will be doing. But in this case, both would be better off if they found a way to agree on mutual cooperation. In general, the Prisoner's Dilemma is defined by two inequations. The first one is the ranking of the elements of the payoff matrix, $T > R > P > S$, as described above. The second inequation is given by $2R > T + S$, which prevents that players are better off when they cooperate and defect alternately.

Mutual cooperation can be reached if players are equipped with a memory keeping track of their interactions in repeated games. Axelrod and Hamilton (1981) found that the "Tit for Tat" strategy, which cooperates in the first round and then simply mimics the opponent's last move, is very successful compared to a wide range of different strategies. However, noise can destroy the dominance of the "Tit for Tat" strategy. Lindgren (1991) introduced a model with a basically unbounded strategy space wherein very complicated strategies can arise which are capable of effectively correcting errors. Even for short memories, error correcting strategies have been analyzed (Nowak and Sigmund, 1992, 1993a). It turned out that a very successful strategy is "Pavlov", which cooperates only if the player and its opponent have chosen the same action in the previous round (Nowak and Sigmund, 1993b).

"Tit for Tat" is an example for direct reciprocity, as it cooperates with others that have also cooperated before. If players can observe others in interactions they can assign reputations to others. This kind of indirect reciprocity can also explain the emergence of cooperation (Nowak and Sigmund, 1998b; Milinski *et al.*, 2002). However, it is controversial what kind of mechanism leads to cooperation in this case (Leimar and Hammerstein, 2001). Recently, it has been shown that a number of different mechanisms can effectively lead to cooperation from indirect reciprocity (Ohtsuki and Iwasa, 2004; Brandt and Sigmund, 2004). Ohtsuki and Iwasa (2004) analyzed systematically all possible assignments of reputation from the last interaction, providing a more general theory of indirect reciprocity.

Cooperation can also be found in models without reciprocity. Riolo *et al.* (2001) have proposed a model in which agents cooperate based on their similarity. However, this model assumes that individuals will always cooperate with others of their own kind. If this assumption is relaxed, the game reduces to a Prisoner's Dilemma again (Roberts and Sherratt,

2002; Hauert, 2002b). Hence, the “Evolution of cooperation without reciprocity” cannot be observed in this model. Nevertheless, models for similarity based cooperation are of general interest. If interactions are not random, clusters of cooperating agents from a single group can be found even in the presence of unconditional defectors not cooperating with their own group. Hence, the similarity based mechanism can lead to higher levels of cooperation in spatially extended systems (Axelrod *et al.*, 2004). In mixed systems without spatial structure, the cooperation in the model of Riolo *et al.* occasionally breaks down. In Traulsen and Schuster (2003) it has been shown that this arises from the destabilizing effect of neutral mutations that lead to a drift towards more tolerant strategies.

A game very similar to the Prisoner’s Dilemma is the snowdrift game². Imagine two drivers caught in a snowdrift. If one of them begins shoveling, the other one can stay in his warm car, since he knows that he will get out. However, if the opponent stays in his car one should begin shoveling to avoid spending the night in the car. The snowdrift game is described by the inequation $T > R > S > P$. In other words, cooperation is the best choice if the opponent defects, but if the opponent cooperates it is best to defect. Although the snowdrift game is closely related to the Prisoner’s Dilemma, there are some striking differences. For example, spatial structure often leads to a lower degree of cooperation in this game (Hauert and Doebeli, 2004; Taylor and Day, 2004), while it increases cooperation under many circumstances in the Prisoner’s Dilemma (Nowak and May, 1992)

In order to reduce the number of free parameters in the Prisoner’s Dilemma, one can introduce a cost c for cooperating with the opponent and a benefit b to quantify the help received from the opponent. In this way, we find for the payoff matrix

$$P = \begin{pmatrix} R & S \\ T & P \end{pmatrix} = \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix}, \quad (1.4)$$

which fulfills the requirements for a Prisoner’s Dilemma if $b > c > 0$. Without loss of generality, we can set $b = 1$, leaving one normalized free parameter, $1 > c > 0$. In this thesis this notation for the Prisoner’s Dilemma and related games is applied. Several results on the emergence of cooperation can be written in a very elegant way, in which the critical parameter is b/c .

- Hamilton (1963) showed that kin selection, i.e. selection between relations, can only work if

$$\frac{b}{c} > \frac{1}{r}, \quad (1.5)$$

²The snowdrift game is also known under a lot of different names, e.g. chicken game or hawk-dove game. Common to these games is that the optimal pure strategy is to choose the opposite of what the opponent does.

where r is the relatedness between individuals. For fixed benefit to cost ratio, this lead to a famous remark of the British biologist J. B. S. Haldane. He stated that he would never give his life for a brother, but he would “jump into the river to save two brothers or eight cousins”.

- Nowak and Sigmund (1998b) have analyzed a system of indirect reciprocity in which agents have a state given by an image score. In this system, cooperation emerges if

$$\frac{b}{c} > \frac{1}{q}, \quad (1.6)$$

where q is the probability that an individual knows the status of others.

- For similarity based cooperation, we find a threshold that determines in which cases a group can be invaded by a small fraction of others. A configuration is stable if

$$\frac{b}{c} > \frac{1}{x}, \quad (1.7)$$

where x is the fraction of agents that refuse to cooperate with other groups (Traulsen and Schuster, 2003).

The Prisoner’s Dilemma is defined as a two player game. The equivalent for more players are public goods games, introduced by Hardin (1968) as “Tragedy of the commons”. Every player has the option to contribute to a common pool at some cost c . The common pool is then increased by a factor of $r > 1$ and divided between all players - even those that did not contribute to the pool. In a population of N players, the n_c individuals contributing to the pool receive a payoff $\pi_c = r c n_c / N - c$, while the remaining $N - n_c$ individuals receive $\pi_d = r c n_c / N > \pi_c$. As in the Prisoner’s Dilemma, the rational strategy is not to contribute, as a contribution to the pool is connected with a lower payoff. However, if everybody contributed to the pool the whole population would be better off. Different strategies have been proposed to solve this kind of social dilemma. An example is reward and punishment (Sigmund *et al.*, 2001; Fehr and Gächter, 2002). If agents have the option to participate voluntarily in the game, high degrees of cooperation can also be reached (Hauert *et al.*, 2002; Szabó and Hauert, 2002; Michor and Nowak, 2002). Hauert *et al.* (2002) introduced a third strategy, the “loner” strategy. The idea is that players can decide whether they enter the public goods game or if they rely on a small but safe payoff. Entering the public goods game, the players still have the option to defect or to cooperate. The option to avoid the “Tragedy of the commons” leads to a cyclic dominance of strategies: If mainly free-riders trying to exploit others are participating in the game, it is best to become a loner. If the population consists of loners only, it makes sense to start a public goods game and to increase the payoff. However,

the public goods game attracts free-riders again that try to exploit the other players. At this point, the cycle begins again. Cyclic games are discussed in detail in Section 1.2.4.

In the seminal paper of Axelrod and Hamilton (1981) on the Prisoner's Dilemma, altruistic behavior has been analyzed in artificial communities. However, cooperation is also frequently observed in nature. For example, altruistic behavior has been reported in baboons (Trivers, 1971; Packer, 1977), and vampire bats (Wilkinson, 1984). Milinski (1987) conducted experiments with sticklebacks. When sticklebacks inspect predators the risk of being recognized is much smaller when two sticklebacks inspect a predator simultaneously. However, in a pair of two sticklebacks the danger of being attacked is reduced if one moves a few centimeters behind the second fish. Milinski experimented with a single fish only and used a mirror to simulate a second stickleback. Different orientations of the mirror can be interpreted as a defecting or cooperating partner. These experiments showed that the sequence of moves of the sticklebacks during their inspection of a predator can be described as a Tit for Tat strategy. However, the fitness of individuals corresponding to the payoff is extremely hard to measure (Nowak and Sigmund, 1999). Hence, it is not always possible to determine the ranking of the elements in the payoff matrix (Milinski *et al.*, 1997). Consequently, it is not clear in which kind of interactions these individuals are involved.

Turner and Chao (1999) have shown experimentally that a certain kind of phages, i.e. viruses that infect bacteria, are actually involved in a Prisoner's Dilemma. In these experiments, two types of bacteriophages are analyzed. In addition to the usual type of $\phi 6$ (the cooperator), a mutant $\phi H2$ (the defector) is present which contributes fewer intracellular products which are required for the replication of phages to the system. This leads to the question why the cooperator is still present. Little is known about the underlying mechanisms (Nowak and Sigmund, 1999), but it could be an example of group selection (Maynard Smith, 1964, 1976; Wilson and Dugatkin, 1997): While host cells with a high fraction of cooperator bacteriophages produce a high number of new phages, defector bacteriophages cannot spread as they do not produce enough offspring.

1.2.4 Cyclic games

Another interesting class of games are cyclic games. The best known game of this type is the two-person game "Rock-Paper-Scissors". Each player chooses simultaneously rock (fist), paper (flat hand) or scissors (two fingers). Scissors is beaten by rock, rock is beaten by paper and paper is beaten by scissors again. In this game each strategy is cyclically dominated by another strategy.

While most social dilemmas are defined in a symmetric setting in which every individual has the same goals described by a single payoff matrix, the simplest cyclic game "Matching Pennies" is an asymmetric conflict (Maynard Smith, 1982) in which both players have

different ambitions. Both players choose an action, “heads” or “tails”, simultaneously. The first player wins if both actions are the same, while the second player wins if different actions have been chosen. If both players choose the strategy “win stay-lose shift”, they will win alternately, as the strategies dominate each other cyclically³. An internal model of the opponent’s learning rule can help to outwit the opponent (Schuster, 2003).

The cyclic dominance does not have to arise directly from the payoff matrix. In (Traulsen and Schuster, 2003) an example is given in which the cyclic dominance is driven by neutral mutations destabilizing a Nash equilibrium that is not an Evolutionary Stable Strategy.

In 1996, a first example for cyclic games in nature has been reported (Sinervo and Lively, 1996; Maynard Smith, 1996). In the side-blotched lizard males have one of three possible throat colors, each associated with a different behavior. Orange-throated males establish large territories holding several females. These populations can be invaded by males with yellow-striped throats, which do not contribute to the defense of the territory. However, a population of yellow-striped males can be invaded by blue-throated males, which defend territories large enough to hold one female which they defend against sneakers. Once sneakers are rare, it is advantageous to defend a large territory with several females and the cycle starts with orange-throated males again. The cycle with three different strategies corresponds to the rock-paper-scissors game, where each strategy is cyclically dominated by another strategy.

Another example for a cyclic game in nature has been given in (Kerr *et al.*, 2002), where dynamics in colicinogenic bacteria populations are analyzed. Colicinogenic bacteria possess a plasmid containing genes that encode the toxic colicin, a colicin-specific immunity protein making the cell immune to the colicin and a lysis protein causing the release of the colicin. In the experiments of Kerr *et al.*, the growth rate of resistant cells (R) was higher than the growth rate of colicinogenic cells (C), but less than the growth rate of sensitive cells (S). In this case, S can displace R (due to S’s growth-rate advantage), R can displace C (due to R’s growth-rate advantage), and C can displace S (as C kills S). Hence, we recover a rock-paper-scissors cycle again. In a mixed system, the resistant strain dominated the population. In spatially extended systems, however, the coexistence of the strains arising from the cyclic dominance was observed. The experiments have shown that local interactions can lead to biodiversity.

³There are several other names for cyclic asymmetric conflicts, in biology a reasoning about parental care leads to a cyclic game and to the name “Battle of the sexes”. In economics, however, the “Battle of the sexes” is a 2×2 game with two pure strategy Nash equilibria.

1.3 Game Theory in spatially extended systems

1.3.1 Motivation

A central assumption of evolutionary game theory is that agents are paired randomly. In reality, interactions are often restricted to small local groups. Although Axelrod and Hamilton (1981) realized that territoriality will have large impact on game theoretic interactions, extensive work on spatial games has started more than a decade later, when Nowak and May (1992) introduced a cellular automaton based on the Prisoner's Dilemma.

Spatial game theory suffers from a wealth of possible algorithms which makes it difficult to derive general conclusions. Possible parameters include the definition of the neighborhood, the rule how new strategies are chosen and the synchronous or asynchronous nature of the update rule (Hauert, 2002a). If memory is included, the number of possible parameters is further increased. The complex spatial evolution of these systems can often only be studied by means of computer simulations (Lindgren and Nordahl, 1994).

Recently, also more complicated spatial structures have been analyzed. The most prominent example are games on networks (Abramson and Kuperman, 2001; Holme *et al.*, 2003; Ebel and Bornholdt, 2002a; Lieberman *et al.*, 2005). As a new degree of freedom is introduced in the topology here, the analysis of spatially extended games on network structures is more challenging than on regular lattices. Another approach is to introduce agents that move in a spatial environment and choose their interaction partner (Aktipis, 2004). These systems can be viewed as a special case of game theoretic interactions on an evolving network structure. If even the network structure is subject to evolution, the system becomes even more complex (Ebel and Bornholdt, 2002b).

1.3.2 Comparison with cellular automata

Spatially extended games with synchronous update are closely related to cellular automata. The introduction of spatially extended games by Nowak and May (1992) is in principle a cellular automaton with an update rule defined by the underlying game. In both cases, a discrete state is assigned to each lattice site in discrete time steps. The new state depends on the state of neighboring sites. However, only a small fraction of possible cellular automata is realized by spatially extended games:

- In spatially extended games, a player usually compares its payoff with all the neighboring players regardless of their spatial relationship. Hence, the standard setup of spatial games describes only isotropic cellular automata.
- Usually, players update according to the payoff of their neighbors, which in turn depends on the strategies of their neighbors. Hence, the update rule has to take into

account the neighbors of the neighbors as well. This is in contrast to a lot cellular automata, as Conway's famous game of life (Gardner, 1970) or the Sierpinski automaton (Wolfram, 1984; Claussen *et al.*, 2004).

Although cellular automata are usually analyzed with two possible states only, more general automata are possible. The same holds for game theory: Although in general $s \times s$ games require s different states, the majority of spatial games only analyzes 2×2 games (Hauert and Doebeli, 2004; Nowak and May, 1992). For $s \times s$ games, the number of necessary update rules is given by s^n , where s is the number of strategies and n is the number of sites involved in the update procedure. Therefore, the complexity of the automata increases rapidly with s . For example, in the simplest spatial automata introduced in (Traulsen and Claussen, 2004), the number of necessary update rules is $4^{5 \times 5} \approx 10^{15}$. For the usual prisoners dilemma in the same setting, "only" $2^{5 \times 5} \approx 3 \times 10^7$ rules are necessary. The complexity increases further, if memory is included (Lindgren and Nordahl, 1994).

1.3.3 Mathematical tools

Due to the wealth of possible algorithms for game theory in spatially extended systems, few general analytical methods exist. Often, these methods are only applicable in very simple systems with various restrictions.

Mean field theories

A first approximation to analyze a spatially extended game theoretic system is given by a mean field theory. For this purpose, the spatial character of the system is neglected and interactions between randomly chosen individuals from a large population are considered. Often, this is termed as a "well-mixed system". Usually, the replicator dynamics is applied for this purpose. In section 1.4.2 this method is discussed in detail.

Pair approximation

An more sophisticated analytical approximation of the spatial dynamics can be obtained through pair approximation, which explicitly takes spatial effects into account (Iwasa, 2000; Sato and Iwasa, 2000; Hauert and Szabó, 2005). Instead of considering the frequency of strategies as in well-mixed populations, i.e. in mean-field theory, pair approximation tracks the frequencies of strategy pairs. Such pair configurations indicate the probability of finding an individual playing strategy j accompanied by a neighbor playing i . In principle, an arbitrary finite set of strategies can be considered. However, even for three strategies, the algebra becomes rather tedious and does often not offer new insight into the character of the system. Pair approximation is based on three conditions: compatibility, symmetry and closure.

Consistency and compatibility with mean-field theory requires that the global fraction of a certain strategy i can be recovered from the frequencies of strategy pairs. Symmetry requires that the probability to find a strategy j in the neighborhood of i is the same as the probability to find a strategy i in the neighborhood of j . Finally, configuration probabilities of larger clusters are approximated by pair configuration probabilities - this is known as closure.

Generally, predictions by pair approximation are less reliable near extinction thresholds because this approach does neither account for corrections arising from loops nor the long range correlations occurring in vicinity of critical transitions. The accuracy of this technique, however, can be improved by considering configuration probabilities of larger clusters.

Although the method is in principle not reduced to two strategies, the analysis of three or more strategies becomes very lengthy.

Mapping to physical systems

Some simple game theoretic systems on two-dimensional lattices can be mapped to spin models (Herz, 1994). However, while the relationship between models from game theory and solid state physics is often interesting from a conceptual point of view (Hauert and Szabó, 2005), few analytical insights can be gained from such a mapping. So far, this mapping has mainly been considered for two strategy systems, which are mapped to two state Ising models. In general, a local external magnetic field has to be assumed for this mapping. In addition, local interactions cannot always be described by a single coupling parameter J_{ij} . For these more general Ising models, a closed analytical solution has not been found so far, limiting the predictive potential of such mappings.

Fundamental clusters

The analysis of fundamental clusters is a straightforward method for spatial game theoretic systems and more general for cellular automata (Hauert, 2001). Configurations of a cluster of individuals with the same strategy in an environment of another strategy are considered. The conditions are derived under which such a cluster grows or shrinks. This analysis is made for a 1×1 cluster, a 2×1 cluster, a 2×2 cluster, ... For larger clusters, this analysis can be made for corners, edges, and other sites independently. This concept shows a strong dependency on the underlying lattice geometry and the neighborhood. Only local development is discussed. This method allows to analyze some general features of the spatiotemporal dynamics, but does not always allow insights on the global dynamics. Although the method is not in general restricted to two strategies only, the analysis of more complicated systems is usually not feasible.

Partial differential equations

Many spatially extended physical systems can be described by partial differential equations, as fluid dynamics by the Navier Stokes equation. A simpler example is the diffusion equation. Many pattern formation phenomena observed in game theoretic systems can also be found in these reaction diffusion systems. For example, spiral waves can be found in a simple reaction-diffusion system with two ingredients only, an activator with concentration $a(\mathbf{r}, t)$ and a controller with concentration $c(\mathbf{r}, t)$. Consider the reaction-diffusion system

$$\dot{a} = D_a \Delta a + \frac{3a - a^3 - c}{\tau_a} \quad (1.8)$$

$$\dot{c} = D_c \Delta c + \frac{a - \delta}{\tau_c}, \quad (1.9)$$

where D_a and D_c are diffusion constants, τ_a and τ_c are time constants describing the reactions and δ is a free parameter. In this system spiral waves can be found, as in the system analyzed in (Traulsen and Claussen, 2004). However, there are several restrictions to this approach in game theory: First, game theoretic systems usually consider a finite strategy set only, whereas the concentrations in a reaction diffusion system change continuously. Hence, the relevant scales of the system have to be large enough to allow a description of concentrations. Second, game theoretic systems often explicitly rely on small local structures and next neighbor interactions. The interaction with a “concentration” of other strategies might change the qualitative dynamics of the system. For example, the notion of a concentration could lead to the system in which selection is not longer restricted to the individual, but to local groups. Such a kind of group selection is usually not desired in spatially extended game theoretic systems. Further, this reasoning becomes very complicated if more than two strategies are involved. These systems are equivalent to reaction-diffusion systems with more than two reacting substances. As these reaction diffusion systems are usually not accessible for analytical solutions, this approach is of limited interest in game theoretic contexts.

Systems with more than two strategies

All the methods introduced in this section are primarily designed for systems with two strategies only. Some of them can be generalized to more complicated systems, but dealing with three or more strategies is challenging and many analytical tools fail in these systems. Usually, only computer simulations are feasible. However, insight can sometimes be gained by introducing new parameters to classify and compare different spatial structures. In (Traulsen and Claussen, 2004) topological charges have been introduced for this purpose in order to locate the tips of spiral waves in the system. Such new parameters have to be defined for each system independently and are usually not applicable in general.

1.4 Mean field theories

1.4.1 Definition of mean field theories

In physical terms, a mean field theory is defined by restricting individual interactions to interactions with an averaged model system. The simplest example is the mean-field theory for the two-dimensional Ising model, where the energy of a spin is computed by assuming that neighboring spins have an averaged orientation. The starting point is to compute the average orientation of a spin in a magnetic field given by the (unknown) average orientation of the remaining spins. The assumption that the considered spin has the same orientation as the average spin leads to a self consistency equation for the spin orientation that can be solved directly. Starting from a regular lattice, the mean field theory becomes exact for high dimensions (usually, the critical dimension for which the mean field theory first becomes exact is $d = 4$). It is also exact if the lattice is either fully connected (i.e. every spin interacts with every other spin) or if random interactions are considered (Hauert and Szabó, 2005).

