Conference
"Evolution of Cooperation - Models and Theories"
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Abstracts

Origins of fair play

Ken Binmore

This lecture is a brief overview of an evolutionary theory of fairness. The ideas are fleshed out in a book Natural Justice, which is itself a condensed version of an earlier two-volume book Game Theory and the Social Contract.

Coordinated contingent punishment is group-beneficial and can proliferate when rare

Rob Boyd
Co-authors: Herbert Gintis, Samuel Bowles

It has recently been proposed that the evolution of human cooperation is based on the group-level advantages afforded by the punishment of free-riders. This explanation has encountered both theoretical and empirical challenges. First, theoretical models make clear that a high frequency of punishers is readily stabilized once attained; but the initial emergence of punishment is a puzzle because rare punishers bear substantial costs. Second, punishment uses scarce resources, and experimental evidence shows that benefits of cooperation are often less than the cost of punishment necessary to sustain it. But in contrast to these models and experiments, in most natural settings punishment of shirkers is contingent and coordinated. As a result, punishment is targeted on shirkers and recognized as legitimate, thus deterring counter-punishment, and is not undertaken when it would not be cost-effective, thus facilitating its proliferation when rare. Here we analyze a model of contingent and coordinated punishment, and show that under parameters approximating ancestral human conditions, punishment can proliferate when rare, and when common it enhances group-average payoffs.

Cooperation and stability through periodic impulses

Ross Cressman
Co-authors: Bo-Yu Zhang, Yi Tao

A great deal of game-theoretic research has been devoted to explain the prevalence of cooperation in biological systems as well as in human society. One reason for the vast literature from members of the game theory community on this topic is that the only rational option for the underlying stage game, the symmetric Prisoner's Dilemma (PD), is to Defect since this strategy strictly dominates Cooperate. To a lesser extent, the question of stability of mixed strategy equilibrium solutions has also created controversy in the game theory community. The controversy here is clearly demonstrated through typical payoffs used in the Battle of the Sexes (BS) introduced by Dawkins where the replicator equation yields periodic solutions around its mixed strategy Nash equilibrium (NE).
Here, we re-examine the PD and BS stage games from the dynamic perspective where, in addition to the continuous trajectories of evolutionary game theory, there are periodic jumps (impulses) in the population size. In particular, we give analytic conditions for

the impulsive coefficients in the PD game for the successful initial invasion of Cooperators into a population of Defectors as well as conditions based on stronger impulsive effects for Cooperators to completely take over the system. We also show that these latter conditions applied to the BS game imply global convergence to a monomorphic system where all males use one pure strategy as well as all females. Moreover, when impulsive effects are weak in the BS game, a globally attracting polymorphic state emerges near the NE.

Runaway selection for cooperation and strict-and-severe punishment

Ulf Dieckmann
Co-author: Mayuko Nakamaru

Punishing defectors is an important means of stabilizing cooperation. When levels of cooperation and punishment are continuous, individuals must employ suitable social standards for defining defectors and for determining punishment levels. Here we investigate the evolution of a social reaction norm, or psychological response function, for determining the punishment level meted out by individuals in dependence on the cooperation level exhibited by their neighbors in a lattice-structured population. We find that (1) cooperation and punishment can undergo runaway selection, with evolution towards enhanced cooperation and an ever more demanding punishment reaction norm mutually reinforcing each other; (2) this mechanism works best when punishment is strict, so that ambiguities in defining defectors are small; (3) when the strictness of punishment can adapt jointly with the threshold and severity of punishment, evolution favors the strict-and-severe punishment of individuals who offer slightly less than average cooperation levels; (4) strict-and-severe punishment naturally evolves and leads to much enhanced cooperation when cooperation without punishment would be weak and neither cooperation nor punishment are too costly; and (5) such evolutionary dynamics enable the bootstrapping of cooperation and punishment, through which defectors who never punish gradually and steadily evolve into cooperators who punish those they define as defectors.

