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EUROCORES Programme

The Evolution of Cooperation and Trading (TECT)

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EUROCORES

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Introduction

Few phenomena attract as much attention from as many different scientific disciplines as the study of cooperation. Cooperation, eventually disguised as 'mutualism', 'symbiosis', 'reciprocity' or 'trading', is a central focus of inquiry or at least an important phenomenon in many scientific disciplines such as anthropology, biology, economics, political science, psychology, sociology, history, artificial intelligence and robotics. Even fields that are less obviously related to behavioural phenomena, such as mathematics and chemistry, explore cooperative interactions.

The fascination with cooperation rests on its puzzling nature: cooperation appears intrinsically unstable and theoretically problematic, yet it is ubiquitous throughout nature and human societies. Cooperating agents typically make an investment in order to have a chance of reaping the benefits of cooperation but risk losing their investment. In addition, the interests of cooperating partners are often at odds.

Cooperative strategies fall roughly into two categories: those that are the product of evolutionary processes, be they natural or cultural, and those that are the result of cognitive processes. The first have been under selective pressure over countless generations and are likely to be more 'rational' than those resulting from cognitive processes. The *raison d'être* of cognitive strategies is their much greater flexibility in novel situations. Inherited cooperative strategies are not well-suited for use in variable environments and unpredictable circumstances. Cognitive processes, however, require costly structures, such as brains, and are slow compared to hard-wired strategies. Therefore cooperation strategies based on rules-of-thumb are likely to prevail as long as they do well enough most of the time.

The idea of developing a EUROCORES research programme on these topics came after a number of successful interdisciplinary meetings, the core of which was formed by anthropologists, biologists, economists and psychologists sharing a common interest in the evolution of strategies that facilitate cooperation. The most important of these meetings was the 90th Dahlem Workshop on Genetic and Cultural Evolution of Cooperation, held in Berlin in June 2002, which led to the publication of a book edited by Peter Hammerstein under the same title (*Genetic and Cultural Evolution of Cooperation.* Cambridge, Mass.: MIT Press, 2003). This book reflects the state of the art at the time when I assembled a group of 24 scientists from 11 European countries and at least as many disciplines which proposed this programme. We decided to add the word 'trading' to the programme's title to stress that we were not only talking about a biological concept, but also about typically human phenomena as seen through the eyes of anthropologists, economists, historians, psychologists and sociologists.

The hypothesis underlying The Evolution of Cooperation and Trading (TECT) programme is that agents of a different nature, ranging from bacteria to multinational alliances of humans, are likely to be equipped with similar evolved strategies designed to solve the same recurring dilemmas. While distantly related species probably use different mechanisms to implement these strategies, more closely related species are more likely to employ the same mechanisms when solving the same problems. These strategies and mechanisms form the focus of research in the EUROCORES programme TECT. Collaborative research projects under TECT are united around one main goal, namely to highlight the evolutionary continuity of cooperation, both genetic and cultural, and to make this continuity an object of study in its own right: What causes the evolution of different mechanisms and strategies? Can we trace the evolutionary history of cooperative mechanisms and does this explain the forms of cooperation we observe today? Can 'bounded rationality' and the breakdown of cooperation in modern human societies be explained by the activation of mechanisms that evolved in past environments? Does evolutionary history repeat itself in the form of a cultural evolution of human trading behaviour? Another important goal of our programme, essential to achieving the first, is to bring together experts from different disciplines in order to encourage, and enable, 'cross-fertilisation' of different traditions, terminologies and methods.

The Call for Proposals, which solicited interdisciplinary research cooperations between empirical and theoretical work, resulted in a high number of excellent proposals. Five Collaborative Research Proposals (CPRs) have been funded since summer 2007, bringing together researchers based in Europe, America, Asia and Africa.

Ronald Noë,
Chair of the TECT Scientific Committee

Programme Description

Coordinated and not coordinated rowing, Heidelberg, Germany

Background and Objectives

The phenomenon of cooperation is a puzzle in many areas of research. It can be observed in organisms from bacteria to multinational alliances in human societies, but in many cases science has as yet failed to explain what it is and why it exists. Cooperators invest in order to obtain a benefit, but risk being exploited by free-riders who reap the benefit without paying the cost. Likewise, traders may make gains, but expose themselves to the risk that the gains are monopolised by their partner. The scientific puzzle is to identify the mechanisms that allow cooperators to reap the benefits of cooperation without being exploited.