The introduction of a mean field theory often assumes implicitly an infinite system, but in general it can be defined for arbitrary system size. Hence, in game theoretic interactions a mean field theory should be possible without the regular assumption of infinite populations. Nowak *et al.* (2004) have introduced a model which can be considered as such a mean field theory in finite populations. In this model, individuals interact with an averaged opponent. The evolutionary dynamics is given by the classical Moran process (Moran, 1962). However, there are many possibilities to define such theories in finite populations. The connection to the usual concepts considering infinite populations is discussed in (Traulsen *et al.*, 2005a).

1.4.2 Replicator dynamics

Often, the replicator dynamics (Taylor and Jonker, 1978; Schuster and Sigmund, 1983; Hofbauer *et al.*, 1979; Hofbauer and Sigmund, 1998; Weibull, 1995) is applied as a mean field theory for the evolutionary dynamics of game-theoretic systems. It describes the evolutionary dynamics in the limit of large populations.

As a simple example, we consider the replicator dynamics for the Prisoner's Dilemma with the payoff matrix equation 1.4. We have only two strategies, cooperators and defectors. Randomly chosen individuals interact. Hence, one variable is sufficient to determine the state of a large population: The fraction of defectors x determines also the fraction of cooperators, $1 - x$. How does x change in time? The basic assumption of the replicator dynamics is that the growth rate of the fraction of a strategy x is proportional to the relative success of the corresponding strategy. A defector expects to meet another defector with probability x . With probability $1 - x$, he will be able to exploit a cooperative individual. In this case, his payoff

will be b . Hence, the defector expects the payoff

$$\pi_D = 0 \times x + b \times (1 - x) = b(1 - x). \quad (1.10)$$

On the other hand, a cooperator will meet a defector with probability x and obtain the payoff $-c$. His partner will be cooperative with probability $1 - x$, leading to the payoff $b - c$. His expected payoff is

$$\pi_C = -c \times x + (b - c) \times (1 - x) = b(1 - x) - c = \pi_D - c. \quad (1.11)$$

Since $\pi_C < \pi_D$, the defectors are always more successful than cooperators. As there are x defectors and $1 - x$ cooperators in the population, the average payoff is

$$\langle \pi \rangle = x\pi_D + (1 - x)\pi_C = (b - c)(1 - x) \quad (1.12)$$

With these payoffs, the replicator dynamics is given by

$$\dot{x} = x(\pi_D - \langle \pi \rangle) = cx(1 - x) \quad (1.13)$$

Equation 1.13 can be viewed as a dynamical system. The system has two fixed points. The fixed point at $x = 0$ is unstable: A small derivation from this fixed point to positive x is amplified and the system leaves the fixed point. This is the situation in which a small fraction of defectors destroys a cooperative population. The second fixed point at $x = 1$ is stable, as a small deviation from this point is dampened again. A small fraction of cooperators cannot invade a population of defectors. However, the average payoff at the unstable fixed point $x = 0$ is higher than the average payoff at the stable fixed point $x = 1$. This recovers the dilemma situation again: In a cooperative population, every individual is tempted to increase its own payoff and to defect. However, if everybody switches to defection this advantage is reversed: Each individual decreased his payoff from $b - c$ to 0 when it tried to increase it to b . Equation 1.13 can even be solved directly. The solution of this differential equation is

$$x(t) = \frac{1}{1 - \frac{x(t_0)-1}{x(t_0)}e^{-c(t-t_0)}} \quad (1.14)$$

This solution describes the approach from an initial point $x(t_0) > 0$ to the stable fixed point at $x = 1$, i.e. the state with defectors only. For $x(t_0) = 0$ we have $x(t) = 0$, since $x = 0$ is a fixed point. In all other cases, the stable fixed point is approached asymptotically in the limit $t \rightarrow \infty$.

Many evolutionary game theoretic models are based upon the replicator dynamics. Although a fruitful place to start, the replicator dynamics make a number of assumptions which can reasonably be questioned for real populations. Essentially, an infinite population is assumed. Although a valid approximation for large population, crucial differences to finite

populations are possible (Nowak *et al.*, 2004; Taylor *et al.*, 2004). In addition, two players are always equally likely to meet and interact. In a spatially extended system this is an unrealistic assumption. Further, mutations are neglected in the replicator dynamics, which often have a crucial influence (Traulsen and Schuster, 2003). Hence, an extincted strategy will never be present in the system.

Nonetheless, the replicator dynamics can serve as a first approximation. As it has been analyzed in great mathematical detail (Hofbauer and Sigmund, 1998; Weibull, 1995), it provides a steady foundation for further analysis.

The general form of the replicator dynamics is the following: Consider a normal-form game within a single population with N different types of individuals. The payoff of each individual depends on the current state of the population. An individual of type i receives the average payoff $\pi_i = \sum_{j=1}^N P_{ij}x_j$, where x_j is the fraction of individuals of type j and P_{ij} is the payoff matrix. The replicator dynamics is given by

$$\dot{x}_i = \eta x_i (\pi_i - \langle \pi \rangle), \quad (1.15)$$

where $\langle \pi \rangle = \sum_{i,j=1}^N x_i P_{ij} x_j$ is the average payoff in the whole population and η is a selection rate. Obviously, we have $\sum_{i=1}^N \dot{x}_i = 0$, i.e. the total population size is conserved. The fraction of individuals that have a fitness above the average fitness increases, while the fraction of individuals with lower than average fitness decreases. A strategy i that is not present at time t_0 will never appear in this dynamics for any $t > t_0$. However, extensions of the replicator dynamics in order to include mutations have been proposed (Page and Nowak, 2002; Stadler and Schuster, 1992).

Often, temporal discretizations of the replicator dynamics are considered. Such a discretization can be intricate, as Eq. (1.19) can have constants of motion which are often not conserved in a time discrete version that results from an Euler discretization (Hofbauer, 1996). These constants of motion arise from a cyclic dominance of strategies, as in the game of rock-paper-scissors. It can be defined by the payoff matrix

$$P = \begin{pmatrix} 0 & +1 & -1 \\ -1 & 0 & +1 \\ +1 & -1 & 0 \end{pmatrix}. \quad (1.16)$$

We identify the fraction of the strategies rock, paper, and scissors with x_1 , x_2 , and x_3 , respectively. x_3 can be computed as $1 - x_1 - x_2$, since $\sum_{i=1}^3 x_i = 1$. For this payoff matrix, equation (1.19) has the constant of motion $H = \ln x_1 + \ln x_2 + \ln x_3$. The invariance of H can be shown in a straightforward way: The time derivative of H reduces to

$$\dot{H} = \frac{\dot{x}_1}{x_1} + \frac{\dot{x}_2}{x_2} + \frac{\dot{x}_3}{x_3} = \pi_1 + \pi_2 + \pi_3 - 3\langle \pi \rangle. \quad (1.17)$$

For the payoff of the strategy “rock” we find $\pi_1 = x_2 - x_3$. The remaining payoffs follow from a cyclic change of the indices: $\pi_2 = x_3 - x_1$ and $\pi_3 = x_1 - x_2$. Obviously, we have $\sum_{i=1}^3 \pi_i = 0$. These symmetry properties lead also to $\sum_{i=1}^3 \pi_i x_i = \langle \pi \rangle = 0$ and hence to the conservation of H , $\dot{H} = 0$. The usual numerical solvers for such differential equations, as Euler or Runge-Kutta discretization, are not recommended for the study of replicator equations with such constants of motion, as they do not take care of the peculiar conservation properties (Hofbauer, 1996).

In general, equation (1.19) can show various different dynamics: In the simplest case, an approach to fixed points is described, as in the prisoner’s dilemma. For more than two strategies, oscillations can appear in cyclic games, as discussed above. Even irregular and chaotic dynamics are possible.

If interactions between two populations are considered, a straightforward generalization of the replicator dynamics is given by the coupled replicator dynamics (Schuster and Sigmund, 1981; Hofbauer, 1996). In this case, the expected payoff of a certain action depends on the strategy distribution of the other population. Hence, the mutual dependence on the payoffs leads to a coupling of the replicator equations for both populations. Consider a game between two populations, X and Y , with the payoff matrices P_{ij}^x and P_{ij}^y , respectively. In general, the number of strategies can be different. Here we restrict ourselves to the case where both populations have the same number of strategies. Every individual is only interacting with the other population. The coupled replicator equations take the form

$$\begin{aligned}\dot{x}_i &= \eta_x x_i \left(\sum_{j=1}^N P_{ij}^x y_j - \sum_{i,j=1}^N x_i P_{ij}^x y_j \right) \\ \dot{y}_i &= \eta_y y_i \left(\sum_{j=1}^N P_{ij}^y x_j - \sum_{i,j=1}^N y_i P_{ij}^y x_j \right)\end{aligned}\quad (1.18)$$

Although these equations are very simple, they can show a wealth of dynamical phenomena, including chaos (Sato *et al.*, 2002; Sato and Crutchfield, 2003). However, it is unclear whether the coupled replicator dynamics is the appropriate description for learning in asymmetric conflicts (Maynard Smith, 1982; Hofbauer, 1996). In games with overlapping generations, the adjusted replicator dynamics (Maynard Smith, 1982; Weibull, 1995) can be a more valid description. In the adjusted replicator dynamics, the evolution equations (1.19) and (1.18) are divided by the average fitness of the corresponding population. For example, equation (1.19) is changed to

$$\dot{x}_i = \eta x_i \frac{\pi_i - \langle \pi \rangle}{\langle \pi \rangle}, \quad (1.19)$$

For the usual replicator dynamics, the effect of this operation corresponds to a re-scaling of time and can usually be neglected. For the coupled replicator dynamics, however, the

stability of fixed points can be altered (Maynard Smith, 1982). The adaptive learning rates discussed in (Traulsen and Schuster, 2003) can be viewed as an interpolation between these two types of dynamics.

It should be noted that other game dynamics have also been discussed, as imitation dynamics, best-response dynamics, and many more (Hofbauer and Sigmund, 1998). However, the standard approach in evolutionary game theory remains the replicator dynamics.

1.4.3 Mathematical tools

From a conceptual point of view, the replicator equations (1.18) and (1.19) are nonlinear first order differential equations. In general, an analytical solution of these systems is not possible. Hence, the analysis is restricted to the qualitative theory of differential equations, i.e. they have to be viewed as nonlinear dynamical systems.

Dynamical systems

A dynamical system in continuous time is defined as

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}), \quad (1.20)$$

where $\mathbf{f}(\mathbf{x})$ is a nonlinear or linear function of the vector \mathbf{x} . Even if a closed solution of (1.20) is not possible, some general properties can be discussed. Of particular interest are the fixed points of the system: If $\mathbf{f}(\mathbf{x}_0) = 0$ the system will remain at \mathbf{x}_0 forever. The nature of the fixed point can be assessed discussing the dynamics near the fixed point. If the fixed point is stable, a small perturbation will lead back to the fixed point. Perturbations of unstable fixed points lead away from these points.

Most of the properties of the systems discussed here can be transferred to discrete time. However, sometimes qualitative differences in the dynamics can appear. A simple example is the logistic growth equation

$$\dot{x} = cx(1 - x), \quad (1.21)$$

which describes the population growth of a population with a maximum size normalized to 1. An analytical solution is possible, see Equation (1.14), and describes the approach to the maximum size. However, the discrete version of the differential equation, known as the logistic map, shows chaotic behavior. Hence, the relationship between time discrete and time continuous systems is not always trivial.

Stability of fixed points

In (Traulsen and Schuster, 2003), a dynamical system is analyzed by discussing the stability of fixed points only. The stability of fixed points can be determined from a linearization

around the fixed point. The linearization of (1.20) at $\mathbf{x}_0 + \mathbf{h}$ with fixed \mathbf{x}_0 and $\mathbf{h} \ll 1$ reads

$$\dot{\mathbf{h}}_j = \mathbf{f}_j(\mathbf{x}_0) + \sum_i \mathbf{h}_i \frac{\partial \mathbf{f}_j}{\partial \mathbf{x}_i}. \quad (1.22)$$

Since $\mathbf{f}_j(\mathbf{x}_0) = 0$ this can be written as

$$\dot{\mathbf{h}} = J \cdot \mathbf{h}, \quad (1.23)$$

where J is the Jacobian at \mathbf{x}_0 . The effect of a small perturbation at the fixed point is now determined by the Jacobian. If all eigenvalues of J have a negative real part, the perturbation will be dampened and the system will move back to the fixed point. If all these eigenvalues have a positive real part, the perturbation will be amplified and the system will leave the fixed point. However, these cases are very special and in general, there will be some eigenvalues with positive real part and some with negative real part. In these cases, the stability is different in different directions. Eigenvalues with positive real part correspond to an unstable situation in the direction of the corresponding eigenvector. Eigenvalues with negative real part correspond to a stable situation in the corresponding direction. For example, one eigenvalue with negative real part and one eigenvalue with positive real part in $d = 2$ correspond to a saddle. The corresponding fixed point is attractive when movement in one direction is considered. In a second direction, the fixed point is unstable.

For completeness, we note that a non-vanishing imaginary part of an eigenvalues leads to a cycling around the fixed point. The real part determines whether the distance to the fixed point increases or decreases in time.

Bifurcations

When the stability of a fixed point is modified due to a change of external parameters, several scenarios are possible: For example, a fixed point can simply vanish or switch stability with another fixed point. Several of these bifurcations are possible, three of them appear in this thesis when the stability of fixed points of replicator equations is discussed. Here, a short sketch of these bifurcations is given. For each bifurcation, a normal form can be defined that describes the simplest possible system with such a bifurcation (Schuster, 1995; Argyris *et al.*, 1995).

- **Pitchfork bifurcation**

In a pitchfork bifurcation, one stable fixed point becomes unstable. At the same point, two new stable fixed points appear. The normal form of a pitchfork bifurcation is given by

$$\dot{x} = \mu x - x^3. \quad (1.24)$$

This dynamical system has only one fixed point at $x = 0$ for $\mu < 0$. Near this fixed point, the third order term in x can be neglected. This shows immediately that this fixed point is stable. For $\mu > 0$ there are three fixed points. A linear stability analysis shows that $x = 0$ is unstable for $\mu > 0$, whereas the other two fixed points at $x = \pm\sqrt{\mu}$ are stable. The situation that a single stable fixed point becomes unstable and is replaced by two symmetric stable fixed points is found in a variety of physical systems. For example, the simplest mean field theory for the Ising model shows such a transition for a critical temperature T_c . Above T_c , the system has only one fixed point describing non-magnetized states. Below T_c , two magnetized states with different magnetic field are possible.

- **Saddle node bifurcation**

In a saddle node bifurcation, a fixed point vanishes at a critical parameter value. The normal form of the saddle node bifurcation reads

$$\dot{x} = \mu - x^2. \quad (1.25)$$

For $\mu < 0$, the system has no real fixed points. For $\mu > 0$, two fixed points appear at $x = \pm\sqrt{\mu}$. A linear stability analysis reveals that the fixed point at $x = -\sqrt{\mu}$ is unstable and the fixed point at $x = +\sqrt{\mu}$ is stable. At the unstable position of an ideal pendulum such a saddle node bifurcation occurs. An ideal pendulum pointing upwards will stay in this position until a small disturbance moves it away from this unstable fixed point. However, if the energy of the pendulum is high enough such that the pendulum rotates, this is not longer a fixed point.

- **Hopf bifurcation**

A Hopf bifurcation describes a situation in which a stable fixed point is replaced by a stable oscillating solution. The normal form of such a system in polar coordinates is given by

$$\dot{r} = \mu r - r^3 \quad (1.26)$$

$$\dot{\theta} = \omega. \quad (1.27)$$

For $\mu < 0$ there is a stable focus at $r = 0$. For $\mu > 0$ this focus becomes unstable. Instead, an cyclic attractor at $r = \sqrt{\mu}$ appears. Hopf bifurcations are typically found when the onset of turbulence is considered.

Stochastic differential equations

In (Traulsen *et al.*, 2004b), an extension of the replicator to a stochastic dynamical system is discussed. There are several mathematical methods for such stochastic dynamical systems

(Gardiner, 1985; Schuster, 2002). Here, stochastic differential equations are introduced.

In one dimension, such a stochastic differential equation is given by

$$\dot{x}(t) = f(x(t)) + g(x(t))\xi(t). \quad (1.28)$$

In most cases, $\xi(t)$ is assumed to be white Gaussian noise with autocorrelation function $\langle x(t)x(t') \rangle = \sigma^2\delta(t-t')$. There are two ways to analyze equation (1.28). It can be considered as a differential equation which can be solved at least formally. However, this solution still has stochastic character. Another possibility is to derive an equation for the evolution of the probability density of the stochastic process.

Let us first concentrate on the first approach and begin with a special example, the Ornstein Uhlenbeck process (Uhlenbeck and Ornstein, 1930). It is defined by

$$\dot{x}(t) = -\frac{1}{\tau}x(t) + \frac{1}{\tau}\xi(t) \quad (1.29)$$

It can be shown that the Ornstein Uhlenbeck process is the only stationary Gaussian Markov process (Doob, 1942). For simplicity, we restrict ourselves to a process with initial condition $x(0) = 0$. The formal solution of (1.29) with this initial condition reads

$$x(t) = \frac{1}{\tau}e^{-t/\tau} \int_0^t e^{s/\tau} \xi(s) ds. \quad (1.30)$$

Integrals over stochastic processes as this one have to be treated with much care. The mathematical precise formulation of $\int \xi(s) ds$ is $\int dW(s)$, where $W(s)$ is the Wiener process. Only stochastic integrals with respect to this process are well defined. The conventional definitions of integrals as e.g. the Riemann integral are no longer valid. Two distinct approaches have been defined: If the problem is discrete in time and the differential equation is only an approximation, the Ito integral widely used in financial mathematics is the correct description (Gardiner, 1985; Deutsch, 2004). In physics, where fluctuations are usually correlated over finite length and time scales (Traulsen *et al.*, 2004a), the Stratonovich integral is the correct mathematical formulation. However, as long as the noise is only additive, i.e. if $g(x(t))$ does not depend on $x(t)$, both mathematical approaches lead to the same results. From (1.30) the average value of the Ornstein Uhlenbeck process can be computed as $\langle x(t) \rangle = 0$. For the autocorrelation function we find omitting the non-stationary terms and using $\langle x(t)x(t') \rangle = \sigma^2\delta(t-t')$

$$\langle x(t)x(t') \rangle = \frac{\sigma^2}{2\tau} e^{|t-t'|/\tau}. \quad (1.31)$$

Hence, the variance of the stationary solution reads $\langle x(t)x(t) \rangle = \frac{\sigma^2}{2\tau}$. The approach to solve the stochastic differential equation directly leads to a stochastic process. The properties of this process can be computed directly.

The second approach is to define an evolution equation for the probabilities of the process. For the general stochastic differential equation (1.28), a so called Fokker-Planck equation can be derived (Gardiner, 1985)

$$\dot{P}(x) = -\frac{\partial}{\partial t} \left(f(x) + \frac{\sigma^2}{2} g(x)g'(x) \right) P(x) + \frac{1}{2} \frac{\partial^2}{\partial t^2} \sigma^2 g(x)^2 P(x) \quad (1.32)$$

The solution of this equation yields the development of the probabilities. For example, for constant $g(x)$ and vanishing $f(x)$ it yields the famous diffusion equation. Often, a stationary solution is considered. For $\dot{P} = 0$ a probability current can be defined that has to be constant in x such that the right hand side vanishes. Arguments on the boundary conditions of the system often lead to the conclusion that this probability current has to be zero and a detailed solution is possible. For the Ornstein Uhlenbeck process, the stationary solution is a Gaussian with variance $\frac{\sigma^2}{2\tau}$. This variance has also been found in the direct approach used above. In (Traulsen *et al.*, 2004b), the stationary solution of the Fokker Planck equation is used to compute the average payoff of a population with adaptive selection rate.