Reference: *Journal of Theoretical Biology* 257: 1–8, 2009

A unifying perspective for understanding the evolution of cooperation

Michael Doebeli

We present a simple framework that highlights the most fundamental requirement for the evolution of cooperation: assortment between cooperative individuals and the helping behaviours of others. We partition the fitness effects on individuals into those due to self and those due to the ‘interaction environment’, and show that it is the latter that is most fundamental to understanding the evolution of cooperation. While kinship or genetic similarity may generate a favourable structure of interaction environments, it is not a fundamental requirement for the evolution of altruism, and even suicidal aid can theoretically evolve without help ever being exchanged between genetically similar individuals. We conclude that in a world in which the concepts of kin and group selection are absent, one is still able to fully understand the evolution of cooperation based on the mechanisms that generate the assortment necessary for cooperation to be favoured by natural selection.

Trusting and being trusted: evidence from genetic and fRMI data"

Armin Falk

In my talk I will briefly discuss two papers that study biological foundations of trust: Trust is a prerequisite for social and economic interactions, both in dyadic as well as in more complex social relationships. The first paper is based on recent studies showing that nasally administered oxytocin increases trust, highlighting the importance of this neuropeptide for cooperative behavior. We therefore hypothesized that the oxytocin receptor (OXTR) gene plays a role in explaining individual differences in trust. To test this hypothesis we conducted a laboratory trust experiment with 100 participants whose OXTR gene was screened. A haplotype block spanning the promoter region of OXTR was significantly related to trusting behavior, yet showed no influence on risk attitudes or on prosocial inclination. Our results indicate that individual differences in the proclivity to trust are influenced by variations in the OXTR gene. The second paper uses functional magnetic resonance imaging techniques (fMRI) to shed light on the neural correlates of being trusted vs. Being controlled. Results suggest that the response to being trusted is based on regions associated with response conflict, executive control, motivation and social intention recognition.

Altruism theories, models, and definitions: prospects for unification

Jeff Fletcher

The evolution of altruistic behavior appears paradoxical: those that sacrifice to help others or put themselves at risk of exploitation via cooperation would seem to be less fit than those with more selfish, exploitative behaviors. Three main theories have emerged to explain how self-sacrificing behaviors in local interactions can nonetheless be selected for overall. These theories are inclusive fitness (kin selection), multilevel selection (group selection), and reciprocal altruism, all of which have been applied to understanding human cooperation. Over the last several decades there has been much disagreement among proponents of these theories. At least part of this debate stems from the use of different models, fitness accounting methods, and definitions of altruism/cooperation used to support each theory. Focusing on what is common among these competing frameworks (a fundamental requirement for assortment between self-sacrificing types and help from others) can move us towards a unification of theories on how altruism and cooperation evolve.

Imitation, evolution, and cooperation

Drew Fudenberg
Co-author: Lorens Imhof

Many forms of social and biological adaptation correspond to "imitation processes" where agents are more likely to adopt more successful and.or more popular strategies. We show how to analyze the long run distribution of these processes, first in general finite populations and then when the population becomes large. With these tools we can analyze the evolution of cooperation in repeated games with a restricted set of strategies; we compare the results to those of models where strategies are allowed to be arbitrarily complex

Rewards vs. punishment to sustain cooperation - experimental evidence

Simon Gaechter

Previous research has shown that punishment can achieve pro-social behaviour. However, punishment is inefficient. Can rewards achieve the same? In this experimental study we compare rewards and punishment as means to sustain pro-social behaviour. The results show that rewards and punishments can achieve this goal both in one-shot and repeated games, provided the "carrot" or the "stick" are big enough. Punishment can be "cost effective" if it serves as a mere threat, whereas costly rewards have to be awarded to be behaviourally effective.