The Evolution of Cooperation and Trading (TECT) programme aims to build a multidisciplinary research framework taking advantage of recent convergent developments in several disciplines. A number of disciplines have adopted a common theoretical framework for explaining biological and cultural evolution that emphasises the properties of interacting, goal-directed agents; e.g. behavioural economics, evolutionary game theory in political science and economics, evolutionary approaches in cognitive and social psychology and neuroscience, replicator chemistry, population dynamic accounts of cultural evolution within anthropology, and the continued importance of evolution in our understanding of cooperative relationships between all kinds of organisms. Methodological advances in several disciplines provide crucial new information about the properties of agents and genetics for inferring evolutionary relationships, new experimental work in economics, the development of neuroimaging methods, the continuing development of methods in cognitive science, and the renaissance of quantitative cross-cultural and comparative research.

Multidisciplinary research into 'cooperation' has become both possible and potentially profitable for the first time. The theoretical convergence allows researchers from a wide range of disciplines to discuss cooperation in a common scientific idiom. This is a crucial development since, in order to appreciate the complexity of cooperation and trading, input is required from beyond biology and economics, from fields such as anthropology, history, sociology, cognitive science, religious studies and psychology. Methodological innovation is also essential because progress depends not only on the profitable exchanges of models and theory among disciplines, but also on the transfer of empirical methods and results from one discipline to another.

Disciplines more closely related to the scope of TECT include in alphabetical order: anthropology (biological, physical, social); biology (behavioural and evolutionary ecology, endocrinology, ethology, palaeontology, physiology; theoretical biology); chemistry (autocatalytic chemistry, replicator and systems chemistry); cognitive sciences (artificial intelligence, evolutionary robotics, embodiment, philosophy of mind); economics (microeconomics, neuro- and endocrino-economics, game theory); history (social and cultural history); linguistics; mathematics (dynamic systems theory; game theory); neurosciences; philosophy of science; political sciences (comparative politics, political theory; law); psychology (economic, social and developmental and evolutionary psychology); and sociology (economic sociology; management studies; theory of organisation).

Scientific Goals

TECT involves Collaborative Research Projects (CRPs) that do not fit easily within existing funding structures because of their multidisciplinary nature. CRPs aim to initiate or strengthen collaborative ties both within and between the social and natural sciences and the humanities, and explicitly address the idea that cooperative phenomena at widely different levels of organisation have their roots in similar evolutionary and developmental processes, be they genetic or cultural.

At the programme level, the multidisciplinary character of TECT is guaranteed through ESF-supported networking activities (workshops, conferences, mutual visits; summer schools; possibly joint publications etc.).

In order to develop the potential for multidisciplinary research, the internal structure of the Collaborative Research Projects has taken the following form:

- Scientists from different disciplinary backgrounds design and conduct studies on cooperation phenomena ranging across different organisms, societies, or systems (or the same entities in different environments). In the programme design phase it had been expected that such a structure would help to obtain information about the nature of underlying mechanisms, to do independent tests of the same hypothesis or model, or to trace the phylogeny of mechanisms. A further goal may be to design artificial cooperative systems.
- Empirical scientists and theoreticians working in different fields, but focusing on the same basic phenomena, design and conduct a research project with strong feedback between the two components, such that theoretical (including modelling) and empirical work evolve together over the course of the programme.
- Senior researchers working in at least two different fields share in the supervision of junior scientists (PhD candidates, post-docs). The junior scientists should ideally spend considerable time in each research group. Similarly, researchers using specific techniques or methods can work as guests in another discipline in order to exchange know-how.

The TECT Call for Proposals had expressly invited research projects which would illuminate challenges facing human society today; e.g. in the medical, social and environmental fields. It was expected that the outcome of such projects would provide a better understanding of cooperation, thus contributing to effective strategies such as controlling the epidemic spread of disease, more efficient organisation of joint endeavours and reduction of intolerance and social conflicts. At least two funded TECT projects are indeed dealing with such topics: Sustaining Eco-economic Norms for a Sustainable environment (SENSE) with its focus on the global commons, and Dynamic Complexity of Cooperation-based Self-organising Networks in the First Global Age (DynCoopNet) with an historical study of patterns of cooperative behaviour in a 'real world' economic and institutional setting.