1.5 Survey of the Publications

1.5.1 Similarity based cooperation and spatial segregation

Studies of public goods games as the Prisoner's Dilemma have often been focused on the effects of memory (Lindgren, 1991; Hauert and Schuster, 1997; Hauert, 1999). Direct reciprocity based on the memory of previous interactions can be very effective in order to induce cooperation. However, memory can only be taken into account when repeated interactions are restricted to few interaction partners. In addition, memory does only work if the opponent is not met for the first time. Therefore, additional mechanisms that induce cooperation have been proposed, as indirect reciprocity (Nowak and Sigmund, 1998b), kin selection (Hamilton, 1964a,b), group selection (Maynard Smith, 1964, 1976; Wilson, 1975) or similarity based mechanisms (Riolo *et al.*, 2001). These similarity based mechanism are subject to this thesis.

However, it is controversial whether cooperation can arise from external traits that are visible to others at all. Dawkins (1976) introduced the famous green beard effect as a thought experiment in sociobiology: Consider a gene that confers on its bearer not only a green beard (or any other visible trait), but also the instinct to help others with green beards. Individuals with such a gene would effectively form a self-serving group, and the gene would spread in the population. However, the idea of a gene that simultaneously produces a signal and a behavior for the signaler is not easy to accept. Any mutation that leads to a green beard, but not to the tendency to cooperate, is advantageous and cooperation would break down rapidly. Hence, it is not clear whether such a cooperation can arise at all.

R. Riolo, M. Cohen and R. Axelrod (Riolo *et al.*, 2001) introduce a more plausible model in which individuals simply like others that are similar to themselves (Sigmund and Nowak, 2001). They are not allowed to cheat, i.e. they always help others that are very similar to themselves. If this requirement is relaxed, the system reduces to the Prisoner's Dilemma. Such a similarity based cooperation can be induced by cultural tags, as clothing, club memberships, or religious beliefs. In the simulations of Riolo *et al.*, each individual has a tag $\tau \in [0, 1]$. An individual i provides help to another individual j only if the difference between their tags is smaller than some tolerance threshold T_i of i , $|\tau_i - \tau_j| \leq T_i$. If an individual provides help to another one, it incurs a cost c , while the other one gains a benefit b . Individuals reproduce with a probability proportional to their payoffs. In order to maintain variability, additional mutations are included. These mutations have a significant influence on the dynamics of the system. Mutations of the tolerance level are realized by introducing a probability distribution around the old tolerance. As no negative tolerance thresholds are allowed, this leads to an increase of the tolerance on average. Hence, there is a net drift from intolerant to tolerant strategies. In order to determine the effect of this drift, it is included

in the well mixed system (Traulsen and Schuster, 2003) as well as in the spatially extended system (Traulsen and Claussen, 2004).

The model of Riolo *et al.* has been criticized, since agents are forced to cooperate with each other (Roberts and Sherratt, 2002; Hauert, 2002b). In Dawkin's picture, any mutation that maintains the green beard, but eliminates the tendency to help others with this trait would easily spread and abandon this kind of similarity based cooperation. In this way, the title of the paper of Riolo *et al.*, "Evolution of cooperation without reciprocity" is misleading. However, the mechanism that maintains cooperation within a group does not necessarily have to be the same as the mechanism that induces cooperation between groups. An individual could take a tag as a first estimation, the cooperation between individuals from the same group could as well be induced by direct or indirect reciprocity or even different mechanisms.

Although the model of Riolo *et al.* is interesting from a conceptual point of view, it does not allow any insights into the driving mechanisms, as it relies solely on computer simulations. However, a detailed analytical description of the model is not possible. Hence, there is a need for a minimal model that allows for an analytical solution. Such minimal models can be very helpful in order to identify the underlying mechanisms that drive the phenomena observed in more complicated models.

Such a minimal model motivated by the work of Riolo *et al.* has been developed in this thesis. In an initial step, the number of different strategies is reduced. This simplification allows to formulate an evolution equation for the probabilities to find a certain strategies in a well mixed system instead of simulating a finite population. Sigmund and Nowak (2001) argued that any spatial distribution would be an obstacle for cooperation. They expected a spatial segregation of different group supporting only others of their own kind. Our simplification allows to analyze this in detail.

The number of possible tags, which is basically unbounded in the model of Riolo *et al.*, has been reduced to two only, red and blue. Hence, it makes only sense to define two tolerance levels. Agents can either cooperate with everybody, $T = 1$, or only with others with the same tag, $T = 0$. In the next step, symmetric interactions are introduced. If two agents are paired, each of them has the possibility to support the other or not. A cooperation results in a cost c for the donor and a benefit b for his partner. The game is described by the payoff matrix depicted in Table 1.1.

As in the model of Riolo *et al.* (2001), agents always cooperate with others with their own tag. What happens if this requirement is relaxed? If intolerant agents do not cooperate at all, the tags lose their meaning: tolerant agents cooperate with everybody. They receive $b - c$ for interactions with other tolerant agents, regardless if they have a blue or red tag. If they encounter an intolerant agent, they pay $-c$. Intolerant agents, on the other hand, receive b if they interact with tolerant agents. They will refuse to cooperate with other intolerant agents, leading to the payoff 0. Hence, the payoff matrix describes exactly the Prisoner's Dilemma

(Tag, T)	(red,1)	(blue,1)	(red,0)	(blue,0)
(red,1)	b-c	b-c	b-c	-c
(blue,1)	b-c	b-c	-c	b-c
(red,0)	b-c	b	b-c	0
(blue,0)	b	b-c	0	b-c

Table 1.1: Payoff matrix of the minimal model for similarity based cooperation.

if intolerant agents do not cooperate at all, making the differences between tags vanish. If unconditional defectors are present in addition to the other strategies, they dominate both other strategies. Hence, cooperation will not evolve. Recently, Axelrod *et al.* (2004) have shown by computer simulations that in spatial systems, the intolerant strategy or ethnocentric strategy can survive and lead to higher levels of cooperation than in spatial systems without any tags.

This simplified model has been used to analyze similarity based cooperation on a spatial lattice by numerical simulations. The analytical methods discussed in 1.3 cannot be transferred to this system, since they are designed primarily for two strategies only, while the minimal model consists of four strategies. The degree of segregation in this model has been quantified numerically using correlation lengths and the spatial dissimilarity index (Duncan and Duncan, 1955). Segregation has also been discussed in the famous paper of Schelling (1971). However, Schelling assumed that segregation is a natural desire of the agents. In our model, segregation arises naturally from the interplay of similarity and mutual cooperation.

In the next step, the drift from intolerant to tolerant strategies discussed above is included in the model. In the spatially extended system, this drift can be realized as a local update mechanism: If all agents in the neighborhood are of the same group, an agent switches to the tolerant strategy. This reasoning leads to a cyclic dominance of strategies: A red intolerant cluster becomes tolerant due to this local drift. Once these agents are tolerant, intolerant blue agents can invade, leading to a blue intolerant cluster. In the next step, the local drift makes this cluster tolerant. Red intolerant clusters invade and the cycle starts again, see Fig. 1.3. This cyclic dominance leads to the emergence of spiral waves in the spatially extended system.

In addition, mechanisms to overcome segregation have been discussed. The basic question is, what ingredients are necessary to create a population that cooperates mutually across segregation borders. In this way, cooperation between groups could be established and the group membership would lose its importance. As a local drift towards more tolerance does not establish cooperation in the system, additional mechanisms are necessary. It turned out that two features have to be present in a system with synchronous update in order to create

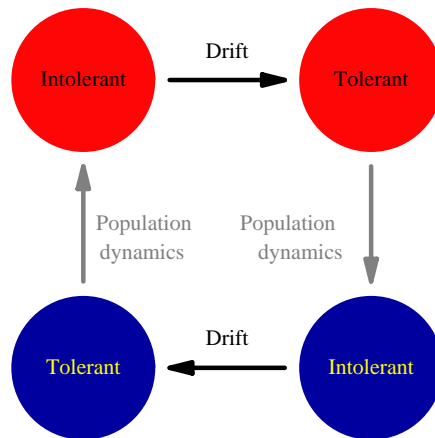


Figure 1.3: Cyclic dominance of the strategies due to the population dynamics and the drift from intolerant to tolerant strategies. Intolerant red clusters become tolerant due to the drift. Red tolerant clusters are attacked by blue intolerant agents, which transform to tolerant agents again. Finally, red intolerant agents can invade again.

a segregated cluster of tolerant agents: Agents need the ability to become tolerant once they are not exploited. In addition, they have to be able to decrease their tolerance when they are likely to be exploited. This reminds of the Tit for Tat strategy of the Prisoner’s Dilemma with memory (Axelrod, 1984): This strategy has the ability to punish others, but also the ability to forgive and return to cooperation. Such a strategy leads to a segregated system of red and blue agents. However, now agents cooperate across segregation borders.

1.5.2 Minimal model for tag-based cooperation

The minimal model for similarity based cooperation described in 1.5.1 is not only useful to analyze spatially extended systems. In well mixed systems, it allows an analytical description of the dynamics of the system.

The computer simulations of Riolo *et al.* (2001) showed characteristic oscillations of the average tolerance, called “Tides of tolerance” by Sigmund and Nowak (2001). The tolerance increases slowly until a wave of intolerance starts spreading reducing the overall cooperation. Sigmund and Nowak conjectured that the upward drift of the tolerance was induced by a combination of mutation pressure and kin selection. However, an explicit explanation of this phenomenon has been lacking. No waves appear if mutations of the tolerance or the tags are omitted (Traulsen and Schuster, 2003). As the simulations in Riolo *et al.* (2001) consider a mixed population, it is possible to construct a mean-field theory for the dynamics. In this mean field theory, an evolution equation for the probabilities of the strategies can be

introduced instead of simulating a finite population. For this purpose, the replicator dynamics discussed in 1.4.2 is chosen. As the dynamical system described by the replicator dynamics cannot be solved analytically in detail, only the stability of fixed points can be discussed. For this purpose, the fixed points have to be determined from a set of four equations describing the evolution of the probabilities for the four strategies. The stability of these fixed point is then determined by a linear stability analysis as described in 1.4.3.

We find stable fixed points of the evolutionary dynamics corresponding to Nash equilibria for the game given by the payoff matrix shown in Table 1.1: If the population consists either of blue or red players only, everybody cooperates and the frequencies of the strategies no longer change. These fixed points are only stable if the fraction of intolerant agents is higher than the cooperation cost divided by the benefit for cooperation. The basins of attraction of the stable red and blue fixed points are separated by a linear plane. Points on this separatrix converge to the mixed Nash equilibrium in which only intolerant agents - 50% red and 50% blue - exist. A linear stability analysis of the mixed Nash equilibrium shows that it is unstable in one direction and stable in the remaining two directions. It turns out that the unstable direction of the Nash mixed equilibrium is the normal of the separatrix dividing the basins of attraction of the red and blue fixed points. This can be shown straightforward by analyzing the dynamics on this plane.

However, the Nash equilibria given by the red and blue fixed points are not strict and the fixed points are hence not Evolutionary Stable Strategies (Maynard Smith and Price, 1973). Consider a population of red intolerant agents only. As red tolerant agent receive the same payoff, neutral mutations can increase the fraction of these agents. If the fraction of tolerant agents is high enough, blue intolerant agents can invade the population, leading to a blue intolerant population. Here, the cycle continues with the roles of red and blue tags exchanged. In order to include the average effect of such neutral mutations into the replicator dynamics, we introduced a drift from intolerant to tolerant strategies. The fraction of red tolerant agents is increased by transforming a fraction ε of the intolerant red agents to tolerant red agents and equivalently for the blue agents. This drift leads the system to unstable fixed points, hence, oscillations emerge from this drift. These oscillations are the deterministic equivalents to the “Tides of tolerance” observed by Riolo *et al.* (2001). The drift towards more tolerance leads to a cyclic dominance in the model: Red intolerant populations become tolerant via this drift, the game dynamics transforms the red tolerant population to a blue intolerant one. Here, the drift increases the tolerance again leading to a blue tolerant population, which is, in turn, attacked by red intolerant agents. The mechanism is the same as in the spatially extended system, only the nature of the drift is different.

The minimal model allows to compute the stability of the fixed points in the model analytically even in the presence of this drift. The stability depends on the drift parameter ε and the cost of cooperation c , see (Traulsen and Schuster, 2003) for details. If these parameters

are varied, the stability of the fixed points is altered and different bifurcations are observed. In particular, the transition to the oscillating state induced by the drift towards tolerance is a saddle node bifurcation with a linear perturbation term. In this bifurcation, a small channel is opened through which the trajectory crosses the separatrix. Depending on the cooperation costs, different dynamical regimes can be observed. For very small cooperation costs, the drift leads to a stabilization of fixed points that are unstable for $\varepsilon = 0$. These fixed points appear if all players cooperate with every other players, regardless of their group membership. For higher cooperation costs, a single attractor can be found in the system. This attractor is found for a wide range of cooperation costs. For even higher costs, the drift cannot longer drive the system through the separatrix and two attractors appear. In one of them, red agents dominate and in the other one blue agents. When c is increased further, these cyclic attractors vanish in a Hopf bifurcation and new fixed points that are created by the drift become stable. Finally, these fixed points join with the mixed Nash equilibrium in a supercritical pitchfork bifurcation, which is the only stable fixed point for very high cooperation costs. Details on these transitions can be found in (Traulsen and Schuster, 2003)

A cyclic dominance as the one induced by the drift from intolerant to tolerant strategies often leads to closed trajectories in mean field theories. The most prominent example is the simple game “Rock-Paper-Scissors” discussed in 1.4.2. A particular interesting example are asymmetric conflicts. In (Traulsen *et al.*, 2004b) it is shown that oscillations in these systems can be dampened in such a way that one player gains an increased payoff.

1.5.3 Stochastic gain in population dynamics

Mean field theories of cyclic games show oscillations in time: The cyclic dominance of the strategies leads to an oscillation of the fraction of the different strategies. From a physicist’s point of view, it is natural to ask how the “energy” of these oscillations can be extracted. An interesting example are asymmetric conflicts. In these game theoretic systems, two players with different roles interact. This could be attackers and defenders, buyers and sellers, or males and females. One example for an asymmetric conflict is the game of “matching pennies”. Consider a town with two pubs. Everybody goes to one of them each night. Person A wants to meet B every night, while B tries to avoid meeting A. This situation can be viewed as a game between A and B: If A and B do the same, A wins and B will choose differently in the future. If they chose different options, A loses and A will switch to the same option as B again. This leads to a cyclic dominance again. In biology, a reasoning over costs of parental care leads to the name “battle of the sexes” for this game (Maynard Smith, 1982).

These asymmetric conflicts are especially interesting, as one can easily analyze situations in which one population of players has a slightly different adaptation mechanism than the population in the second role. A first question is how the oscillations induced by the cyclic

dominance can be exploited by one population. This way, the oscillations would be dampened and the average payoff of this population would increase. In this situation, it is not enough if one population simply has a different selection or learning rate. In this case, their strategies oscillate with different frequencies, but the dynamics is still periodic. A simple approach is to introduce a selection rate that changes with the success of the population. If the population is in a good state, the selection becomes weaker. The escape from unfavorable states is accelerated by higher selection rates. Such a behavior is motivated by the “win stay—lose shift” strategy from reinforcement learning (Sutton and Barto, 2000). In mathematical terms, the selection rate η can be written as

$$\eta = \eta_0 (1 - \tanh[\alpha \Delta\pi]), \quad (1.33)$$

where η_0 is a base selection rate, α is a perception ability and $\Delta\pi$ is the difference between the average payoffs of two interacting populations. For $\alpha \rightarrow 0$ the selection rate remains constant. For $\alpha \rightarrow \infty$ the population is not changed by selection if $\Delta\pi > 0$, while it evolves with a rate $2\eta_0$. It has been shown that such a learning rate can stabilize the mixed Nash equilibrium in the game of matching pennies (Traulsen *et al.*, 2004b). In particular, the Nash equilibrium is stabilized in such a way that one population has an increased payoff when the Nash equilibrium is approached. However, the Nash equilibrium is not always approached in systems with adaptive selection rates. For example, in the game of “Rock-Paper-Scissors”, trajectories exist on which $\Delta\pi = 0$, e.g. where both populations use exactly the same strategies. This has previously been conjectured (Sato *et al.*, 2002).

The solution of the coupled replicator dynamics of this system shows that the system always stays at the mixed Nash equilibrium which has been stabilized by the adaptive selection rates. In realistic systems, disturbances are expected which lead the system away from this fixed point again. For small fluctuations, the system stays near the Nash equilibrium, where both populations have the same success. Very strong fluctuations dominate over the selection mechanism and adaptive selection rates do not have any influence. Intermediate levels of fluctuations, however, can be exploited: If the time interval between large disturbances is long enough such that the system settles back at the stable fixed points, these fluctuations can be exploited. There are several sources for such fluctuations. They can result from errors of players, changes in the environment or external shocks. Randomness can also arise from finite populations (Claussen and Traulsen, 2005) or from payoff matrices with random entries (Eriksson and Lindgren, 2001). We follow the usual approach to include noise as a Langevin term to the usual replicator equations (Foster and Young, 1990; Fudenberg and Harris, 1992; Cabrales, 2000). In this way, the usual deterministic replicator equation is replaced by a stochastic differential equation, as discussed in 1.4.3. These stochastic differential equations are combined with adaptive selection rates in asymmetric conflicts. The adaptive selection rates lead to the exploitation of such fluctuations. This effect has been found numerically in

different games, as well in cyclic games as matching pennies and in the Prisoner's Dilemma. For non-cyclic games, even a rough analytical approximation for the average payoff under the influence of noise is possible (Traulsen *et al.*, 2004b). In principle, the mechanism can also be transferred to finite populations. For example, one could adapt the selection pressure on one population in a Moran process, as introduced in (Nowak *et al.*, 2004).

A mechanism that exploits fluctuations can in principle be applied to realize increased earnings in real markets, which can under some circumstances be described by games. In particular, the "Minority game" often serves as a model for a simple market (Challet and Zhang, 1997; Challet *et al.*, 2000). So what hinders us from applying this mechanism at the stock market and becoming rich? First, our model assumes an infinite population size and introduces artificially external disturbances. It is not clear whether such kind of fluctuations are present and if they are stronger than fluctuations from an inherent noise arising from finite populations (Claussen and Traulsen, 2005). However, First numerical simulations indicated that the stochastic gain effect can also be observed in finite populations.

2 Publications

This chapter contains the following publications:

- Arne Traulsen and Jens Christian Claussen,
Similarity based cooperation and spatial segregation,
Physical Review E **70**, 046128 (2003)
(Virtual Journal of Biological Physics Research **8** (9), 2004)
- Arne Traulsen and Heinz Georg Schuster,
Minimal model for tag-based cooperation,
Physical Review E **68**, 046129 (2003)
(Virtual Journal of Biological Physics Research **6** (9), 2003)
- Arne Traulsen, Torsten Röhl, and Heinz Georg Schuster,
Stochastic gain in population dynamics,
Physical Review Letters **93**, 028701 (2004)
(Virtual Journal of Biological Physics Research **8** (2), 2004)

2.1 Similarity based cooperation and spatial segregation

PHYSICAL REVIEW E 70, 046128 (2004)

Similarity-based cooperation and spatial segregation

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We analyze a cooperative game, where the cooperative act is not based on the previous behavior of the coplayer, but on the similarity between the players. This system has been studied in a mean-field description recently [A. Traulsen and H. G. Schuster, Phys. Rev. E **68**, 046129 (2003)]. Here, the spatial extension to a two-dimensional lattice is studied, where each player interacts with eight players in a Moore neighborhood. The system shows a strong segregation independent of parameters. The introduction of a local conversion mechanism towards tolerance allows for four-state cycles and the emergence of spiral waves in the spatial game. In the case of asymmetric costs of cooperation a rich variety of complex behavior is observed depending on both cooperation costs. Finally, we study the stabilization of a cooperative fixed point of a forecast rule in the symmetric game, which corresponds to cooperation across segregation borders. This fixed point becomes unstable for high cooperation costs, but can be stabilized by a linear feedback mechanism.

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I. INTRODUCTION

The study of complex systems with game-theoretic interactions has recently attracted a lot of attention in statistical physics, biology, behavioral sciences, and economics. In contrast to standard game theory [1] the focus has recently been on evolutionary game theory [2–6]. In particular, the prisoner's dilemma [7] has become the metaphor for the evolution of cooperation in populations of selfish individuals. If the game is not repeated, the dominating strategy is to defect. However, repeated interactions of individuals memorizing the past can establish high levels of cooperation from direct reciprocity [7]. Reciprocity works also indirectly if individuals can observe the behavior of others and cooperate with respect to the reputation of others [8,9].