The evolution of private property

Herbert Gintis

Experimental studies have shown that subjects exhibit a systematic endowment effect. No acceptable explanation for the existence of this behavior has been offered. This paper shows that the endowment effect can be modeled as respect for private property in the absence of legal institutions ensuring third-party contract enforcement. In this sense, ``natural" private property has been observed in many species, in the form of recognition of territorial incumbency. We develop a model loosely based on the Hawk-Dove-Bourgeois game and the War of Attrition to explain the natural evolution of private property.

Poison-antidote systems in nature and culture

Peter Hammerstein

In host parasite interactions there is usually little scope for cooperation. It would seem maladaptive, for example, if hosts actively provided their parasites with resources, helped them to survive and facilitated their transmission into offspring. Intracellular bacteria of the genus *Wolbachia* demonstrate impressively, however, that this view of host parasite relationships is far too simple. Many strains of *Wolbachia* are known for a dual way in which they manipulate their hosts. In males they “poison” the sperm. In a female’s egg they offer an “antidote” if the egg is infected. Females of an infected population would then often be under selection to “pay protection money” in order to “buy” the rescue of eggs in fusions with manipulated sperm. Less figuratively speaking, our models show for a wide range of parameters that natural selection would program females to support the bacteria even if the latter significantly reduced female fecundity. This is probably one of the main reasons why more than half of all insect species seem to be infected with *Wolbachia*. The bacterial poison-antidote system can strongly influence host evolution since it facilitates genetic divergence, local adaptation, and speciation. *Wolbachia* are not the only organisms employing a poison-antidote system. In particular, human business often prospers on the basis of structurally similar manipulations.

Koehncke, A., Telschow, A., Werren, J.H. & Hammerstein, P. (2009). Life and death of an influential passenger: *Wolbachia* and the evolution of CI-modifiers by their hosts. *PLoS ONE* 4(2), e4425.

Hilgenboecker, K., Hammerstein, P., Schlattmann, P., Telschow, A. & Werren, J.H. (2008). How many species are infected with *Wolbachia*? - a statistical analysis of current data. *FEMS Microbiology Letters*, 281, 215–220.

Spatial dynamics of ecological public goods

Christoph Hauert

Public goods model the production, consumption and exploitation of common resources ranging from extra-cellular products in microorganisms to global issues of climate change. Individuals can cooperate and sustain common resources at some cost or defect and exploit the resources without contributing. This generates a conflict of interest, which characterizes social dilemmas: individual selection favors defectors but for the community it is best if everybody cooperates. Traditional models of public goods do not take into account that benefits of the common resource enable cooperators to maintain higher population densities. This leads to a natural feedback between population dynamics and interaction group sizes as captured by 'ecological public goods'. Here we show that the spatial evolutionary dynamics of ecological public goods in 'reaction-diffusion' systems promotes cooperation based on different types of pattern formation processes. In spatial settings individuals can migrate (diffuse) in order to populate new territories. Slow diffusion of cooperators fosters aggregation in highly productive patches (activation), whereas fast diffusion enables defectors to readily locate and exploit these patches (inhibition). These antagonistic forces promote co-existence of cooperators and defectors in static or dynamic patterns, including spatial chaos of ever changing configurations. The local environment of cooperators and defectors is shaped by the production or consumption of common resources. Hence, diffusion induced self-organization into spatial patterns not only enhances cooperation but also provides a simple mechanisms for the spontaneous generation of habitat diversity, which denotes a crucial determinant of the viability of ecological systems.

The coevolution of cooperation and dispersal in social groups and its implications for the emergence of multicellularity

Michael Hochberg
Co-authors: Michael Taborsky, Daniel Rankin

One of the central puzzles in explaining transitions in individuality for entities ranging from complex cells, to multicellular organisms and societies, is how different autonomous units relinquish control over their functions to others in the group.. In addition to the necessity of reducing conflict over effecting specialized tasks, differentiating groups must control the exploitation of the commons, or else be out-competed by more fit groups. We employ an optimization model to show the conditions under which different within-group social behaviors may be selected to disperse, thereby not affecting the commons and functioning as germ line. We find that partial or complete dispersal specialization of cheaters is a general outcome. Our findings suggest two forms of conflict access to resources within groups and representation in germ line may be resolved in tandem through individual and group-level selective effects.