Research Topics

The TECT Programme revolves around a number of interrelated themes and specific research areas, which may all benefit from coordinated input from bio-, human and social sciences and sustained modelling efforts:

1. Integrating methods and disciplines

A number of competing approaches have been used to explain the occurrence of cooperative behaviour, but none is fully supported by observational and experimental data. Consequently, there is a great deal of controversy over which models are most appropriate, whether the assumptions on which these models rest are accurate, and whether appropriate empirical tests are being performed.

TECT encourages theoretical and empirical scientists to work closely together in order to:

- improve the fit between theory and data,
- generate new theoretical insights based on sound empirically demonstrated assumptions,
- expand the range of empirical observations on which such theoretical models can be tested.

Questions of relevance include the following: does the spatial structure of a population influence patterns of cooperation and competition in the real world in the same way that it does in computer simulations? Does the exercise of power by one or more individuals influence how the gains from trade and from other forms of cooperation are distributed among the participants? Is human pro-social behaviour driven by adaptive emotional mechanisms, does it reflect a concern for the actor's reputation in his community or is it all a 'big mistake' caused by the faltering of ancient psychological adaptations in the artificial atmosphere of the laboratory?

TECT aims at exploring the degree to which cooperative behaviours across species reflect the operation of the same underlying strategies, and, by the same token, to test whether superficially similar strategies actually share the same underlying deep structure. A wide range of topics can be addressed under this heading, e.g.: bacteria and plants have been shown to cooperate, but do the same evolutionary processes explain the cooperative behaviour of cleaner fish, capuchin monkeys and humans? How does a species' history determine the form of cooperation observed, and how robust are cooperative mechanisms across organismic groups? To what degree do species other than our own have roles, norms and institutions? Does the structure of social relationships allow policing to develop as a stabilising factor? Does inter-specific cooperation differ in essence from intra-specific cooperation? To what degree do co-evolutionary and niche-constructing processes drive the patterns we see in nature?

Collaborative Research Projects under TECT bring together descriptive empirical work with theoretical models; TECT researchers test and refine the assumptions on which these models are based. Where the fit between theory and data cannot be improved, it is hoped that TECT can open new theoretical directions to be pursued, informed by real world patterns and aimed at providing testable hypotheses and predictions.

2. The evolutionary, historical and developmental origins of cooperation and trading

Tracing the roots of cooperation and trading is one of the keys to understanding the mechanisms by which they operate. TECT aims at gaining a better understanding of the phylogenetic pathways that cooperation has followed over evolutionary time, the ontogenetic pathways by which cooperative behaviour develops over the course of an individual lifespan, and the historical pathways by which different patterns of cooperation and trade emerge within and across cultures.

For example: how do oxytocin titres influence the degree of trust between cooperating partners? Are such mechanisms operating in other animals? Can we trace these mechanisms back to a common ancestral function (e.g., the promotion of parent-offspring bonds)? How does an organism's evolutionary history constrain and enhance the mechanisms that can evolve? How does an organism's developmental history link to these evolutionary and/or historical processes? Are there 'scale-free' patterns discernible in these data where we can identify similar processes operating at, for example, the microscopic scale of interacting molecules as well as the political interactions of nation states?

The TECT Call for Proposals encouraged the adoption of an explicit multi-level approach to these issues, where evolutionary, developmental and historical processes are investigated as issues in their own right, but with the explicit aim of linking them together in coherent evolutionary, historical sequences.

Bay of Póvea in Northern Portugal. Instead of the docks we associate with twentieth-century seaports, many ports of the first global age consisted mostly of protected beaches with associated warehouses and repair facilities. Customs officials had difficulty patrolling such open areas, which provided possibilities for clandestine economic activities. Póvea de Varzim received its royal charter of self government in 1514 and emerged as one of the busiest ports in its region.

3. Mechanisms of cooperation

Investigating patterns of cooperation at various levels should allow the identification of their origins and the tracking of both evolutionary and historical lineages. However, to understand it fully, more detailed research is needed on the proximate mechanisms by which organisms implement cooperative strategies. The TECT Call for Proposals invited investigations of the morphological, physiological, neurological and cognitive basis of cooperation in specific systems (e.g. symbiosis; mycorrhisa markets; cooperative hunting etc.), in order to identify these mechanisms and link them to the processes and patterns identified by other TECT themes.