Real world interactions are often restricted to small local groups. Realizing that territoriality can have strong influences on the evolution of cooperation, Axelrod proposed the study of a spatially extended prisoner's dilemma [7]. Nowak and May studied a cellular automaton based on the prisoner's dilemma [10]. They found that reducing interactions to small local groups can promote cooperation, as cooperative clusters minimize their contacts with neighboring defectors. Their paper initiated an intensive research on spatially extended games on two-dimensional lattices [11–14] and network topologies [15–18]. However, spatial structure does not necessarily lead to an increased level of cooperation [19].

Another mechanism that can promote cooperation among related individuals is kin selection [20]. Although kin selection is controversial in biology, indications for similarity-based interaction mechanisms have been found on the molecular level [21,22]. Riolo *et al.* introduced a model in which agents are equipped with traits that allow one to discriminate between different groups of players [23]. It has been argued that the model is of limited biological relevance,

as agents are forced to cooperate within their own group [24,25]. However, cooperation can evolve from a combination of kin selection and reciprocity, which can promote such an intragroup cooperation. The mechanism that leads to cooperation does not have to be the same for interaction within groups and between groups. In spatially extended systems agents can only prosper if they get sufficient support from their neighbors. Hence, cooperation based on similarity will lead to a segregation of different groups in spatially extended system [26].

Although the importance of group memberships is stressed in the social sciences [27], segregation is usually not desired in social systems. We raise the question on the minimal requirements for agents in order to avoid this kind of segregation. We introduce a forecast rule that helps to overcome the segregation, leading to a population in which agents support others regardless of their group membership. The corresponding spatial pattern can be stabilized by a linear global feedback.

II. DEFINITION OF THE MODEL

The evolution of cooperation in large populations is usually analyzed in systems based on public goods games [28]. For each cooperation a cost $c_i > 0$ depending on the tag of the player is incurred which results in a benefit $b > c_i$ for the interaction partner. For simplicity, we restrict ourselves to two groups of agents only, red and blue. In every group there are two kinds of players. Intolerant players support only others with the same tag ($T=0$). Tolerant players ($T=1$) support any other player, regardless of his group membership. The payoff of every player depends on the strategies of his interaction partners. We introduce n_1^r , n_0^r , n_1^b , and n_0^b for the number of interaction partners that are tolerant red, intolerant red, tolerant blue, and intolerant blue, respectively. The payoff can be written as

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$$\Pi(x) = \begin{cases} (b - c_r)(n_0^r + n_1^r + n_1^b) - c_r n_0^b & \text{for } x = (\text{red}, 1), \\ (b - c_r)(n_0^r + n_1^r) + b n_1^b & \text{for } x = (\text{red}, 0), \\ (b - c_b)(n_0^b + n_1^b + n_1^r) - c_b n_0^r & \text{for } x = (\text{blue}, 1), \\ (b - c_b)(n_0^b + n_1^b) + b n_1^r & \text{for } x = (\text{blue}, 0). \end{cases} \quad (1)$$

In the following we restrict ourselves to $c_r = c_b = c$. The system with $c_r \neq c_b$ is analyzed in Sec. IV. In a single interaction the payoff is $b - c$ if both players cooperate with each other, $-c$ indicating that the player has been exploited and b indicating that the player has exploited his interaction partner. The payoff is zero when both players refused to cooperate. The tolerant strategies are dominated by the intolerant strategies, as the payoffs of the $T=1$ strategies are never higher than the payoffs of the $T=0$ strategies. In well-mixed systems without spatial structure this leads to bistability. One group becomes extinct and the other group dominates in the two evolutionary-stable Nash equilibria with intolerant players of one tag only. An alternating dominance of both groups can be generated if there is a drift towards more tolerance [29].

III. SPATIALLY EXTENDED SYSTEM

Players are arranged on a two-dimensional regular cubic lattice with periodic boundary conditions. The system size is $N = L \times L$. Each player interacts with his eight nearest neighbors (Moore neighborhood)—i.e., $n_0^r + n_1^r + n_0^b + n_1^b = 8$. After interacting with all the neighbors, the players update their strategy synchronously. This corresponds to discrete, non-overlapping generations. Strategies are updated due to the deterministic “best takes over” rule [30]; i.e., i switches to the strategy among its nearest neighbors that reached the highest payoff:

$$s_i^{t+1} = s_j^t \quad \text{where } j = \underset{j \in NN(i)}{\operatorname{argmax}} \Pi_j^t. \quad (2)$$

If several nearest neighbors with different strategies have the same success, players keep as much of their identity as possible. Choosing between switching tag or tolerance, players will switch their tolerance. This ensures that the update rule remains deterministic. However, these additional rules apply only in very rare cases. Note that the new strategy of a player depends on the strategies in his 5×5 neighborhood, as the payoffs in his 3×3 neighborhood are involved. Self-interactions can be neglected in our case. Hence, the game can be described as a deterministic cellular automaton with 4^{24} update rules. This is in contrast to the usual prisoner’s dilemma, where “only” 2^{24} update rules are necessary [10]. A modification of the cooperation cost leads to a modification of the update rules; see the Appendix for details. The extension of the usual prisoner’s dilemma to four strategies complicates the application of many tools for spatial games, as pair approximation [13,14,31], fundamental clusters [32,33], or mapping to Ising models [12].

A. Segregation in the basic system

As the tolerant strategies can easily be exploited by intolerant players from the other group, they can only survive

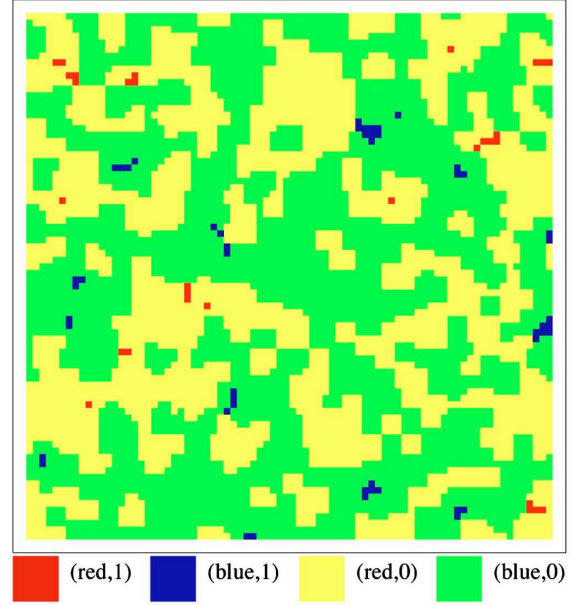


FIG. 1. (Color online) Basic system without mutations. Only ten generations after a random initialization the system reaches a static state. The tolerant players can only survive if they have sufficient support from their neighbors ($c=0.3$, $b=1.0$, $L=80$).

with sufficient support from surrounding players (cf. Fig. 1). Hence, the majority of players will be intolerant when the system reaches a static state. A 3×3 cluster of intolerant agents can always survive, as the player in the center has the highest possible payoff in his neighborhood. In general, a tolerant player not interacting with intolerant players of the other tag can always survive. If he interacts with such players, the cooperation cost determines which kind of clusters are stable.

As expected [26], the system shows a strong segregation. Segregation between different agents in cellular automata has already been observed in the seminal paper of Schelling [34]. However, in our case segregation is not directly based on observable traits of others, but on mutual support. Most of the players are intolerant. Players that support others across the segregation borders are always exploited; they cannot survive if the cooperation cost is too high. This is consistent with the mean-field theory [29], where only fixed points with intolerant players of one tag are stable.

The situation is slightly different if stochastic mutations are included, as the system no longer becomes static. Tolerance mutations increase the fraction of the tolerant agents, as there is no equilibrium between tolerant and intolerant agents. The tolerance mutations lead towards such an equilibrium, while the population dynamics works against this equilibrium. Mutations of the tags can also destabilize clusters, as they introduce new agents into an environment that cannot produce such agents by the population dynamics.

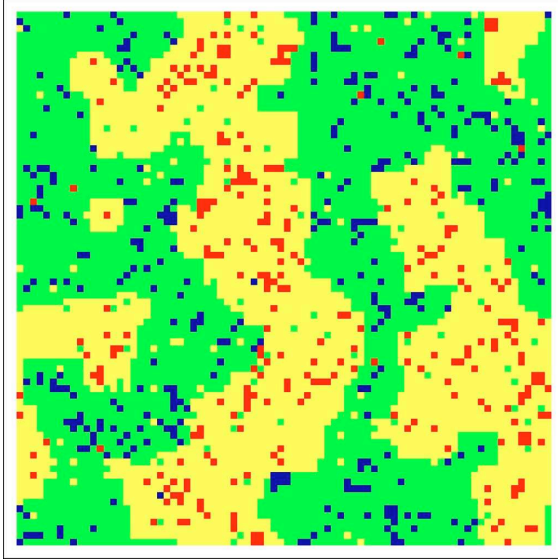


FIG. 2. (Color online) Basic system with mutations. With 2% probability, the tag and tolerance are modified independently. As in the system without mutations, the different tags segregate in space. One hundred generations after a random initialization, the majority of small clusters seen in the system without mutations (cf. Fig. 1) has vanished due to the destabilizing effect of the mutations. This leads to a longer correlation length; see text. Colors are as in Fig. 1 ($c=0.3$, $b=1.0$, $L=80$).

This leads to the disappearance of small clusters (cf. Fig. 2).

The degree of segregation can be quantified utilizing the “spatial dissimilarity index” D [35], defined as

$$D = \frac{1}{2} \sum_j \left| \frac{N_r^j}{N_r} - \frac{N_b^j}{N_b} \right|, \quad (3)$$

where N_r^j (N_b^j) is the number of red (blue) agents in subregion i and N_r (N_b) is the total number of red (blue) agents. Choosing a 3×3 neighborhood as subregion we find $D = 0.715 \pm 0.001$ ($c=0.3$, $N=1000$) indicating a strong degree of segregation, compared to

$$D = \frac{1}{9} \frac{1}{512} \sum_{j=0}^9 \binom{9}{j} |2j - 9| = \frac{35}{128} \approx 0.273$$

for a random population. D decreases less than 5% when c is increased ($D=0.729 \pm 0.001$ for $c=0.05$ and $D=0.707 \pm 0.001$ for $c=0.95$).

Another possible measure for the segregation is the correlation length λ . For simplicity, the correlations have only been computed for one direction. The probability that an agent in the distance of d has the same color decays as $p \propto e^{-d/\lambda}$. For $c=0.3$ we find a correlation length of $\lambda = 5.85 \pm 0.02$. The correlation length decreases slightly with increasing c ($\lambda = 6.25 \pm 0.02$ for $c=0.05$ and $\lambda = 5.65 \pm 0.02$ for $c=0.95$). As discussed above, mutations lead to the elimination of small clusters. Consequently, the correlation length

is increased by mutations. After 100 time steps we find $\lambda = 8.95 \pm 0.03$ ($c=0.3$; tags and tolerances are mutated with probability 2%), which is significantly higher than the correlation length in the system without mutations. The segregation properties are not altered if an asynchronous update is applied instead.

Overall, the segregation properties and correlation length are governed by the length defined by the size of the neighborhood window. They are only marginally influenced by the cooperation cost c .

B. Emergence of spiral waves from a local conversion mechanism

The well-mixed system was analyzed rigorously under the influence of biased conversions towards tolerance [29]. These biased conversions show an alternating dominance of both groups in the mixed system.

Let us now introduce a local conversion mechanism that promotes tolerance in a similar way. We assume that an agent in a neighborhood consisting only of players of his own tag becomes tolerant, if he did not switch his strategy in the same time step due to selection. As only intolerant players utilize the ability to distinguish between tags this could be motivated by assuming some costs for this cognition system. These conversions lead to a rock-paper-scissors-like cycle with four strategies: If the neighbors are red, red agents become tolerant. In a red tolerant neighborhood intolerant blue agents have the highest payoff. If these dominate the neighborhood, the blue players should switch to the tolerant strategy. Finally, in such a neighborhood the intolerant red agents gain the highest payoff. This in contrast to [36], where cyclic dominance is explicitly included in a system with asynchronous update.

This cycle leads to the emergence of rotating spirals. The arms of these spirals are traveling waves, as in the game of rock, paper, scissors [37,38] or in public goods games with volunteering [14,39]. The front of such a wave consists of intolerant agents; these are followed by tolerant agents of the same tag (cf. Fig. 3). These players can be exploited by intolerant players with a different tag; hence a new front with a different tag can invade.

In the case of asynchronous update spirals are replaced by larger structures moving through the system. However, the mechanism for the movement of these structures is the same as for the spiral waves.

To locate the spiral tips quantitatively, the strategies $(r,1)$, $(r,0)$, $(b,1)$, and $(b,0)$ are associated with discrete indices 0, 1, 2, and 3, respectively. Interpreting those as four possible angles of a two-dimensional vector field, the curl can be calculated from a counterclockwise Stokes path on a 2×2 block. For a continuous field of phases ϕ the topological charge of a closed path Γ is defined by

$$q = \frac{1}{2\pi} \oint_{\Gamma} \vec{\nabla} \phi \cdot d\vec{r}. \quad (4)$$

In our case, both space and phase are discrete; the phase is measured in units of $\pi/2$. Along the Stokes path we compute the phase differences

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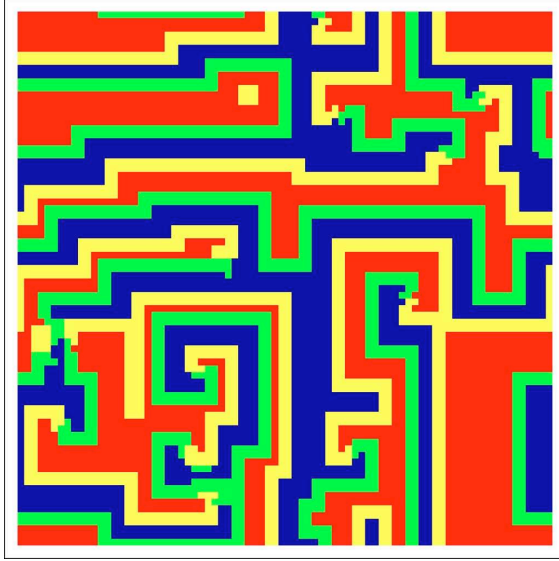
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FIG. 3. (Color online) System with local conversions towards tolerance. Colors are as in Fig. 1. Agents become tolerant if their new neighborhood has the same color, this leads to a rock-paper-scissors-like cycle. Spirals that generate traveling waves appear ($c=0.3$, $b=1.0$, $L=80$).

$$\begin{aligned}
 \Delta\phi_1 &= x_{i+1,j} - x_{i,j}, \\
 \Delta\phi_2 &= x_{i+1,j+1} - x_{i+1,j}, \\
 \Delta\phi_3 &= x_{i,j+1} - x_{i+1,j+1}, \\
 \Delta\phi_4 &= x_{i,j} - x_{i,j+1}.
 \end{aligned} \tag{5}$$

In the discrete case a phase difference of two steps, or angle π , may occur and consistently can be interpreted as a zero contribution to the Stokes integral (leading to the possibility of half-valued partial charges as discussed below). Thus the phase differences are mapped on differences Δq_i according to Table I. The topological charge is given by $q = \Delta q_1 + \Delta q_2 + \Delta q_3 + \Delta q_4$. A typical spiral tip consists of two equal topological charges $q = \pm \frac{1}{2}$ in nearby positions. In the stationary regime, the generic case is a pairing of two spirals with different chiralities—i.e., different topological charges $q = \pm 1$ —near each other. For completeness, it should be noted that the resulting curl field is defined on the dual lattice shifted from the original one by a vector $(\frac{1}{2}, \frac{1}{2})$.

A comparison between the strategy distribution and the corresponding charge distribution is shown in Fig. 4.

TABLE I. Mapping of phase differences $\Delta\phi_i$ to charge differences Δq_i .

$\Delta\phi_i$	-3	-2	-1	0	+1	+2	+3
Δq_i	$+\frac{1}{4}$	0	$-\frac{1}{4}$	0	$+\frac{1}{4}$	0	$-\frac{1}{4}$

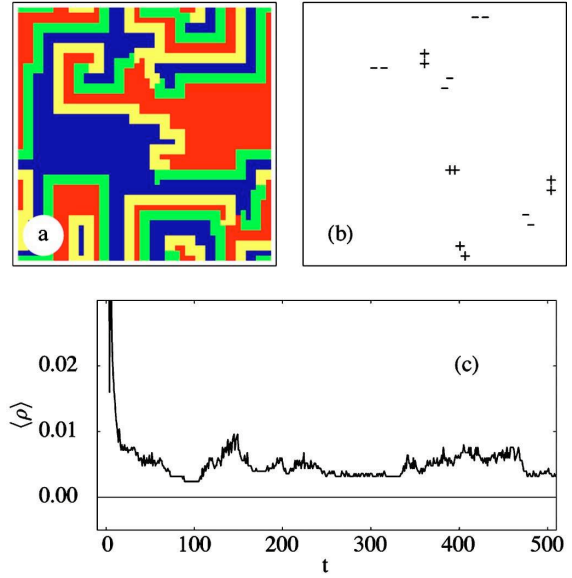


FIG. 4. (Color online) Topological charges: Colors are as in Fig. 1. (b) shows the spatial distribution of charges for the strategy distribution shown in (a). The sign + (−) indicates a topological charge of $q = +\frac{1}{2}$ ($q = -\frac{1}{2}$). Full charges are not stable and disappear immediately after their generation. (c) shows a typical time development of the average charge density $\langle\rho\rangle$. Initially, $\langle\rho\rangle$ drops rapidly. As topological charges are generated and annihilated, the charge density fluctuates until the system reaches a stationary state ($L=50$).

For a random initialization we find a topological charge density of $\langle\rho\rangle = 0.219 \pm 0.003$, which is consistent with the theoretical average value for independent topological charges $\langle\rho\rangle = \frac{7}{32} = 0.21875$. The spatial game dynamics quickly reduces the initial topological charge density. However, topological charges are generated and annihilated in an irregular manner until the system reaches a stationary state; see Fig. 4.

IV. ASYMMETRIC SPATIAL SYSTEM

It seems natural to assume that the two different groups can have two different costs of cooperation. For different costs c_r and c_b in Eq. (1) we find several distinct dynamical regimes, as dominance of red players, spiral waves, etc. (cf. Fig. 5 for details).

Three different classes of transitions can be observed in Fig. 5. As in the symmetric game, the update rule is modified if one of the cooperation costs crosses a threshold cost as explained in the Appendix. Such transitions are vertical and horizontal lines in Fig. 5—e.g., the black dotted line in region (B_r) at $c_r = \frac{1}{3}b$. Note that the transitions shown in Fig. 9 (curve L) can be observed on the diagonal $c_r = c_b$ in Fig. 5. A second kind of threshold is determined by c_r/c_b . These thresholds govern the dynamical behavior and divide the phase plane in Fig. 5 into seven distinct regions. For $c_b/c_r > \frac{8}{3}$ red agents dominate the population; for $c_b/c_r > \frac{8}{3}$

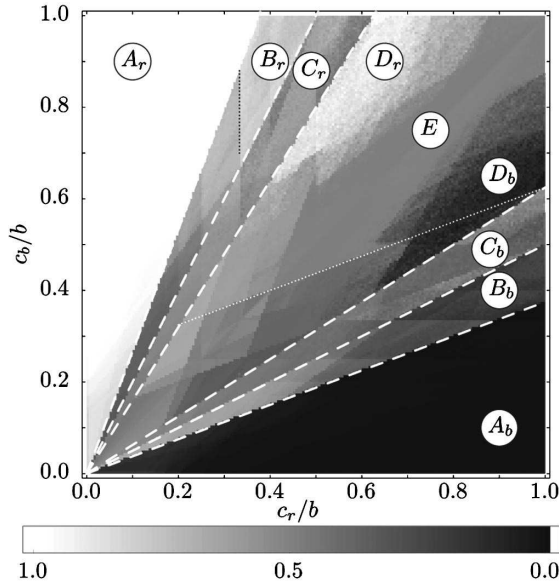


FIG. 5. Asymmetric system: fraction of red agents (encoded in a grayscale) in dependence of the cooperation costs c_b and c_r . In region (A_r) the population is dominated by red agents; for small c_b intolerant blue agents can survive. In region (B_r) intolerant blue players form channels in a sea of tolerant red agents. In (D_r) red tolerant agents dominate again. Region (E) shows spiral waves as the symmetric game, cf. Fig. 3. Region (C_r) shows coexistence of spiral waves from (E) and channels from (B_r). For $c_b < c_r$ the dynamics is the same with the role of red and blue agents exchanged. Structures inside the regions are determined by changes of the update rule. The borders of these structures, e.g. the dotted lines in regions (D_b)/(E) and (B_r), are given by linear equations $c_b = a + bc_r$, see text for details ($L=100$, averages over 50 time steps and 100 independent realizations).

stationary clusters of intolerant blue agents can survive. At $c_b/c_r=2$ traveling waves can appear which suppress stationary clusters of intolerant blue agents at $c_b/c_r < \frac{8}{5}$. However, if the cooperation costs are sufficiently high, one group can take over the whole population after a transient period [region (D_r) in Fig. 5]. For $c_b < c_r$ the roles of red and blue are exchanged. Finally, we have a third class of transitions which is given by linear equations $c_b = a + bc_r$. Here, the transition threshold is given by a certain slope $\Delta c_b / \Delta c_r = \text{const}$ as for the second kind of transitions. However, now one of the costs has to exceed a certain threshold as for the first kind of transitions—e.g., the white dotted line in region (D) of Fig. 5 is given by $c_b = \frac{1}{4}b + \frac{3}{8}c_r$.