Paradox of nutrient removal in coupled socio-economic and ecological dynamics for lake water pollution

Yoh Iwasa
Co-authors: Y. Ohno-Suzuki, H. Yokomizo

We study coupled socio-economical and ecological dynamics for lake water pollution. Players choose between cooperative (but costly) option and economical option, and their decision is affected by the fraction of cooperators in the community and by the importance of water pollution problem. When an opportunity for choice arrives, players take the option with the higher utility. This social dynamics is coupled with the dynamics of lake water pollution. First, oscillation of large amplitude is generated if social change occurs faster than ecosystem responses. Second, the model can show

"paradox of nutrient removal". If phosphorus is removed more effectively either from the inflow or from the lake water, the pollution level may increase (rather than decrease) due to the decline in people's willingness to cooperate. Third, we compare the effectiveness of alternative methods in improving water quality: to reduce the cooperation cost by subsidy, to enhance people's concern to water pollution problem, and to promote the conformity among people. We also discuss how to reduce the conflict among people.

Conditional cooperation, recognition and chromodynamics

Vincent A.A. Jansen
Co-authors: William Lee, Minus van Baalen

The evolution of altruism and cooperation poses a long-standing evolutionary paradox. One of the solutions that has been proposed is recognition: if individuals could direct their altruistic behaviour to other altruists, thus avoiding being exploited by selfish, non-altruistic individuals altruistic and cooperative behaviour could, in theory, evolve. The simplest recognition system is a conspicuous, heritable tag. I will present simulation results for the evolution of cooperation under recognition and show how the evolution of cooperation is enhanced be recognition, and how tag diversity allows altruism to evolve and be maintained, leading to complicated dynamics of the different tags. We will show how this relates to kin selection, and discuss possible examples in which recognition could play an important role.

Revision games: cooperation via the revisions of strategies

Michihiro Kandori
Co-author: Yuichiro Kamada

We analyze a situation where players in advance prepare their actions in a game. After the initial preparation, they have some opportunities to revise their actions, which arrive stochastically. Prepared actions are assumed to be mutually observable. We show that players can achieve a certain level of cooperation in such a class of games.

Can mate choice ever be group selected?

Hanna Kokko
Co-author: Katja Heubel

The debate over the importance of different levels of selection shows no signs of dying away. Much of the mathematical analysis of examples has relied on rather abstract concepts of 'public goods' or 'altruism'. Concrete examples are relatively few. Here we ask whether mate choice could ever exhibit group selected evolution. Our case study is a fish species complex in which local extinctions can occur unless males avoid mating with the 'wrong' kind of females. The 'wrong' females are those of the Amazon molly, which is an all-female fish species with an unusual kind of asexuality: it needs sperm from related species to trigger embryogenesis, without using the genes in the sperm at all. Males who mate with Amazon females enable Amazons to ecologically outcompete their own, sexual species (because asexual reproduction is doubly efficient compared to sexual reproduction). To avoid extinction, males should 'cooperate': they should all refuse to mate with Amazon females even if this comes at a short term cost to their own reproductive success. Such a cost can exist despite the fact that males gain no reproductive success through Amazons because a male who scrutinizes females carefully before mating may lose real (conspecific) mating opportunities. Mating in this system resembles a tragedy of the commons in two different ways: (1) rampant reproduction of the Amazons makes their host species go extinct yet Amazons depend on this host because only they can provide a critical resource for reproduction (sperm).

(2) Males who are not selected to cooperate (discriminate) strongly enough allow a 'parasitic' species to outcompete their own females, and for these males conspecific females are a critical resource for any real reproductive success. We will present solutions to the puzzle that this unusual species complex can persist at all, and discuss why males in nature show some discrimination (but not complete enough to drive Amazons extinct).

Saltation vs. gradualism in the evolution of mutualistic mimicry

Olof Leimar

An interesting form of cooperation occurs when several senders share the same or a similar signal. The sharing is advantageous if it tends to enhance a beneficial response to the signal. The process through which sharing evolves from a situation with distinct signals, in which the signaling populations reside at separate adaptive equilibria, is comparable to a transition between adaptive peaks. Whether such evolutionary transitions occur as saltations or through gradual change depends on the properties of signal receivers. This question has long been debated for the example of mutualistic, Müllerian mimicry, which is one of the most thoroughly studied instances of signal sharing in nature. I will discuss theories and models relating to this example, combining ideas about the psychology of receivers with evolutionary genetics of signaling populations. In particular, I will discuss the so-called two-step hypothesis of Müllerian mimicry evolution, which states that mimicry starts with a major mutational leap between adaptive peaks, followed by gradual fine-tuning of the mimetic resemblance. Based on the theoretical analysis, I will sketch a theory of the evolution of mimicry rings.

Inter-generational equity and the problem of discounting

Simon Levin

A central problem in evolutionary theory and economic theory alike involves the optimal tradeoff between current consumption and future needs. In either case, those future needs belong in part to future generations, including one's own descendants. This introduces a range of discounting problems: discounting one's own future, discounting the interests of one's offspring, and discounting the interests of others. This lecture will explore these issues, based on work with Kenneth Arrow, Adi Livnat, and Steve Pacala.

Evolution of repeated games

Eric Maskin

We characterize the payoffs that correspond to evolutionarily stable strategies in two-player symmetric repeated games when players discount the future and make mistakes with positive probability.

The importance of individual differences in conflict and the evolution of cooperation

John McNamara

Game theoretical models often ignore differences between individuals. Using a series of examples I will demonstrate that such differences are not innocuous noise, but can fundamentally change the nature of a game. Differences promote the need to have extensive interactions to find out about a partner, so changing the strategy set and hence the outcomes of the interaction. Difference can mean that it may be worth taking risks that a partner is cooperative, and can completely reverse the direction of evolution in a simple prisoner’s dilemma game. Differences promote choosiness, and the co-evolution

of choosiness and cooperativeness can lead to high levels of cooperation when repeated interaction with the same partner are possible. Finally, differences in personality promote the need to be socially sensitive; and once individuals are socially sensitive, this can lead to the maintenance of differences.

Biological markets: a paradigm with empirical support

Ronald Noë

Biological market (BM) theory aims to explain the evolution and maintenance of cooperation. BM is a 'partner choice' model, because the choice among different potential partners is assumed to be the pivotal mechanism governing cooperative interactions. Partner choice and the (threat of) partner switching have a controlling effect on the behaviour of current partners, as in partner control models, but also lead to outbidding competition between potential partners. On an evolutionary time scale partner choice can lead to selection for specific traits that benefit the choosing party, much like female choice selects for male traits favourable to females under sexual selection. On short time scales outbidding competition drives an adaptation of the exchange rates of goods and services to fluctuations in supply and demand of such commodities. Several empirical examples of both phenomena have been published till date in systems ranging from nutrient exchange mutualisms between plants and bacteria or fungi, protection mutualisms between ants and other insects or plants, helper systems in mongoose, grooming exchanges in primates, mating markets in birds and humans and so forth. This wide empirical support stands in sharp contrast to other popular theories of cooperation, most of which belong to the 'partner control' family of models.
After this first wave of empirical studies that were inspired by the biological market paradigm to look at known phenomena in a new way, the time is ripe for a number of further developments, such as (1) the development of both more general models of the adaptation of exchange rates to fluctuating market situations and more specific models that are tailored to particular forms of cooperation. (2) Attention to the proximate mechanisms involved in tracking fluctuations in supply and demand. (3) Negotiation tactics and the problem of honest communication, notably in organisms that use cognitive mechanisms.