It is also possible to describe the phases in the asymmetric system by topological charge densities introduced in Sec. III B (cf. Fig. 6).

V. FORECAST RULE

Here, we return to a system where both cooperation costs are the same. Let us assume that the local conversion rule

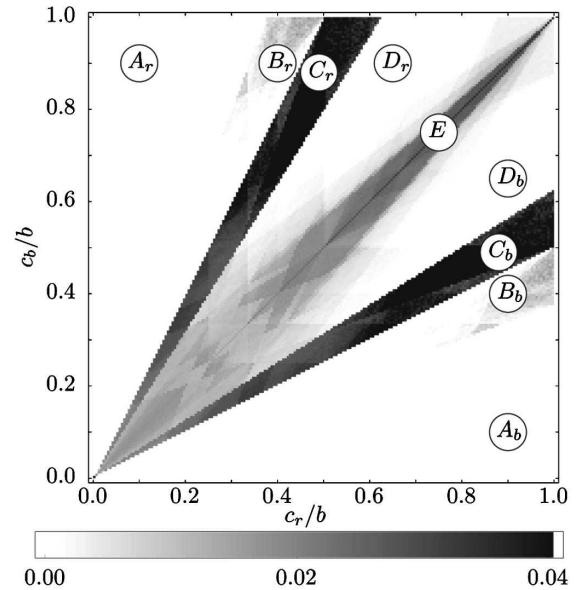


FIG. 6. Asymmetric system: average charge density in dependence of the cooperation costs c_b and c_r . The regions are the same as in Fig. 5. Topological charges can only be found when traveling waves are present—i.e., in regions (C) and (E). The absence of topological charges corresponds to the dominance of one group in the limit $t \rightarrow \infty$. The highest charge densities are observed in the (C) regions and in (E) near the diagonal $c_r = c_b$ ($L=100$, averages over 50 time steps and 100 independent realizations).

towards tolerance is based on the *new* strategies of the neighbors and applies also for players that switched their strategies due to selection. Hence, now the update depends on the strategies in a 7×7 neighborhood. Such a mechanism can be viewed as a primitive forecast. Players become tolerant if they expect their neighborhood to cooperate with them in the next generation. Even in this setting the local conversion rule leads to the emergence of spiral waves.

It is straightforward to add an equivalent mechanism that increases the fraction of intolerant agents. Tolerant agents can become intolerant in order to protect themselves against exploiters that refuse to cooperate. Therefore, we decrease the tolerance of an agent if at least two neighbors will probably exploit him in the next time step.

A. Cooperative fixed point

For $c < 0.4b$ we observe cooperation across the segregation borders for synchronous update. For asynchronous updates this fixed point does not become stable. The forecast rule leads to a stable coexistence of red and blue tolerant agents that provide help for everybody in their neighborhood (cf. Fig. 7). As a discrimination between different agents is no longer necessary, this can be seen as a primitive mechanism to overcome segregation. However, although the behavior of all agents is independent of the tags, the different tags are still segregated in space. The typical correlation lengths

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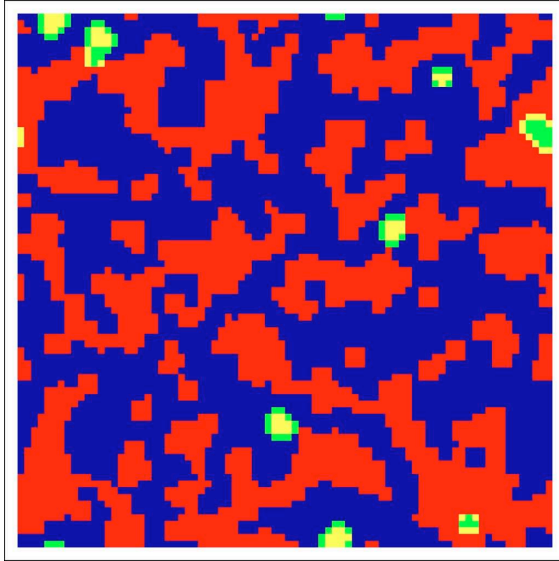


FIG. 7. (Color online) System with forecast rule. Colors are as in Fig. 1. Agents become tolerant if their neighborhood has the same color and intolerant if at least two neighbors will refuse to cooperate. This mechanism allows the coexistence of red and blue tolerant agents; here, the intolerant agents have been eliminated by the mechanism, leading to a static state ($c=0.3$, $b=1.0$, $L=80$).

are larger than in the system without conversion mechanisms. For $c=0.3$ we find $\lambda=8.32\pm 0.02$. The spatial dissimilarity index is only slightly higher; we observe $D=0.719\pm 0.005$. Surprisingly the mechanism that enables agents to become intolerant increases the total fraction of tolerant agents, as it helps to stabilize tolerant domains. It is interesting that a mechanism that increases intolerance helps to eliminate intolerance. However, the mechanism bears some resemblance to the “tit-for-tat” strategy in the iterated prisoner’s dilemma [7], which punishes others for not cooperating, but can also forgive defectors reestablishing coop-

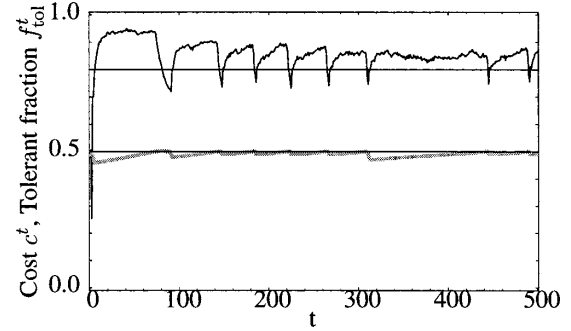


FIG. 8. Time evolution of the system with linear feedback. Cost of cooperation (gray) and fraction of tolerant agents (black). The fraction of tolerant agents decreases rapidly when the cost reaches the threshold $c=0.5$ ($f_{\text{tol}}^*=0.8$, $\alpha=0.01$, $c^0=0.5$, $N=200$).

eration. One can even observe different stationary structures that change periodically in which intolerant agents survive; these resemble the “blinkers” in the “game of life” [40]. For $c>0.4b$ the system reaches a stationary state only in very rare cases. However, parts of the system are still dominated by tolerant agents. In the case of $c>0.5b$ this is no longer the case; here, intolerant agents are found in the whole system.

Note that such a forecast rule cannot stabilize the cooperative fixed point in the spatial prisoner’s dilemma [10], as defectors have always a higher payoff than neighboring cooperators.

B. Feedback stabilization

For cooperation costs $c>0.5b$ the tolerant fixed point is unstable. However, we can enforce cooperative behavior by global feedback on the cooperation costs. In social systems this corresponds to adapting taxes with respect to the state of the society. Specifying a desired fraction of tolerant agents f_{tol}^* we update the cost depending on the current fraction of tolerant agents f_{tol}^t as

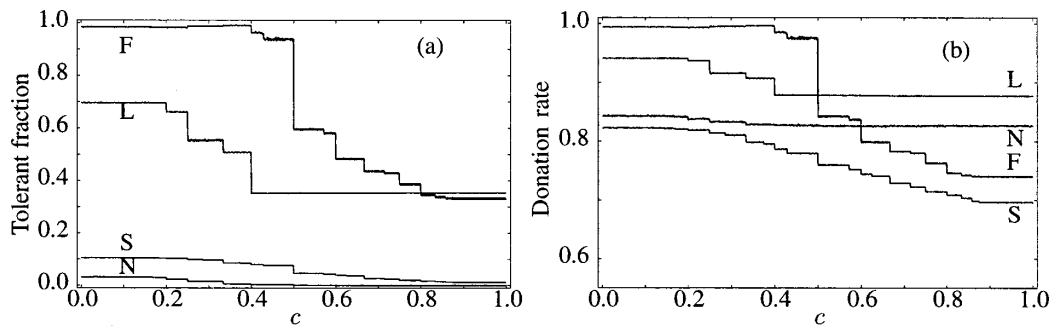


FIG. 9. Dependence of different order measures on the cost of cooperation, c , for four different update rules. (a) shows the fraction of tolerant agents in the system. The donation rate—i.e., the fraction of interactions in which a player cooperated with his coplayer—is shown in (b). The order measures are shown for the system without mutations (N), with stochastic mutations (S), with the local conversion mechanism described in Sec. III B (L), and with the forecast rule (F) from Sec. V. The sharp steps correspond to modifications of the update rules ($b=1.0$, $L=100$, spatial averages over 50 independent realizations and 50 update steps after a transient period of 50 update steps).

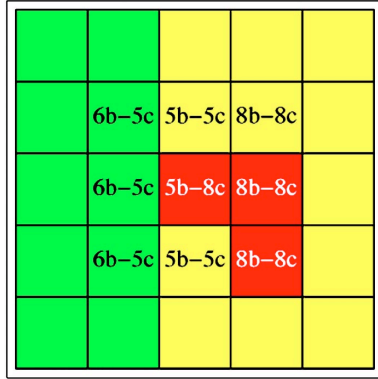


FIG. 10. (Color online) Example for a modification of the update rule. Colors are as in Fig. 1. The numbers are the payoffs Π for this neighborhood. This situation is stable for $c \leq 2/3b$, as the players with $\Pi = 6b - 5c$ that exploit the player in the center do not have the maximum payoff $\Pi = 8b - 8c$.

$$c^{t+1} = c^t + \alpha(f_{\text{tol}}^* - f_{\text{tol}}^t)c^t. \quad (6)$$

For each f_{tol}^* , the cost fluctuates around a threshold that is determined by a change of the update rule (cf. the Appendix), as shown in Fig. 8 for $f_{\text{tol}}^* = 0.8$. This mechanism can stabilize points with $f_{\text{tol}}^* < 1$ even for $c > 0.5b$. For each f_{tol}^* the cost fluctuates around a threshold that is determined by a change of the update rule (cf. the Appendix).

For the mean-field theory we have a fixed point for $f_{\text{tol}} = 1$ [29], which is only stable for very low cooperation costs. However, this fixed point cannot be stabilized with the linear feedback from Eq. (6).

VI. CONCLUSIONS

We have investigated spatial segregation, pattern formation, and control in a spatial version of a public goods game with cooperation based on the similarity between players. This type of model may establish a useful approach for a large variety of economical and social systems, where agents may act not only upon economical considerations, but also based on similarity or group membership. Generalizations to more detailed agents can be performed in a straightforward manner, yet our four-state model already is capable of showing different phase states from stationary segregation to complex spatiotemporal behavior.

Particularly, it is interesting to note that a simple forecast rule can help to overcome segregation and lead to a stable pattern of cooperating agents, as regions with limited cooperation at the borders between groups are eliminated. How-

ever, the different groups are still segregated in space.

APPENDIX: INFLUENCE OF THE COST OF COOPERATION

Due to the discrete nature of the total payoff, sharp steps appear when the cost of cooperation, c , varies. As examples, we consider the dependence of the fraction of tolerant agents, f_{tol} , and the donation rate—i.e. the fraction of cooperative interactions—on the cost of cooperation (see Fig. 9). Due to the symmetry between tags, the fraction of red and blue tolerant agents can be computed from the fraction of tolerant agents, $f_{\text{tol}}/2$, on average. In the same manner the fraction of intolerant agents of each group can be computed as $(1 - f_{\text{tol}})/2$. The donation rate includes additional information on the spatial distribution of the agents. The steps that are observed in the order measures correspond to modifications of the update rule, as described in [10]. The steps occur at the same positions for all order measures. However, the step size is different for the fraction of tolerant agents and the donation rate (see Fig. 9).

Consider a player x with a payoff $\Pi(x)$ and a second player y with the payoff $\Pi(y)$ and a different strategy. If a third player z with a payoff $\Pi(z) < \Pi(x), \Pi(y)$ in the neighborhood of these two players searches for the best strategy, his update rule changes at $c = c^*$ if the sign of $\Pi(x) - \Pi(y)$ changes at $c = c^*$. The corresponding values for c/b are given by

$$X^b b - X^c c = Y^b b - Y^c c, \quad (A1)$$

where $0 \leq X^b (Y^b) \leq 8$ is the number of agents that support $x(y)$ and $0 \leq X^c (Y^c) \leq 8$ is the number of agents that are supported by $x(y)$. For the situation shown in Fig. 10 we find for the center player $\Pi(z) = 5b - 8c$, for his left neighbor $\Pi(x) = 6b - 5c > \Pi(z)$, and for his right neighbor $\Pi(y) = 8b - 8c > \Pi(z)$. Hence, we find a modification of the update rule for

$$c^* = \frac{X^b - Y^b}{X^c - Y^c} b = \frac{2}{3} b. \quad (A2)$$

For $c > c^*$ the center player will switch tolerance and group membership. Other transitions can be found in the same way, although the method of fundamental clusters [33] is more complicated due to the high number of possible configurations.

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2.2 Minimal model for tag-based cooperation

PHYSICAL REVIEW E **68**, 046129 (2003)**Minimal model for tag-based cooperation**

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Recently, Riolo *et al.* [Nature (London) **414**, 441 (2001)] showed by computer simulations that cooperation can arise without reciprocity when agents donate only to partners who are sufficiently similar to themselves. One striking outcome of their simulations was the observation that the number of tolerant agents that support a wide range of players was not constant in time, but showed characteristic fluctuations. The cause and robustness of these tides of tolerance remained to be explored. Here we clarify the situation by solving a minimal version of the model of Riolo *et al.* It allows us to identify a net surplus of random changes from intolerant to tolerant agents as a necessary mechanism that produces these oscillations of tolerance, which segregate different agents in time. This provides a new mechanism for maintaining different agents, i.e., for creating biodiversity. In our model the transition to the oscillating state is caused by a saddle node bifurcation. The frequency of the oscillations increases linearly with the transition rate from tolerant to intolerant agents.

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I. INTRODUCTION

The emergence of cooperation in evolving populations with exploitative individuals is still a challenging problem in biological and social sciences. Most theories that explain cooperation are based on direct reciprocity, as the famous iterated prisoner's dilemma [1]. Cooperation can also arise from indirect reciprocity when agents help others only if these are known to be sufficiently altruistic [2]. In most of these models a finite population of agents is simulated, pairs of agents meet randomly as potential donor and receiver. A donation involves some cost to the donor while it provides a larger benefit to the receiver. Agents reproduce depending on their payoffs after a certain number of such meetings. Obviously, selfish individuals who do not donate would quickly spread in the population if help is not channeled towards more cooperative players. If agents do not meet repeatedly—as in a large population—direct reciprocity does not work. Indirect reciprocity can solve this problem when donations are given only to those individuals who are known as sufficiently helpful. This mechanism effectively protects a cooperative population against exploiters [2].

Riolo *et al.* [3] introduced a model in which cooperation is not based on reciprocity, but on similarity. In this model donations are channeled towards individuals who are sufficiently similar to the donor. To distinguish between different groups of individuals every agent i has a tag $\tau_i \in [0,1]$. School ties, club memberships, tribal costumes, or religious creeds are all tags that induce cooperation. In addition, agents have a tolerance threshold $T_i \geq 0$, which determines the tag interval that the agent classifies as its own group. An agent i donates to another agent j if their tags are sufficiently similar, $|\tau_i - \tau_j| \leq T_i$. The cost of such a donation for i is $c > 0$ while the benefit for j is $b > c$. For simplicity, b is normalized to 1, since a multiplication of payoffs with a constant factor does not change the game. Initially, the tag and the tolerance threshold are uniformly distributed random

numbers. In each generation every agent acts as a potential donor for P other agents chosen at random. Hence it is, on average, also chosen P times as a recipient. After each generation each agent i compares his payoff with the payoff of another randomly chosen agent j and adopts T_j and τ_j if j has a higher payoff. In addition, every agent is subject to mutation. With probability 0.1 an agent receives a new τ drawn from a uniform distribution and also with probability 0.1 a new T which is Gaussian distributed with standard deviation $\sigma = 0.01$ around the old T . If this new T becomes smaller than zero, it is set to 0. Obviously, it seems to be the best strategy for an individual to donate as little as possible, i.e., to have a very small T . However, the whole population would be better off if everybody would cooperate. This “tragedy of the commons” can be solved in different ways, e.g., by volunteering [4–6].

Riolo *et al.* solve this problem by channeling help towards others who are sufficiently similar to the donor. Instead of a cooperative population, the formation and decay of cooperative clusters is observed for certain parameter ranges (high P and low c , see Fig. 1). The average tolerance of a cooperative cluster grows slowly over time. Occasionally, it declines sharply. This decline occurs when the cluster is exploited by agents that are sufficiently similar to the cluster's agents to get support, but do not help themselves. However, the mechanism that generates these tides of tolerance remained unclear [7].

Here we develop a minimal model for tag-based cooperation, which displays these “tides of tolerance” if there is a net average drift towards more cooperation. We find that these fluctuations vanish if such a drift is not included in the model. The importance of this observation stems from the fact that if we have species that can distinguish between themselves and others and donate only to others with the same tag, then this would in the long run lead to a single group of cooperating species having a single tag. But if we introduce a small rate of biased conversions from intolerant to tolerant species, we observe a waxing and waning in time of species with different tags. In other words, the small conversion rate leads to a coexistence of different species, where

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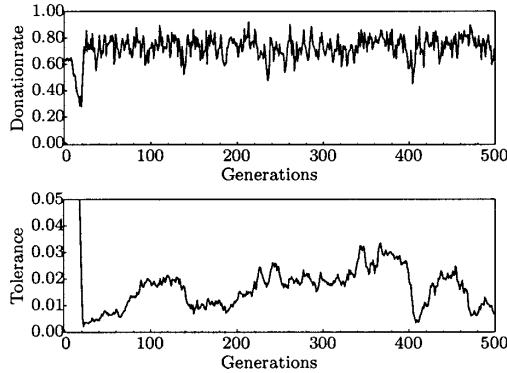


FIG. 1. Population dynamics for the first 500 generation of the model of Riolo *et al.* [3]. The average tolerance and the donation rate—i.e., the fraction of encounters that lead to a donation—show fluctuations. When a cooperative cluster becomes dominant, its tolerance increases until the cluster becomes extinct ($c=0.1$, $b=1.0$, and $P=3$).

different species appear cyclically at different times. This constitutes a new mechanism that generates biodiversity in a group of competing species.

This paper is organized as follows. First, the model of Riolo *et al.* is simplified in order to allow an analytical treatment. Then the system without the effects of mutations is analyzed. Thereafter, we introduce a drift that increases the tolerance and leads to oscillations of tolerance. We show that the truncated mutations in the model of Riolo *et al.* also lead to such a drift.

II. SIMPLIFIED REPLICATOR MODEL

A. Definition of the model

Here we simplify the model of Riolo *et al.* [3] in order to allow for an analytical treatment. In a first step we restrict the game to only two tags, red and blue. Similarly, we allow only two tolerances. The agents can either only donate to others bearing the same tag if they have zero tolerance $T=0$ or to every other agent ($T=1$). This leads to four possible strategies. Then we allow partners to donate and to receive in a single interaction instead of defining different roles for donors and receivers. We end up with the payoff matrix

(Tag, T)	(Red, 1)	(Blue, 1)	(Red, 0)	(Blue, 0)
(Red, 1)	$b - c$	$b - c$	$b - c$	$-c$
(Blue, 1)	$b - c$	$b - c$	$-c$	$b - c$
(Red, 0)	$b - c$	b	$b - c$	0
(Blue, 0)	b	$b - c$	0	$b - c$

The strategies with $T=1$ are obviously dominated by the strategies with $T=0$, because the payoff of an intolerant player is always larger than the payoff of the corresponding tolerant player. There are pure Nash equilibria for the intolerant strategies (red, 0) and (blue, 0). In addition, there is an

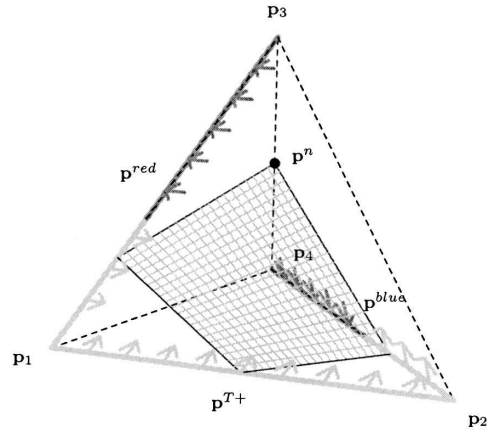


FIG. 2. The trajectories of the replicator dynamics move from the inside of the simplex onto the boundaries. The corners represent the pure strategies \mathbf{p}_i . Arrows indicate the stability of the fixed points at the edges. There are two stable attractors called \mathbf{p}^{red} and \mathbf{p}^{blue} (dark gray) corresponding to stable lines of fixed points of Eq. (2). At the top only players with red tags survive whereas at the bottom only players with blue tags can exist. The two basins of attractions of these stable attractors are separated by a planar separatrix given by Eq. (3). This separatrix is the basin of attraction for the fixed point in the Nash equilibrium indicated by a black circle ($c=0.4$ and $b=1.0$).

evolutionary unstable mixed Nash equilibrium if these two strategies are used with probability $\frac{1}{2}$.

If the intolerant agents do not even cooperate within their own group we recover the prisoner's dilemma [8], see Appendix A.

Instead of simulating a finite group of agents, we calculate only the evolution of the probability that an agent uses a certain strategy. In the following, p_1 and p_2 are the frequencies of tolerant red and tolerant blue agents, respectively. p_3 and p_4 are the frequencies of the corresponding red and blue intolerant agents. As $p_1 + p_2 + p_3 + p_4 = 1$, the state of the system is completely determined by $\mathbf{p}^t = (p_1^t, p_2^t, p_3^t)$. The trajectory can therefore be visualized as a trajectory in the three-dimensional simplex shown in Fig. 2.

In order to apply standard replicator dynamics [9] we calculate the mean payoffs from the payoff matrix as

$$\begin{aligned}
 \Pi_1^t &= (b - c)(p_1^t + p_2^t + p_3^t) - cp_4^t, \\
 \Pi_2^t &= (b - c)(p_1^t + p_2^t + p_4^t) - cp_3^t, \\
 \Pi_3^t &= (b - c)(p_1^t + p_3^t) + bp_2^t, \\
 \Pi_4^t &= (b - c)(p_2^t + p_4^t) + bp_1^t,
 \end{aligned} \tag{1}$$

$$\langle \Pi \rangle^t = \sum_{i=1}^4 p_i^t \Pi_i^t,$$

where Π_i is the payoff of the strategy with frequency p_i . Using Eq. (1) the replicator equations can be written as

$$p_i^{t+1} = p_i^t + p_i^t \beta (\Pi_i^t - \langle \Pi \rangle^t), \quad (2)$$

where $i=1, \dots, 4$. Here β determines the time scale. In the following, we set $\beta=1$. Our main interest is the attractors of the system, and a modification of β would only modify the velocities on the attractor.

B. Fixed points and separatrix

The dynamics of the system (2) can roughly be characterized as follows, see Fig. 2. Most initial conditions lead to fixed points where only one tag survives. The frequency of intolerant players is typically higher than the frequency of tolerant players here. There is a separatrix that divides the basins of attraction of the two tags. On one side of the separatrix red players will survive and on the other side blue players. In addition, we find several fixed points on the edges described in the following.

As in any replicator system, the mixed Nash equilibrium $\mathbf{p}^n = (0, 0, \frac{1}{2})$ is a fixed point. Here the basin of attraction is the separatrix. The separatrix shown in Fig. 2 can be calculated from the stability of this fixed point, which is discussed for a more general case in Appendix B. \mathbf{p}^n is always part of the separatrix, its normal corresponds to the eigenvector $\mathbf{e}_3 = (1-c, 1+c, 2)$ of the corresponding Jacobi matrix J^n with the eigenvalue $\lambda_3 = (3-c)/2 > 1$. We find the equation

$$p_3^s = \frac{1}{2} [1 - (1-c)p_1^s - (1+c)p_2^s] \quad (3)$$

for points on the separatrix. As we have $[\mathbf{p}^{t+1}(p_1^s, p_2^s, p_3^s) - \mathbf{p}^t(p_1^s, p_2^s, p_3^s)] \cdot \mathbf{e}_3 = 0$, the system never leaves this plane again.

In addition, there are two fixed lines if only one tag is present: $\mathbf{p}^{red} = (1-x, 0, x)$ and $\mathbf{p}^{blue} = (0, 1-x, 0)$, where $0 \leq x \leq 1$ is the fraction of intolerant players. The stability of the fixed points on these lines depends on x . For $1-x > c$, the points are unstable and intolerant players with the opposite tag can invade (see Appendix B). Finally, there is an unstable fixed line for a completely tolerant population $\mathbf{p}^{T+} = (1-y, y, 0)$, where $0 \leq y \leq 1$. The stability of this fixed line is discussed in Appendix B.

So far, the system does not show any oscillation. It simply relaxes to one of the fixed points described above. In the following section a mechanism that generates oscillations will be discussed.

III. INTRODUCTION OF A BIASED DRIFT

In order to generate oscillations in the system we have to destabilize the attracting fixed points and force the system through the separatrix. This can be realized by introducing first *ad hoc* a drift that increases the fraction of tolerant agents at the cost of the intolerant fraction of the same tag. If we introduce such biased conversions into our model, Eq. (2) becomes

$$p_1^{t+1} = p_1^t + p_1^t (\Pi_1^t - \langle \Pi \rangle^t) + \varepsilon p_3^t, \quad (4)$$

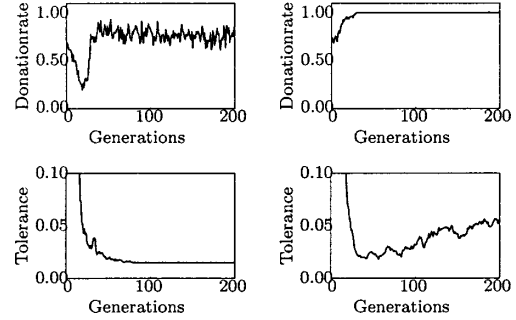


FIG. 3. Population dynamics for the first 200 generation of the model of Riolo *et al.* [3] without tolerance mutations (left) and without tag mutations (right). Without tolerance mutations the donation rate fluctuates due to tag mutations. After less than 100 generations all players inherit the same tolerance. Without tag mutations the donation rate quickly rises to 100% when all players have the same tag. The fluctuating tolerance does no longer influence the system ($c=0.1$, $b=1.0$, and $P=3$).

$$p_2^{t+1} = p_2^t + p_2^t (\Pi_2^t - \langle \Pi \rangle^t) + \varepsilon (1 - p_1^t - p_2^t - p_3^t),$$

$$p_3^{t+1} = p_3^t + p_3^t (\Pi_3^t - \langle \Pi \rangle^t) - \varepsilon p_3^t.$$

The solution of these equations shown in Figs. 4 and 5 display oscillations in tolerance. These oscillations can be considered as the deterministic equivalent to the tides of tolerance in Ref. [3].

In the model of Riolo *et al.* [3] such a drift is generated by truncated mutations. The average tolerance is usually of the order of σ . Therefore the truncation of negative tolerances decreases the probability for mutations that lower the tolerance, and leads to a drift towards higher tolerances. We repeated the simulations of Riolo *et al.* and found that 50.0% of the tolerance mutations increase T while only 39.8% decrease T . The average mutation increases T by 1.3×10^{-4} ($c=0.1$, $P=3$, average over 10 000 realizations with 30 000 generations each). If we omit the tolerance mutations in the model of Riolo *et al.*, one (low) tolerance is quickly inherited by the whole population, see Fig. 3. The majority of players belongs to a dominant cluster. The mean tag of this cluster—and hence the donation rate—drifts slowly due to mutations of the tags. Without mutations of the tags one tag is inherited by the whole population after a short initial period. Consequently, the donation rate becomes 100%, and tolerance mutations do no longer influence the system.

A. Qualitative behavior

The attractor of the system (4) is shown in Fig. 4, and the time evolution of the strategies can be seen in Fig. 5. If initially all strategies are present, the system shows periodic oscillations for small ε and $c=0.1$. One tag becomes dominant. The fraction of tolerant players increases due to the biased conversions imposed by $\varepsilon > 0$ and intolerant players with the opposite tag can invade and destroy the cluster, giving rise to a new dominant cluster with the opposite tag. This attractor shown in Fig. 4 has essentially the whole sim-

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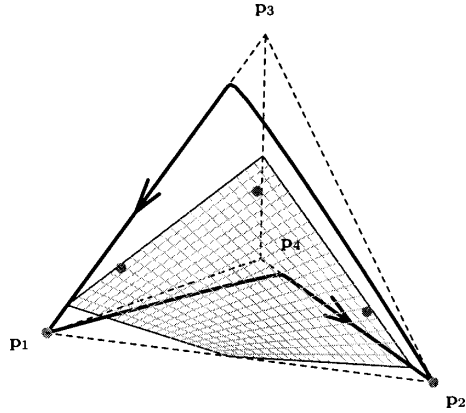


FIG. 4. Attractor of the system (4) for $c=0.1$. The black line is the attractor, the gray points are the fixed points. The plane is the separatrix for $\varepsilon=0$. The arrows indicate how the biased conversions drive the system through the separatrix to the corner with only tolerant individuals. Here individuals with the other tag can invade and steer the system to a corner with mostly intolerant individuals. Biased conversions lead to a tolerant corner again and the circle continues ($\varepsilon=0.01$, $c=0.1$, and $b=1.0$).

plex as a basin of attraction. Only for very small or very high values of c other fixed points become stable. The system can be analyzed in two parts for $\varepsilon \ll 1$. Near the edges \mathbf{p}^{red} and \mathbf{p}^{blue} , the replicator dynamics becomes irrelevant and the system is mainly driven by biased conversions. Further away from these edges the system is driven by the replicator dynamics. Here the dynamics is not altered by the biased conversions.

Our biased conversions lead the system from an edge that is dominated by one color to an edge that is dominated by the other color. For small c the trajectory leaves these edges near the corners of the pure tolerant strategies, cf. Fig. 4. However, these corners are never crossed as they are fixed points.

B. Fixed points

Let us now analyze the system (4) in more detail. The fixed line $\mathbf{p}^{T+}=(1-y,y,0)$ of Eq. (2) is still a fixed line of Eq. (4). For $c < 2\varepsilon$, a fraction of the fixed line remains stable, see Appendix B for details. However, as we are interested in $\varepsilon \ll 1$ the fixed line is usually unstable. Due to the flow from intolerant to tolerant players, the edges \mathbf{p}^{red} and \mathbf{p}^{blue} are no longer fixed. The fixed point $\mathbf{p}^n=(0,0,\frac{1}{2})$ in the mixed Nash equilibrium moves away from the edge for $\varepsilon > 0$ and is now given by $\mathbf{p}^d=(\varepsilon/c, \varepsilon/c, \frac{1}{2}-\varepsilon/c)$. The stability of this fixed point is discussed in Appendix B.

In addition, we find two more fixed points \mathbf{p}^{s+} and \mathbf{p}^{s-} . For $\varepsilon=0$ they correspond to the points where the population with only one tag loses stability. These fixed points can be calculated analytically, see Appendix C for details. The expansion for $\varepsilon \ll 1$ of \mathbf{p}^{s+} is

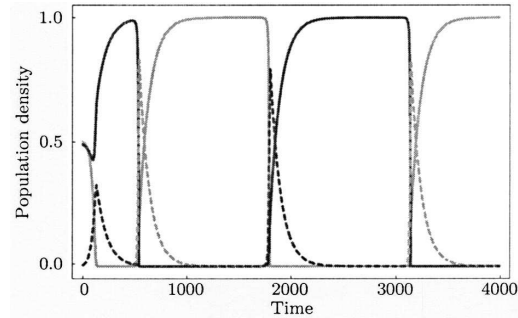


FIG. 5. The waxing and waning of the four different groups of agents (red agents: black, blue agents: gray, full lines: $T=1$, and dashed lines: $T=0$) are caused by the following mechanism. A cluster of tolerant red agents is invaded by intolerant blue agents who convert via directed mutations to their tolerant counterpart, giving rise to a blue cluster which is then invaded by red intolerant agents. Although initially the number of red and blue tolerant agents differed only by 1%, a tiny number (0.5%) of intolerant agents of each tag is enough to generate large clusters that are segregated in time ($\varepsilon=0.01$, $c=0.1$, and $b=1.0$).

$$\mathbf{p}^{s+} \approx \begin{pmatrix} 1 - c - \frac{2\varepsilon}{c} + \frac{\varepsilon^2}{(c-1)c^2} \\ \frac{\varepsilon^2}{c^2 - c^3} \\ c + \frac{(1-2c)\varepsilon}{c - c^2} - \frac{\varepsilon^2}{(c-1)^2 c} \end{pmatrix}. \quad (5)$$

Due to the symmetry in the tags \mathbf{p}^{s-} can easily be calculated by exchanging p_1 with p_2 and p_3 with $p_4=1-p_1-p_2-p_3$. As described above, we find $\mathbf{p}^{s+}=(1-c,0,c)$ for $\varepsilon=0$. Increasing ε moves it towards \mathbf{p}^d . For $\varepsilon=c(1-c)/4$ $\mathbf{p}^{s\pm}$ and \mathbf{p}^d collapse, here \mathbf{p}^d becomes stable.

For $c < 0.73$ we have no fixed points that are stable in all directions. The whole simplex is essentially the basin of attraction of the attractor shown in Fig. 4.

C. Bifurcation at $\varepsilon=0$

The transition from the system without biased conversions (i.e., $\varepsilon=0$) to the system with biased conversions can be analyzed in detail by considering the Poincaré map shown in Fig. 6.

At $\varepsilon > 0$ the fixed lines where only one tag is present vanish. This is caused by a saddle node bifurcation [10]. A fixed line disappears at this bifurcation, and a small channel is opened through which the system moves slowly to the other side of the separatrix. The width of this channel is controlled by ε . For small ε a linear dependence between ε and the oscillation frequency of the attractor is observed as shown in Fig. 7. Such a linear dependence is expected in a saddle node bifurcation with linear perturbation terms εp_3 and εp_4 [11].

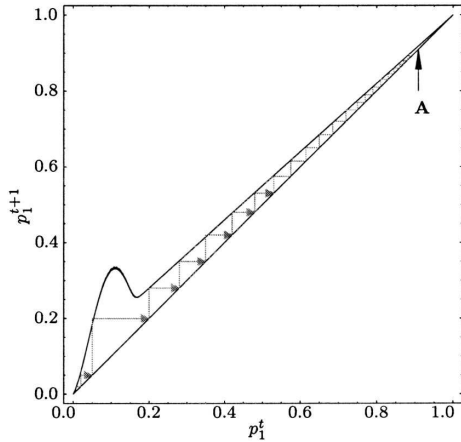


FIG. 6. The Poincaré map of the p_1 shows the “channel” through which the trajectory crosses the separatrix. The black lines are the function and the bisector. The distance between the function and the bisector has been magnified by a factor of 10. Therefore the course of iteration is drawn only schematically. A marks the point where the separatrix is crossed due to biased conversions from p_3 to p_1 . Here p_1 increases further, as the fraction p_4 that exploits p_1 is still very small. For $\varepsilon=0$ the function and the bisector will match, the separatrix can no longer be crossed ($\varepsilon=0.01$, $c=0.1$, and $b=1.0$).

In our model two small channels are opened by $\varepsilon > 0$, as the separatrix is crossed twice in one oscillation. The reinjection in our model is caused by the replicator dynamics, which drives the system to the channel of the opposite tag. The dependence of the oscillation frequency on the parameter ε for $c=0.1$ is shown in Fig. 7. For values of $\varepsilon > 0.02$, the dynamics changes. Here the fixed points \mathbf{p}^{T+} that be-

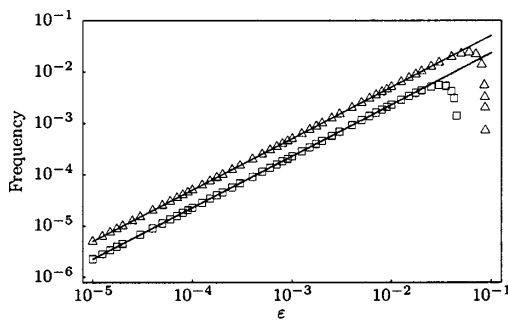


FIG. 7. Dependence of the oscillation frequency on the mutation rate ε . The squares and the triangles are the numerical values for $c=0.1$ and $c=0.2$, respectively. The line is a fit of the frequencies for $\varepsilon \leq 0.01$. For small ε the frequency increases as $f = \alpha \varepsilon^\beta$. We found $\beta = 1.0036 \pm 0.0003$ for $c=0.1$ and $\beta = 1.0021 \pm 0.0002$ for $c=0.2$. A linear dependence is expected if the perturbation is linear in ε , as in our case. For high values of ε the fixed line \mathbf{p}^{T+} becomes partially stable for $\varepsilon = c/2$ and begins to influence the system. Therefore the frequency decreases ($b=1.0$).

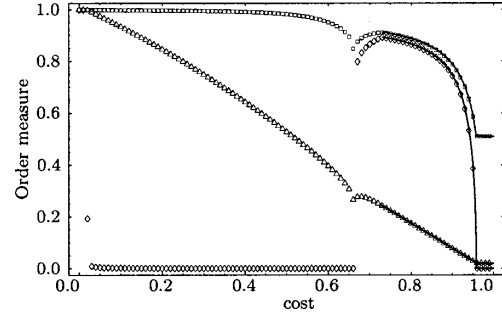


FIG. 8. Influence of the cost c on the donation rate (squares), the fraction of tolerant players (triangles), and the asymmetry between the tags (diamonds). All symbols are averages over 10 000 initial conditions and 100–10 000 time steps. The number of time steps is taken as a uniformly distributed random number to exclude effects resulting from changes of the oscillation frequency. The lines are the analytical results for $c > 0.73$, see Appendix C. The fraction of tolerant players decreases as the time intervals where the tag is invaded become longer. This has also an effect on the donation rate. For $c \approx 0.66$ a large change of the symmetry parameter is observed when one symmetric attractor is replaced by two attractors which are not symmetric. The fraction of tolerant players and the donation rate decrease slightly at $c \approx 0.66$. The donation rate and the symmetry parameter increase until the fixed points \mathbf{p}^{\pm} become stable at $c \approx 0.73$. Here these parameters decrease again. When \mathbf{p}^d finally becomes stable at $c = (1 + \sqrt{1 - 16\varepsilon})/2 \approx 0.96$, the symmetry is complete again ($\varepsilon=0.01$ and $b=1.0$).

come stable for $\varepsilon = c/2$ begin to influence the dynamical system.

D. Influence of the cost of cooperation c

Here we analyze the influence of the cost of cooperation (c) on our system by defining different measures of order in our model and by observing the influence of c on these measures. The donation rate is the probability that one player donates to another, $d = \langle 1 - p_3(p_2 + p_4) - p_4(p_1 + p_3) \rangle$. The fraction of tolerant individuals can be measured as $p_{tol} = \langle p_1 + p_2 \rangle$, and the asymmetry between the tags as $a = |\langle p_1 + p_3 \rangle - \langle p_2 + p_4 \rangle|$. Here $\langle \cdot \rangle$ denotes a time average. In addition, an average over different initial conditions is necessary.

Figure 8 shows that these measures display changes at $c \approx 0.02$, $c \approx 0.66$, $c \approx 0.73$, and $c \approx 0.96$. We now discuss the reasons for these transitions. For $c < \varepsilon$ the points $\mathbf{p}^{T+} = (1 - y, y, 0)$ are stable fixed points. In the case of $\varepsilon < c < 2\varepsilon$ only a part of this fixed line is stable, see Appendix B for details. For $c > 2\varepsilon$ these fixed points become unstable, this leads to a decrease of the asymmetry between tags at $c = 2\varepsilon$.