Spatial selection

Martin Nowak

Spatial selection is a mechanism for the evolution of cooperation. Cooperators can prevail over defectors by forming clusters. Individual cooperators within clusters can obtain a higher payoff then defectors. Spatial selection works with unconditional strategies and is only based on individual selection. It is different from group selection and kin selection. I will discuss spatial games, games on graphs, games in phenotype space and evolutionary set theory. I will present a general principle that applies to all of those approaches.

Indirect reciprocity provides only a narrow margin of efficiency for costly punishment

Hisashi Ohtsuki
Co-authors: Yoh Iwasa, Martin A. Nowak

Indirect reciprocity is a key mechanism for the evolution of human cooperation. Our behavior toward other people depends not only on what they have done to us, but also on what they have done to others.
We extend the standard model of indirect reciprocity to include the option of costly punishment as well as cooperation and defection. It has been suggested that costly

punishment between individuals can promote cooperation. Here we study the role of costly punishment in indirect reciprocity. We analyze all social norms, which depend on the action of the donor and the reputation of the recipient. We allow errors in assigning reputation. We characterize all strategies that allow the evolutionary stability of cooperation. Some of those strategies use costly punishment, while others do not. We find that punishment strategies typically reduce the average payoff of the population. Consequently, there is only a small parameter region where costly punishment leads to an efficient equilibrium.

Evolutionary dynamics of collective action

Jorge M. Pacheco

Collective action often requires the participation of several individuals, who should decide whether to participate or not in a joint enterprise. Public Goods Games provide the appropriate mathematical tool to address these types of problems, which may deal with situations ranging from family issues to global warming. Evolutionary game theory predicts that the temptation to forgo the public good mostly wins over collective cooperative action, something which is often confirmed in behavioural economic experiments. Here I will address 2 important aspects of evolutionary game theory which have been neglected so far in the context of public goods games: On one hand, the fact that often there is a threshold above which a public good is reached. On the other hand, the fact that individuals often participate in several games, related to their social context and pattern of social ties, defined by a social network. In the first case, the existence of a threshold dictates a rich pattern of evolutionary dynamics: in finite populations, whenever public goods require participation of nearly the entire community, the direction of natural selection can be inverted compared to standard expectations. In networked games, cooperation blooms whenever the act of contributing is more important than the effort contributed.

The evolution of kin recognition genes

David Queller
Co-authors: Xiaoyun Liao, Joan Strassmann

Some organisms have genetic kin recognition mechanisms, in which they use genetically variable cues to assess relatedness of unknown individuals. How such systems evolve is unclear. In particular, Crozier's paradox asserts that common cue alleles will be favored, destroying the variation upon which recognition depends. We reformulate this problem with a model that considers all three components of recognition: production of cues, perception of them, and action. A key insight is that, in the context of a functioning system, the cues are greenbeard alleles. Although they do not themselves directly cause all three components, the difference a cue allele makes is that other copies of its same allele get aided. This greenbeard nature is why common alleles are fixed. Our model explores how perception alleles at other loci, which accept or reject matches at cue alleles, can modify this dynamic to give stable kin recognition. We also report an empirical study system in which some of these processes may be explored: social amoebae in the genus Dictyostelium. First we report a true green-beard locus, the cell adhesion gene csaA, in which one allele is more altruistic, but acts in a way that ensures the benefits go to others who share that allele. This appears fixed in the population and probably only acts against rare mutants. But D. discoideum also has active kin recognition, which we believe is also controlled by cell adhesion genes, lagB lagC, and perhaps others. These are extremely variable, and studies of their knockouts and transformants support their role in kin recognition, which this species uses to aggregate preferentially with kin.