For cooperation costs $c > 2\varepsilon$, the typical qualitative behavior is described above. The attractor of such a system can be seen in Fig. 4. For higher costs c , the intolerant players can invade earlier as their advantage is larger. In the following we restrict ourselves to the case of $\varepsilon = 0.01$. The quali-

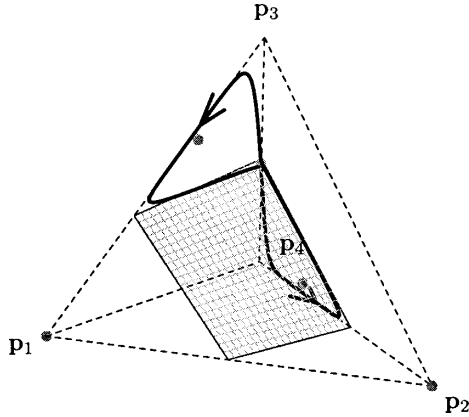


FIG. 9. Attractor of the system (4) for $c=0.66$. The black line is the attractor. The gray points are the fixed points. The plane is the separatrix for $\epsilon=0$. The arrows indicate the parts of the attractor where it is mainly driven by the biased conversions. The system does no longer cross the separatrix near the edges $p_1+p_3=1$ and $p_2+p_4=1$. Near the fixed point \mathbf{p}^d the trajectory almost closes itself. For higher values of c there are two separated attractors ($c=0.66$, $\epsilon=0.01$, and $b=1.0$).

tative behavior does not change until $c \approx 0.661$. The attractor for $c=0.66$ can be seen in Fig. 9.

For $c > 0.661$ the biased conversion can no longer drive the system through the separatrix. Two different attractors are observed for different initial conditions. In the original model this behavior corresponds to the establishment of one cooperative cluster which becomes tolerant due to the truncated mutations. Intolerant individuals with the other tag try to invade, but the dominant cluster becomes more intolerant again and prevents an invasion. At $c \approx 0.73$ the fixed points $\mathbf{p}^{s\pm}$ become stable (see Appendix C). For higher values of c , oscillations are no longer observed. For one eigenvalue of the corresponding Jacobi matrix J^s , we had $|\lambda_1| < 1$ even for smaller c . In addition, there is a pair of complex conjugated eigenvalues that crosses the unit circle at $c \approx 0.73$. Hence we are observing a Hopf bifurcation here. For $c > 0.73$ the system spins into the fixed points $\mathbf{p}^{s\pm}$. For $c \approx 0.93$ the imaginary parts of the eigenvalues vanish. At $c = (1 + \sqrt{1 - 16\epsilon})/2 \approx 0.96$, the stable fixed points $\mathbf{p}^{s\pm}$ collapse with the unstable fixed point \mathbf{p}^d in a supercritical pitchfork bifurcation. For higher values of c the fixed point \mathbf{p}^d is stable.

IV. SUMMARY AND OUTLOOK

We developed a minimal model for cooperation based on similarity. This model shows oscillations in the population of tolerant agents as two different groups dominate the population successively. The mechanism that drives these oscillations is a drift towards more tolerance. Without such a drift a cooperative cluster cannot be destabilized and will not give

way to a new cooperative cluster. In other words, the temporally segregated dynamical coexistence of different tags is only possible if such a drift towards more tolerance exists. Without such a drift only one species would be selected. This is similar to the dynamical coexistence of species in the rock-paper-scissors game [12]. The drift provides a new mechanism for maintaining a dynamical biodiversity in biological systems [13].

This mechanism prevents a single species from taking over the whole population as it makes the dominant cluster vulnerable. Agents can therefore exploit the cluster by accepting support without supporting the cluster. These free riders consequently destroy the cooperative cluster again. The cooperative cluster can only defend itself if the cost for cooperation is sufficiently high. In this case the free riders cannot take over the whole population.

The main results do not change if the number of tags is increased. However, the analytical treatment becomes much more complicated, as we have to deal with $n-1$ coupled nonlinear equations in the case of n tags. Yet, a population model seems to be more appropriate in the case of more tags, as our model shows a subsequent realization of all tags in the same order.

If one analyzes a system with a spatial distribution of agents instead of the well-mixed case described above, one observes strong segregation between tags. Tolerant players need to protect themselves against intolerant exploiters by building a border of intolerant agents around them. The spatially distributed system and the strategies that help to overcome the segregation will be discussed in Ref. [14].

ACKNOWLEDGMENTS

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APPENDIX A: PRISONERS DILEMMA

The introduction of “never cooperate” agents which do not donate at all [15] instead of the zero-tolerance agents eliminates the difference between tags and leads to the payoff matrix

(Tag, T)	(Red, +1)	(Blue, +1)	(Red, 0)	(Blue, 0)
(Red, +1)	$b - c$	$b - c$	$-c$	$-c$
(Blue, +1)	$b - c$	$b - c$	$-c$	$-c$
(Red, 0)	b	b	0	0
(Blue, 0)	b	b	0	0

which describes the prisoner’s dilemma [1,8].

APPENDIX B: FIXED POINTS OF THE REPLICATOR DYNAMICS

The stability of the fixed points with only one tag can be calculated as follows. For $\mathbf{p}^{red}=(1-x,0,x)$ and $\varepsilon=0$, we find the Jacobian matrix

$$J^{red} = \begin{pmatrix} 1+(1-x)(c-x+cx) & 0 & (c-1)x^2 \\ c-cx & 1-x & cx \\ (1-x)(c-x+cx) & 0 & 1+(c-1)x^2 \end{pmatrix}, \quad (\text{B1})$$

with the eigenvalues $\lambda_1=1$, $\lambda_2=1-x$, and $\lambda_3=1+c-x$. The fixed point is marginally stable as long as $x \geq c$, for $x < c$ it becomes unstable. The reasoning can be adopted for the fixed line $\mathbf{p}^{blue}=(0,x,0)$.

A fixed point that is conserved for $\varepsilon > 0$ can be found if all players are tolerant. For $\mathbf{p}^{T+}=(1-y,y,0)$, the Jacobian matrix is given by

$$J^{T+} = \begin{pmatrix} 1+(c\bar{y}+y)\bar{y} & -\bar{c}\bar{y}y-\varepsilon & 0 \\ (c\bar{y}+y)\bar{y} & 1-\bar{c}\bar{y}y-\varepsilon & 0 \\ 2\bar{y}y\bar{c}+c\bar{y}+\varepsilon & -2\bar{y}y\bar{c}-cy-\varepsilon & 1+cy-\varepsilon \end{pmatrix}, \quad (\text{B2})$$

where $\bar{y}=1-y$ and $\bar{c}=1-c$. The eigenvalues of this matrix are $\lambda_1=1$, $\lambda_2=1+cy-\varepsilon$, and $\lambda_3=1+c(1-y)-\varepsilon$. $\lambda_i < 1$ ($i=1,2,3$) is not possible for $\varepsilon=0$. Hence the fixed line is unstable for $\varepsilon=0$. For $\varepsilon > 0$ there is an interval of stability given by $1-\varepsilon/c < y < \varepsilon/c$. If this inequality and $0 \leq y \leq 1$ are both fulfilled by y , the biased conversions ensure stability of the fixed point although the replicator dynamics alone would make this point unstable. The first inequality can only be fulfilled for $c < 2\varepsilon$. For $c < \varepsilon$ it is always fulfilled and the whole fixed line \mathbf{p}^{T+} is stable.

The fixed point given by $\mathbf{p}^d=(\varepsilon/c,\varepsilon/c,1/2-\varepsilon/c)$ reduces to the mixed Nash equilibrium for $\varepsilon=0$. The Jacobi matrix at this fixed point is

$$J^d = \begin{pmatrix} 1 + \frac{3c\varepsilon + \varepsilon - c^2}{2c} & \frac{-(1+c)\varepsilon}{2c} & \frac{(1-c)(c-2\varepsilon)}{4c} \\ \frac{(1+c)\varepsilon}{2c} & 1 + \frac{c\varepsilon - \varepsilon - c^2}{2c} & \frac{(1+c)(c-2\varepsilon)}{4c} \\ \frac{(1+c)\varepsilon}{c} & \frac{-(1+c)\varepsilon}{c} & 1 + \frac{(1-c)(c-2\varepsilon)}{2c} \end{pmatrix}. \quad (\text{B3})$$

The eigenvalues of this matrix are

$$\lambda_1 = 1 - \frac{\gamma}{2},$$

$$\lambda_2 = 1 + \frac{\gamma(2c-1) - \sqrt{\gamma(\gamma+8\varepsilon c+8\varepsilon c^2)}}{4c},$$

$$\lambda_3 = 1 + \frac{\gamma(2c-1) + \sqrt{\gamma(\gamma+8\varepsilon c+8\varepsilon c^2)}}{4c}, \quad (\text{B4})$$

where $\gamma=2\varepsilon-c$. For $\varepsilon=0$ we have $\lambda_1=\lambda_2=1-c/2 < 1$ and $\lambda_3=\frac{3}{2}-(c/2) > 1$. The third eigenvalue corresponds to an unstable direction. The corresponding eigenvector is $\mathbf{e}_3=(1-c,1+c,2)$, which is the normal of the separatrix for $\varepsilon=0$. In the case of $\varepsilon > 0$ we have $\lambda_i < 1$ for $i=1,2,3$ only if $c > (1+\sqrt{1-16\varepsilon})/2$. Hence \mathbf{p}^d becomes stable where it coincides with the fixed points \mathbf{p}^{s+} described in Appendix C. In all other cases, at least one eigenvalue of J^d is outside the unit circle.

APPENDIX C: ADDITIONAL FIXED POINTS

Numerical simulations show that the additional fixed points for $\varepsilon > 0$ can always be found in the plane spanned by $(1-c,0,c)$, $(0,1-c,0)$, and $(0,0,\frac{1}{2})$. Together with $p_1^{t+1}=p_1^t$ and $p_3^{t+1}=p_3^t$ we have three equations that describe these points. Two of the solutions are fixed points not described above. The first fixed point \mathbf{p}^{s+} can be written as

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$$\mathbf{p}^{s^+} = \begin{pmatrix} \frac{\alpha + \sqrt{\alpha\beta} - 2\varepsilon}{2c} \\ \frac{\sqrt{\alpha\beta} + 2(\alpha - \varepsilon) - (\alpha^2 + 4\alpha\beta + 4\alpha\sqrt{\alpha\beta})^{1/2}}{2c} \\ \frac{(1-c)(c^2 - \beta - 2\sqrt{\alpha\beta}) + (\alpha^2 + 4\alpha\beta + 4\alpha\sqrt{\alpha\beta})^{1/2}}{4\alpha} \end{pmatrix}, \quad (\text{C1})$$

where $\alpha = c(1-c)$ and $\beta = \alpha - 4\varepsilon$. \mathbf{p}^{s^-} can be calculated by exchanging p_1 with p_2 and p_3 with $p_4 = 1 - p_1 - p_2 - p_3$. These fixed points have only real coordinates for $\beta \geq 0$. For $\beta = 0$ we have $\mathbf{p}^{s^+} = \mathbf{p}^{s^-} = \mathbf{p}^d$.

The eigenvalues of the Jacobi matrix at the fixed points \mathbf{p}^{s^\pm} can be calculated numerically. For $\varepsilon = 0.01$ the fixed points are only stable if $c > 0.73$. At $c = (1 + \sqrt{1 - 16\varepsilon})/2 \approx 0.96$ they collapse with \mathbf{p}^d in a supercritical pitchfork bifurcation and form a single stable fixed point.

For $c > 0.73$ the fixed points \mathbf{p}^{s^\pm} are the only stable attractors and the order measures described in Sec. III D can be calculated analytically. We find for $c < 0.96$

$$d = 1 - p_3(p_2 + p_4) - p_4(p_1 + p_3) = \frac{5\alpha - 4\varepsilon(1+c) + 2\sqrt{\alpha\beta} - (\alpha^2 + 4\alpha\beta + 4\alpha\sqrt{\alpha\beta})^{1/2}}{4\alpha}, \quad (\text{C2})$$

$$p_{\text{tol}} = p_1 + p_2 = \frac{3\alpha - 4\varepsilon + 2\sqrt{\alpha\beta} - (\alpha^2 + 4\alpha\beta + 4\alpha\sqrt{\alpha\beta})^{1/2}}{2c}, \quad (\text{C3})$$

$$a = |p_1 + p_3 - p_2 - p_4| = \frac{-\alpha + (\alpha^2 + 4\alpha\beta + 4\alpha\sqrt{\alpha\beta})^{1/2}}{2\alpha}. \quad (\text{C4})$$

For $c > 0.96$ the fixed point \mathbf{p}^d becomes stable and we find $d = \frac{1}{2} + (\varepsilon/c)$, $p_{\text{tol}} = 2(\varepsilon/c)$, and $a = 0$.

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2.3 Stochastic gain in population dynamics

Stochastic Gain in Population Dynamics

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We introduce an extension of the usual replicator dynamics to adaptive learning rates. We show that a population with a dynamic learning rate can gain an increased average payoff in transient phases and can also exploit external noise, leading the system away from the Nash equilibrium, in a resonancelike fashion. The payoff versus noise curve resembles the signal to noise ratio curve in stochastic resonance. Seen in this broad context, we introduce another mechanism that exploits fluctuations in order to improve properties of the system. Such a mechanism could be of particular interest in economic systems.

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Game theory [1] describes situations in which the success or payoff of an individual depends on its own action as well as on the actions of others. This paradigm can be applied to biological systems, as evolution through natural selection can be viewed as an optimization process in which the fitness landscape changes with the state of the adaptive populations [2]. Evolutionary game theory focuses mainly on systems with a single fitness function for all individuals, which is identified with the payoff function of a game [3–5]. In nature, often different populations with different ambitions interact with each other, as shoppers and sellers [6], attackers and defenders [6], or males and females [5]. Here the payoff functions are different for the interacting populations. A mean-field description of such asymmetric conflicts is given by the coupled replicator equations [4,5,7]. These equations have a very rich dynamical behavior and can even display Hamiltonian chaos [8,9]. In previous work [3–5] it has been tacitly assumed that both populations have the same adaptation mechanisms. But it seems to be natural that different mechanisms are applied by the interacting populations, e.g., different adaptation rates. Here we analyze such systems for the case that both populations have slightly different adaptation mechanisms. We assume that one population can control its own adaptation rate. This alters the velocity when the system is approaching the stable Nash equilibria [10] in strategy space, leading to an increased average payoff.

In real systems, fluctuations disturbing the system are to be expected. Such disturbances can arise from a variety of effects, e.g., errors of the players [11], deviations from a perfectly mixed population, or immigration of individuals with different strategy distributions. So far, stochastic extensions to the replicator dynamics have mainly been analyzed in the context of equilibrium selection [12,13]. Here we show that a population with an adaptive learning rate can obtain an increased payoff if these fluctuations are present. For small noise intensities the average payoff increases, while very large fluctuations can no longer be exploited, leading to a decrease of the average payoff.

This recalls the stochastic resonance effect [14–17], where the signal to noise ratio of a system is improved for intermediate noise intensities. In contrast to the usual stochastic resonance, a periodic force is not involved here, making the mechanism more similar to coherence resonance [18]. Seen in this broader context, we introduce another mechanism that exploits fluctuations in order to improve the performance of the system.

We consider two adaptive species X and Y —each with different strategies—that are involved in a repeated game. Both populations have different objectives described by payoff matrices P_x and P_y . The fraction of individuals x_i that adopt a certain strategy i grows proportional to the relative payoff of the strategy i ; the same holds for Y . In the presence of noise, this coevolution can be described by the coupled replicator equations

$$\begin{aligned}\dot{x}_i &= x_i \eta_x [\Pi_i^x - \langle \Pi^x \rangle] + \xi_i^x, \\ \dot{y}_i &= y_i \eta_y [\Pi_i^y - \langle \Pi^y \rangle] + \xi_i^y,\end{aligned}\quad (1)$$

where η_x and η_y are the learning rates of the populations. We assume for simplicity that the noise ξ_i^x is Gaussian with autocorrelation $\langle \xi_i^k(t) \xi_j^l(s) \rangle = \sigma^2 \delta_{ij} \delta_{kl} \delta(t-s)$ as in Ref. [12]. We also follow Ref. [12] in choosing reflecting boundaries. The payoffs are defined as $\Pi_i^x = (P_x \cdot \mathbf{y})_i$, $\langle \Pi^x \rangle = \mathbf{x}^T \cdot P_x \cdot \mathbf{y}$, and similarly for y .

We extend the usual replicator dynamics by introducing adaptive learning rates as

$$\eta_x = 1 - \tanh(\alpha_x \Delta \Pi), \quad (2)$$

where $\Delta \Pi = \langle \Pi^x \rangle - \langle \Pi^y \rangle$ is the time dependent difference between the average payoffs of the populations and $\alpha_x \geq 0$ is a “perception ability” of the population. In order to maintain the basic features of the replicator dynamics, the learning rate must be a positive function with $\langle \eta \rangle = 1$, which is ensured by Eq. (2). For $\alpha_x > 0$ the population X learns slower if it is currently in a good position; otherwise, it learns faster. The value of α_x determines how well a population can assess its current state. The adaptive learning rate leads to a faster escape

from unfavorable states, while on the other hand the population tends to remain in preferable states. Other choices for η_x which ensure these properties mentioned above will not alter our results. In the following, we focus on a setting where only one population has an adaptive learning rate η_x as in Eq. (2).

The noise introduced above drives the system away from the Nash equilibrium and leads for small amplitude to a positive gain of the population with an adaptive learning rate, whereas for large noise amplitudes the fluctuations smear out the trajectories in phase space so strongly that they can no longer be exploited. Hence, we expect an optimal noise effect for intermediate values of σ . In order to be able to compare the payoffs of both populations, we assume that the dynamics starts from the Nash equilibrium.

As a first example, we consider the zero-sum game “matching pennies” [3,19]. Here both players can choose between two options ± 1 . Player one wins if both players select the same option and player two wins otherwise. The game is described by the payoff matrices

$$P_x = \begin{pmatrix} +1 & -1 \\ -1 & +1 \end{pmatrix} = -P_y. \quad (3)$$

The replicator equations follow from Eqs. (1) and (3) as

$$\begin{aligned} \dot{x} &= -2\eta_x x(2y-1)(x-1) + \xi_x, \\ \dot{y} &= +2\eta_y y(2x-1)(y-1) + \xi_y, \end{aligned} \quad (4)$$

where $x = x_0$ and $y = y_0$. Let us first consider the zero noise limit in the case $\eta_x = \eta_y = 1$. As for all zero-sum games, i.e., $P_x = -P_y^T$, the system (1) without noise becomes Hamiltonian and has a constant of motion [20]. Here the constant is given by $H(x, y) = -2 \ln[x(1-x)] - 2 \ln[y(1-y)]$. The trajectories oscillate around the Nash equilibrium at $x = y = 1/2$. $H(x, y)$ is connected to the temporal integral of the average payoff $\langle \Pi_x \rangle = (\mathbf{x}^t)^T \cdot P_x \cdot \mathbf{y}^t$ during a period with $\langle \Pi^x \rangle > 0$,

$$\int_{t_0}^{t_1} \langle \Pi^x \rangle dt = -\frac{H(x_0, \frac{1}{2}) - H(\frac{1}{2}, \frac{1}{2})}{4}, \quad (5)$$

where $(x, y) = (x_0, \frac{1}{2})$ at t_0 and $(x, y) = (\frac{1}{2}, x_0)$ at t_1 .

If we include adaptive learning rates (2) into the system, we find $\dot{H}(x, y) = -2 \tanh(\alpha_x \Delta \Pi) \Delta \Pi \leq 0$, vanishing for $\alpha_x = 0$. Hence, adaptive learning rates dampen the oscillations around the Nash equilibrium, and the trajectories in the $x-y$ plane spiral towards the Nash equilibrium where $\langle \Pi_x \rangle = \langle \Pi_y \rangle = 0$ (see Fig. 1). In addition, this leads to an increased payoff of one population. As the matrices (3) describe a zero-sum game, it is sufficient for a population if it knows its own current average payoff $\langle \Delta \Pi \rangle = 2\langle \Pi_x \rangle$.

Numerical simulations for $\alpha_x > 0$ show that the temporal integral of the payoff becomes

$$\left\langle \int_{t_0}^{t_1} \langle \Pi_x \rangle dt \right\rangle_{(x_0, y_0)} = -\frac{1}{8} [H(x_1, y_1) - H(x_0, y_0)]. \quad (6)$$

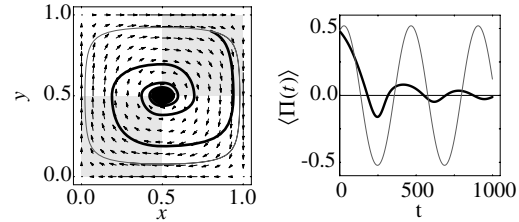


FIG. 1. Matching pennies: Comparison between the behavior of a population with a constant learning rate [i.e., $\alpha_x = 0$ (thin lines)] and a population with an adaptive learning rate [perception ability $\alpha_x = 10$ (thick lines)]. The opponent has in both cases a constant learning rate $\eta_y = 1$. Left: Trajectories in strategy space. Arrows show the vector field of the replicator dynamics. Population X has positive (negative) average payoff in gray (white) areas. Right: Time development of the average payoff of the population X. The adaptive learning rate increases the time intervals in which the corresponding population has a positive payoff, dampening the oscillations around the Nash equilibrium [21].

The averaged initial value $H(x_0, y_0)$ can be calculated as $\int_0^1 dx_0 \int_0^1 dy_0 H(x_0, y_0) = 8$. For $t \rightarrow \infty$ the system relaxes to the Nash equilibrium where $H = 8 \ln 2$. Hence, we find for the average cumulated payoff with $\langle \int_{t_0}^{\infty} \langle \Pi_x \rangle dt \rangle_{(x_0, y_0)} \leq -\frac{1}{8} (8 \ln 2 - 8) \approx 0.307$. Numerical simulations yield 0.308 ± 0.005 independent of α . We conclude that a population can increase its average payoff if it has an adaptive learning rate $\alpha_x > 0$ and if the game does not start in the Nash equilibrium. The adaptation parameter α influences only the time scale on which the Nash equilibrium is approached.

Small noise intensities drive the system away from the fixed point and the population with the adaptive learning rate gains an increased payoff. If the noise amplitude σ becomes too large, the trajectories will be smeared out homogeneously over the positive (gray) and negative (white) payoff regions in phase space (Fig. 1). This implies that the average gain of population one decreases to zero; cf. Fig. 2. Although the average payoff is very small even for the optimal noise intensity, the cumulated payoff increases linearly in time. This means that for long times the gained payoff accumulates to a profitable value.

As a second application we analyze the effect of adaptive learning rates and noise on the prisoner’s dilemma. We use the standard payoff matrix [22]

$$P_x = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} = P_y, \quad (7)$$

where rows and columns are placed in the order “cooperate” and “defect.” As this game is not a zero-sum game, the population with the adaptive learning rate must be able to compare its own average payoff with the opponent’s average payoff. The replicator dynamics of this system is determined by Eqs. (1) and (7),

$$\begin{aligned} \dot{x} &= x\eta_x(x-1)(1+y) + \xi_x, \\ \dot{y} &= y\eta_y(y-1)(1+x) + \xi_y. \end{aligned} \quad (8)$$

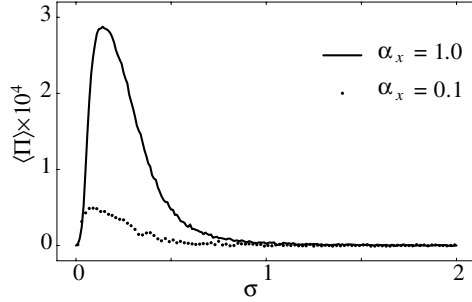


FIG. 2. Matching pennies: Average payoff of a population with an adaptive learning rate against a population with a constant learning rate under the influence of noise for different noise intensities ($\alpha_y = 0$, averages over 2×10^4 initial conditions and 2×10^4 time steps; see [21] for further details).

There is a stable fixed point in the Nash equilibrium $x = y = 0$ where both players defect and an unstable fixed point for mutual cooperation, i.e., $x = y = 1$.

The average payoff difference under the influence of noise is similar as in matching pennies. Small fluctuations lead the system slowly away from the Nash equilibrium and tend to increase the payoff. If the fluctuations are too large, they disturb the population with adaptive learning rates and the payoff decreases again (see Fig. 3). Interestingly enough, here too much noise even leads to a decreasing payoff difference.

In order to describe the “stochastic gain” effect analytically, we introduce a simplified model. A linearization of Eq. (8) around the stable Nash equilibrium leads for constant learning rates to $\dot{x} = -\eta_x x + \xi_x$ and $\dot{y} = -\eta_y y + \xi_y$. We now analyze a game in which the replicator dynamics is given by these linear equations and include adaptive learning rates based on the payoffs for the prisoner’s dilemma. With $\Delta \Pi = -5(x - y)$ the adaptive learning rate η_x becomes $\eta_x = 1 + \tanh[5\alpha(x - y)] \approx 1 + 5\alpha(x - y)$ for $\alpha, x, y \ll 1$. The simplified system can be viewed as a small noise expansion of the prisoner’s dilemma, where the trajectory stays close to the Nash equilibrium. For $\eta_y = 1$ the simplified noisy replicator equations read

$$\dot{x} = -x - \alpha' x(x - y) + \xi_x, \quad (9a)$$

$$\dot{y} = -y + \xi_y, \quad (9b)$$

where $\alpha' = 5\alpha$. The effect of different constant learning rates is discussed in Ref. [23]. The mechanism we introduce here is more intricate, as the adaptive learning rate leads to a dynamical adjustment of the learning rate, and the average of $\eta_x = 1 + \alpha'(x - y)$ over all possible strategies is $\eta_x = 1$.

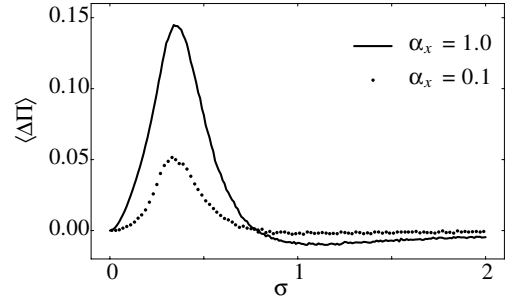


FIG. 3. Prisoner’s dilemma: Average payoff difference of a population with an adaptive learning rate against a population with a constant learning rate for different noise intensities. The negative payoffs arise from the fact that we have $\eta_x < \eta_y$ for $x < y$ ($\Delta t = 0.01$, $\alpha_y = 0$, averages over 2×10^4 initial conditions and 2×10^4 time steps).

Equation (9b) describes an Ornstein-Uhlenbeck process [24]; here the dynamics is restricted to $0 \leq y \leq 1$. The Fokker-Planck equation [25] for $p_y = p_y(y, t | y_0, t_0)$,

$$\dot{p}_y = \frac{d}{dy} \left(y p_y + \frac{\sigma^2}{2} \frac{d}{dy} p_y \right), \quad (10)$$

has the stationary solution $p_y^s = \mathcal{N}_y e^{-y^2/\sigma^2}$, where $\mathcal{N}_y^{-1} = \int_0^1 e^{-y^2/\sigma^2} dy$. We find the mean value $\langle y(\sigma) \rangle$ as

$$\langle y \rangle = \int_0^1 dy y p_{y,y} = \frac{\sigma(1 - e^{-\sigma^{-2}})}{\sqrt{\pi} \operatorname{erf}(\frac{1}{\sigma})}. \quad (11)$$

y is a correlated stochastic process which appears in Eq. (9a) as a multiplicative noise. Numerical simulations indicate that we may neglect the stochastic nature of y and replace it by $\langle y \rangle$ for small α . This leads to an approximated Fokker-Planck equation for $p_x = p_x(x, t | x_0, 0)$,

$$\dot{p}_x = \frac{d}{dx} \left[-a(x) p_x + \frac{\sigma^2}{2} \frac{d}{dx} p_x \right], \quad (12)$$

where $a(x) = -x - x\alpha'(x - \langle y \rangle)$. Since x is (similarly to y) also restricted to $0 \leq x \leq 1$, we find the stationary solution

$$p_x^s = \mathcal{N}_x \exp \left[-\frac{x^2}{\sigma^2} - \frac{2\alpha' x^3}{3\sigma^2} + \frac{\alpha' \langle y \rangle x^2}{\sigma^2} \right] \quad (13)$$

with the normalization constant \mathcal{N}_x . Since x is typically of the order of σ for $\sigma \ll 1$, the term x^2/σ^2 is finite. Therefore, we can expand Eq. (13) for $\alpha' \ll 1$ and obtain by expanding $\langle x \rangle$ again an analytical expression for $\langle \Delta \Pi \rangle = -5(\langle x \rangle - \langle y \rangle)$,

$$\langle \Delta \Pi \rangle = -5\alpha' \frac{d}{d\alpha'} \langle x \rangle = 5\alpha' \left[\frac{\sigma^2}{2} - \delta^3 \sigma \gamma (1 - \gamma)^2 + \delta^2 (1 - \gamma) \left[\frac{5}{3} \gamma - \frac{7}{6} \sigma^2 (1 - \gamma) \right] - \delta \gamma \left(\frac{2}{3\sigma} + \sigma \right) \right], \quad (14)$$

where $\delta = \frac{1}{\sqrt{\pi} \operatorname{erf}(1/\sigma)}$ and $\gamma = e^{-1/\sigma^2}$. The asymptotics of Eq. (14) can be computed as $\langle \Delta \Pi \rangle = \alpha'/(24\sigma^2)$ for $\sigma \gg 1$ and

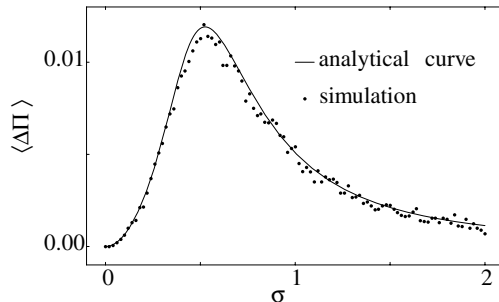


FIG. 4. Simplified model: Comparison of the average payoff difference $\langle \Delta \Pi \rangle$ from a simulation of Eqs. (9a) and (9b) and the analytical function Eq. (14) ($\Delta t = 0.01$, $\alpha' = 5\alpha = 0.1$, averages over 4×10^4 time steps and 4×10^4 realizations).

$\langle \Delta \Pi \rangle = \alpha' \left(\frac{5}{2} - \frac{35}{6\pi} \right) \sigma^2$ for $\sigma \ll 1$. We stress that this simplified system which consists of a stable fixed point with a linear adaptive learning rate in the presence of noise is the simplest possible model that describes the stochastic gain effect. Figure 4 shows a comparison between the analytical payoff difference Eq. (14) and a simulation of Eqs. (9a),(9b).

To summarize, we have introduced an extension to the usual replicator dynamics that modifies the learning rates using a simple “win stay–lose shift” rule. In this way, a population optimizes the payoff difference to a competing population. This simple rule leads to a convergence towards the mixed Nash equilibrium for the game of matching pennies [26]. Even in games with stable Nash equilibria as the prisoner’s dilemma, transient phases can be exploited, although the basins of attraction are not altered, as, e.g., in Ref. [23]. Weak external noise drives the system into the transient regime and leads to an increased gain for one adaptive population.

In conclusion, we have found a learning process which improves the gain of the population with an adaptive learning rate under the influence of external noise. Fluctuations lead to an increased payoff for intermediate noise intensities in a resonancelike fashion. This phenomenon could be of particular interest in economics, where interactions are always subject to external disturbances [6,13,27].

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$$\begin{aligned} x_i^{t+1} &= x_i^t + x_i^t [\Pi_i^x - \langle \Pi^x \rangle] \frac{1}{C/\eta_x + \langle \Pi^x \rangle}, \\ y_i^{t+1} &= y_i^t + y_i^t [(\Pi_i^y)^+ - \langle \Pi^y \rangle^+] \frac{1}{C/\eta_y + \langle \Pi^y \rangle^+}, \end{aligned} \quad (15)$$

with $C \gg 1$ and where $(\Pi_i^y)^+ = (P_y \cdot \mathbf{x}^{t+1})_i$, $\langle \Pi^y \rangle^+ = (\mathbf{y}^t)^T \cdot P_y \cdot \mathbf{x}^{t+1}$. Here we choose $C = 100$.

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3 Discussion

3.1 Conclusions

In this thesis, a minimal model for similarity based cooperation motivated by the model of Riolo *et al.* (2001) has been introduced and analyzed. Cooperation does not evolve if agents are not forced to cooperate within their own group (Hauert, 2002a; Roberts and Sherratt, 2002). In our simplified model we can show this explicitly by reducing the payoff matrix to a Prisoner's Dilemma. It has been argued that this reduces the biological relevance of such models. However, there can be situations in which this approach is justified. One possibility is that different mechanisms for the evolution of cooperation between groups and within groups are present. For example, in small groups direct or indirect reciprocity can work, whereas strangers are first assessed from their group membership. Another possibility are groups in which it is difficult to refuse to cooperate with others from the own group, e.g. to refuse to speak the own native language.

For mixed systems with random interactions the minimal model for similarity based cooperation introduced in this thesis can be solved analytically. This analytical insight allows to identify the driving mechanisms that lead to this kind of dynamical behavior. We have shown that oscillations are only observed if a drift towards more tolerant strategies is present that destabilizes fixed points. This understanding of the key features of the model allows to construct more complicated and realistic models again.

In spatially extended systems, similarity based cooperation leads to the absence of cooperation between groups and segregation (Sigmund and Nowak, 2001). If the drift towards more tolerant strategies is implemented as a local update mechanism, it leads to the emergence of spiral waves in the system based upon a cyclic dominance of strategies. Further, different mechanisms to overcome the segregation are discussed. The minimal model allows to analyze related models on spatial lattices. One key question is whether tags can increase the cooperation at all. If they allow to induce cooperation between small groups in a population of non-cooperative individuals, this is obviously the case. Recently, it has been shown that even if unconditional defectors are present, i.e. if agents are not forced to cooperate within their own group, tag based mechanisms can lead to high degrees of cooperation (Axelrod *et al.*, 2004). The similarity based cooperation mechanism has been analyzed both in spatial systems with finite populations and in the limit of infinite populations. The differences

in the dynamics of these systems have two main reasons: First, the population is finite. A second point is the restriction of interactions to a small fraction of the population. The latter requirement can easily be relaxed applying game dynamics in finite populations. This part of evolutionary game theory has attracted growing attention recently (Nowak *et al.*, 2004; Taylor *et al.*, 2004; Fudenberg *et al.*, 2004; Claussen and Traulsen, 2005).

In the second part of this thesis, asymmetric conflicts have been discussed. In these systems, two populations with different selection mechanisms can be analyzed directly. It has been shown that an adaptive selection rate can help to exploit external fluctuations. These adaptive selection rates can be viewed as an interpolation between two previously discussed game dynamics: the standard replicator dynamics (Hofbauer and Sigmund, 1998) and the adjusted replicator dynamics (Maynard Smith, 1982). The stochastic gain effect is found with the assumption that stochastic elements of the dynamics can be captured by adding a Langevin term of Gaussian distributed noise to the replicator equations, as previously proposed (Fudenberg and Harris, 1992). There are several other examples for positive effects of randomness as noise induced pattern formation, coherence resonance or stochastic resonance. However, the stochastic gain effect is the first example for a game theoretic system that shows such a feature. In all these systems, the response of the system is improved by noise. There are several sources for such a kind of noise: External fluctuations can influence the system, errors of individuals or deviations from a mixed system can lead to disturbances. A particular interesting case is the noise arising from finite populations, where a certain noise is always present. The introduction of the Moran process to frequency dependent selection by Nowak *et al.* (2004) provides a standard model for game theory in finite populations. The frequency dependent Moran process includes a quantity that can be defined as intensity of selection. This allows to address the stochastic gain problem in finite populations. First numerical simulations indicate that also internal fluctuations can be exploited by populations with adaptive selection pressure.

However, the stochastic gain effect leads to several other interesting questions. One question is of course whether the stochastic gain effect can be realized in game theoretic systems describing economic interactions. In this case, it might be possible to transfer it to real world markets. However, these systems usually consider a different situation in which a single trader interacts in a large market with a vanishing influence on the market development. In these situations, individual payoffs are hard to compare. Hence, the selection rate can no longer depend on payoff differences. However, the selection rate could be adjusted depending on a market index. It remains to be seen whether such a strategy can be successful in real markets. A probably more serious problem, is the definition of an equilibrium. While in zero sum games the payoffs of the other party can easily be accessed, it is not clear what it means to be “in an advantageous situation” at a market, as these markets are usually not stationary. However, traders have their personal perception of the market situation and apply

similar mechanisms, although they do not necessarily have a solid mathematical basis. In conclusion, the application of this mechanism seems to be in principle possible. However, more work into this direction has to be made and there is no simple way to get rich from fluctuations.

3.2 Outlook

The similarity based cooperation mechanism allows to analyze the dynamics of such systems in detail. So far, it has been analyzed in a well mixed system and on a simple lattice. To incorporate the nature of real world interaction structures, more realistic geometries have to be considered, as small world networks.

This thesis has been restricted to systems in which individuals always cooperate with others from their own group. In spatially extended systems, interesting phenomena can be observed when this requirement is relaxed. In particular, Axelrod *et al.* (2004) have shown numerically that tags can increase the level of cooperation. This feature is also found in our model. However, a detailed comparison between spatially extended systems with and without tags is lacking so far. Numerical simulations of our model show that tags can promote cooperation even for parameter values that do not promote cooperation if tags are not present in the system. This feature has to be analyzed and quantified in detail.

The introduction of tags that differentiate groups leads to the possibility to impose a selection mechanism on these groups depending on their composition. Based on the work in this thesis, a model in which group selection emerges from individual selection by a population structure has been developed (Traulsen *et al.*, 2005b; Traulsen and Nowak, 2005).

The stochastic gain effect has only been analyzed in systems based on the replicator dynamics so far. This basically assumes an infinite population. The next step is to transfer this model to finite populations. As a first step, the relationship between different game dynamical formulations in finite and infinite populations has been analyzed (Traulsen *et al.*, 2005a). In finite populations, a quantity for the pressure of selection can be defined. An adaptive selection rate would naturally modify this parameter and analyze a dynamic adjustment of the pressure of selection. In finite populations, a certain randomness is always present. However, such an inherent noise is not always captured by additive Langevin terms of Gaussian white noise (Claussen and Traulsen, 2005). However, first numerical simulations indicate that such noise arising from the inherent stochasticity can effectively be exploited by adaptive selection rates. The stochastic gain effect for finite populations is a first requirement to transfer the mechanism to game theoretic interactions that mimic real world markets, as the minority game.

For the field of evolutionary game theory, there are still challenges in the future. So far,

evolutionary game theory lead to a better qualitative understanding of many biological systems. However, quantitative experiments are extremely difficult since the fitness of individuals is very hard to measure. An increased cooperation with experimentalists is necessary. The theory is so far mainly restricted to well mixed systems or simple spatial lattices. To capture the geometry of real biological and social interactions, a generalization to more universal systems as networks is necessary. However, in game theoretic systems on networks only few analytical results are possible (Matsen and Nowak, 2004; Lieberman *et al.*, 2005).

The complexity of biology requires many more extensions of evolutionary game theory. For example, the complex genotype-phenotype mapping has been ignored so far. Hence, more work is necessary on the interaction of strategies that are encoded in genomic sequences.

Another important point already raised above is the relationship between finite and infinite populations. Most evolutionary game dynamics have been studied in infinite populations so far. Finite population effects often lead to surprising results (Nowak *et al.*, 2004) and may challenge traditional results from evolutionary game theory. For example, the concept of evolutionary stability has to be altered when effects of a finite population size are considered.

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Selbständigkeitserklärung

Ich erkläre, dass ich die vorgelegte Arbeit – abgesehen von der Beratung durch meinen Betreuer Prof. Dr. Heinz Georg Schuster – selbständig und nur unter Benutzung der angegebenen Literatur angefertigt habe.

Die den Veröffentlichungen zugrunde liegende Forschungsarbeit wurde – abgesehen von der Beratung durch Prof. Dr. Heinz Georg Schuster – ausschließlich von mir selbst durchgeführt. Ausnahmen sind die folgenden Veröffentlichungen:

- Bei dem Artikel „Similarity-based cooperation and spatial segregation“ hat Dr. Jens Christian Claussen zur quantitativen Analyse beigetragen.
- Bei dem Artikel „Stochastic gain in population dynamics“ war Dipl.-Phys. Torsten Röhl an der Modellbildung beteiligt.

Weiterhin versichere ich, dass die vorliegende Dissertation weder ganz noch zum Teil bei einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt worden ist.

Ich habe keine früheren Promotionsversuche unternommen.

Kiel, den 2. Januar 2005