Evolutionary game theory on graphs, network reciprocity and emergence of cooperation

Anxo Sánchez
Co-authors: Carlos P. Roca, José A. Cuesta

In the past few years much work has been devoted to understanding the emergence of cooperation through network reciprocity, i.e., by studying evolutionary games among individuals whose interactions are governed by a network. While this line of research has produced a number of interesting and inspiring results, a complete picture of the observed phenomenology and the mechanisms behind it is lacking. In this talk, we will provide evidence that such a complete picture can not be found because evolutionary game theory on graphs depends crucially on details. Extensive simulations allow us to conclude that the enhancement or inhibition of cooperation is strongly affected by the type of network, the type of evolutionary dynamics and the social dilemma under study. Therefore, modeling the emergence of cooperation in a sensible way requires looking at a wide range of social dilemmas and not at a particular one, while having in mind a specific context for application.

Evolution of generous cooperative norms by cultural group selection

Istvan Scheuring

Evolution of cooperative norms is studied in a population where individual and group level selection are both in operation. Individuals play indirect reciprocity game within their group. Individuals are well informed about the previous actions and reputations, and follow second order norms. Individuals are norm-followers, and imitate their successful group mates. In contrast to previous models where norms classify actions deterministically, we assume that norms determine only the probabilities of actions, and mutants can differ in these probabilities. The central question is how a selective cooperative norm can emerge in a population where initially only non-cooperative norms were present. It is shown that evolution leads to a cooperative state if generous cooperative strategies are dominant, although the "always defecting" and the "always cooperating"-like strategies remain stably present. The characteristics of these generous cooperative strategies and the presence of always defecting and always cooperating strategies are in concordance with experimental observations.

Helping neighbors: a game theoretic analysis

Tom N. Sherratt
Co-author: Mike Mesterton-Gibbons

Individuals often chase away potential predators or parasites, and in so doing not only help themselves but also their neighbors (“not in my backyard”). More dramatically, in some animal species territory owners have been observed to leave their own territories in order to help their neighbors ward off conspecific challengers (the “dear enemy” effect). To characterize the properties of these systems we have explored a series of game theoretical models. A simple co-evolutionary model involving a mobile biting parasite identifies the inter-related conditions under which: (i) hosts should pay costs to punish the parasite, (ii) punishment benefits others and (iii) how the parasites should react. The model predicts that punishment should not evolve when the parasite is highly mobile and the host population is large – predictions supported by data on the sabre-toothed blenny and its hosts. To understand why neighbors might come to the aid of nearby residents, we explored triadic games involving challengers, residents and potential allies. Seeing off a neighbor’s intruder may evolve when it is ultimately less costly than re-negotiating boundaries with a potentially larger usurper. However, such

intervention only pays when the resident does not stand a reliable chance of winning alone. The model readily explains occasional intervention in the Australian fiddler crab, and why the ally tends to be larger than both the assisted neighbor and the intruder. In both of the above cases, the stability of giving aid to neighbors does not depend on reciprocation since cooperation arises as a by-product mutualism. More generally, explicit consideration of cooperative systems in the natural world may shed light on the nature and stability of human cooperation.

Reputation, incentives, and moral assessment

Karl Sigmund

The first part of this talk deals with the role of incentives and opportunism for the evolution of cooperation. Under individual selection, opportunistic agents (prone to be swayed by positive or negative incentives) emerge if players can build up reputation. Punishment takes over, and the population will eventually be dominated by players who cooperate except if they know that they can get away with defection. If the information level is below a certain threshold, the possibility of rewarding cooperation plays an important, but transient role. In the second part, reputation-based assessment systems are compared for the simplest binary model of indirect reciprocity. While two different assessment rules can coexist, the population evolves towards moral consensus. The first part is based on joint work with Christian Hilbe, the second with Satoshi Uchida.

Inventing new signals

Brian Skyrms

A model of inventing new signals is introduced in the context sender-receiver games with reinforcement learning. If the invention parameter is set to zero, it reduces to basic Roth-Erev learning applied to acts rather than strategies, as in Argiento et. al.(2009). If every act is uniformly reinforced in every state it reduces to the Chinese Restaurant Process - also known as the Hoppe- Pólya urn - applied to each act. The dynamics can move players from one signaling game to another during the learning process. Invention helps agents avoid pooling and partial pooling equilibria.

Spatial evolutionary prisoner's dilemma game with pairwise cooperative strategy updates

György Szabo
Co-author: Attila Szolnoki

Evolutionary Prisoner's Dilemma games are studied with players located on a square lattice. The players follow one of the two strategies (unconditional cooperation and defection) and their income comes from one-shoot games with the neighbors. During the evolution of strategy distribution two randomly chosen neighboring players are allowed to update their strategy cooperatively and simultaneously (instead of imitating the better one). In the iterated elementary evolutionary processes both players evaluate the current (initial) payoff, they choose a new strategy pair at random and determine the corresponding (final) payoffs assuming quenched strategies in their neighborhood. The new strategy pair is adopted with a probability dependent on the difference of their summed payoffs between the final and initial state. Their choice is motivated by maximizing their summed income. The effect of noise is quantified by a "temperature" parameter in the Fermi-Dirac function providing smooth transition from 0 to 1 in the strategy adoption probability. Using this strategy update the system avoids the "tragedy of the community" where all players defect. Instead of it the cooperators and defectors form an ordered structure resembling an anti-ferromagnetic state. The latter state

ensures the maximum total payoff in the community if the temptation to choose defection exceeds a threshold value (T+S>2R).

Random exploration of strategies in games of cooperation

Arne Traulsen

Most models based on evolutionary game theory focus on imitation. But is imitation of better strategies the right way to model human behavior? In contrast to genetics, social mutation rates may be high. Increasing mutation rates can lead to unexpected outcomes in games of cooperation. This can be illustrated in a public goods game with cooperators and defectors as well as punishers and the option to abstain from the game. For small mutation rates, cooperation (and punishment) only evolve if the game is voluntary, whereas moderate mutation rates can lead to high levels of cooperation even in compulsory public goods games. High mutation rates also blur the effect of population structure, such that the dynamics becomes more similar to the dynamics in well-mixed populations.

To punish or leave? Conditional dissociation in the evolutionary emergence of cooperation

Fernando Vega-Redondo

Co-authors: Segismundo S. Izquierdo, Luis R. Izquierdo, Jörgen W. Weibull

The paper shows that conditional dissociation, i.e. an agent's option to leave her partner in response to the latter's behaviour, may play an important role in the evolutionary emergence of cooperation. For, even if individuals can punish uncooperativeness (e.g. through a Tit-For-Tat strategy), it is a simple form of conditional dissociation that governs the spread and stability of extensive cooperation. Formally, we study a population of individuals who are paired to play a prisoner's dilemma in discrete time periods. After every interaction, each individual is given the option to change her partner for the next period. Individuals die at a constant rate and reproduction is proportional to payoffs, with possible mutations. This ergodic process exhibits two predominant dynamic regimes: a non-cooperative one and a (partially) cooperative one, whose attractiveness, persistence and level of cooperation crucially depend on individuals' lifespan. We also provide an analytical approximation to the level of cooperation.

In-group cooperation and reputational psychology

Toshio Yamagishi

Most models of indirect reciprocity assume transparency of behavior to all the other members of a community, which is not likely to be true in real social life. It is almost impossible to constantly observe and remember behaviors of all the other members of a community. Instead, community members are likely to use a summary indicator of each individual's behavioral tendency or his/her reputation as the basis of indirect reciprocity. If this is the case, human cooperation based on indirect reciprocity requires that humans have sensitivity toward reputational implications of their behavior, especially in front of members of their group. This sensitivity should manifest itself as sensitivity to cues suggesting the presence of monitoring of their behavior by other community members. I am going to present results of a series of experiments demonstrating that the cooperation level with in-group members is affected by the presence of such cues, but cooperation with out-group members is not affected by such cues.