Among the research areas presenting major problems for comparability of non-human and human organisms, the nature and function of emotions involved in decision making has long remained under-studied; e.g. fear of deception, anger after being cheated, envy of a partner's payoff, jealousy of a partner's social relationships. Another such emotional complex is formed by the mechanisms underlying choice, which can be separated into 'liking' (learning preferences) and 'wanting' (implementing preferences). One of the crucial questions is whether these emotional mechanisms are designed specifically for cooperation, or have they been co-opted from other functions?

Conversely, are mechanisms evolved for cooperation generalised to other domains, and how effective are they? Do hormonal influences on cooperation serve a different function to those governed by neuronal processes? How does the time-scale of interaction affect the likelihood that physiological versus cognitive mechanisms will be engaged? It had been expected that some projects would use brain-scanning techniques (PET, fMRI) which can monitor the brain activities of individuals while they engage in cooperation and trading, and may enable an assessment of the cognitive demands of such tasks, and the degree to which emotional and cognitive responses are integrated.

The cognitive processes underlying cooperative strategies have long been neglected. Theoreticians tended to focus on functional fitness-based explanations for cooperative strategies, which are necessarily silent on how organisms actually implement the strategies they use. However, since organisms are constrained by both task demands and time available, mechanism and function are linked fundamentally. Recent work points to the need to study the 'fast and frugal heuristics' of bounded rationality.

For example, can such heuristics account for human performance in one-shot games? Does the use

Tour de France, Osthoffen.

of similar heuristics also explain the behaviour of other organisms, or perhaps groups of organisms, in natural and experimental settings? If so, what environmental cues do individuals use for judging what kind situations they are in? Similarly, do individuals distinguish between anonymous and recognisable partners that are encountered repeatedly? Do cooperating individuals communicate about their interaction; if so, in what form, and to what level of trustworthiness? To what degree do temperamental differences across individuals influence the cognitive mechanisms used? Do the demands of cooperation require increased cognitive capacity? Do cooperating members of different species communicate in order to coordinate?

4. Biological model systems of human cooperation and trading

The TECT Call for Proposals had specifically invited studies of biological systems that can be manipulated easily, either in the laboratory or in the field. These would, the understanding was, serve as model systems and alternatives to computer simulations, notably for the understanding of human behaviour in the context of markets and situations of collective action and the production of common goods.

For while theoretical model systems risk overlooking essential elements and building on unrealistic assumptions, experiments with real-life agents rely on strategies and mechanisms tested over the millennia by natural selection. Despite the great heuristic value such model systems provide, only very few studies have adopted this perspective.

The nature and scope of the issues that can be investigated include:

- Inter-specific mutualisms, in which nutrients are traded against nutrients, can be compared to markets in which tangible goods are traded against common currencies (e.g. Ricardo's principle of comparative advantage applying to the trading between plants and mycorrhisal fungi and rhisobia under experimental conditions).
- Biological systems in which nutrients are traded against protection (e.g. ants interacting with either plants or various other insect species) or against parasite removal (e.g. cleaning mutualisms) can be considered as models for markets in which tangible goods are traded against services.
- Collective action problems can be investigated using the formation of fruiting bodies in micro-organisms: under specific circumstances, individual bacteria in-

vest in the production of this common good in the absence of any direct returns.
- The conditions under which cooperation emerges in non-cooperative species can be explored using micro-organisms or, indeed, any species with a fast generation time.

TECT brings together an inventory of promising systems developed for other purposes to be tested for their potential, rather than devise new systems from scratch. It is hoped that among the outcomes of the programme will be a model system that could easily be kept and manipulated in the laboratory and be used to answer many of the questions suggested above.

This text is based on a longer text developed by the coordinating proposer of TECT, Ronald Noë, with input from the co-proposers Louise Barrett (Liverpool), Redouan Bshary (Neuchâtel), Tim Clutton-Beck (Cambridge), Robin Dunbar (Liverpool), Ernst Fehr (Zurich), Dario Floreano (Lausanne), Peter Hammerstein (Berlin), Peter Henzi (Preston), Laurent Keller (Lausanne), Karin Knorr-Cetina (Konstanz), Olof Leimar (Stockholm), Ruth Mace (London), Rui F. de Oliveira (Lisbon), Boguslaw Pawlowski (Wroclaw), Carel van Schaik (Zürich), Paul Seabright (Toulouse), Karl Sigmund (Vienna), Pavel Stopka (Prague), Eörs Szathmary (Budapest), Eric van Damme (Tilburg), Gregory Velicer (Tübingen), Elisabetta Visalberghi (Rome) and Franjo Weissing (Groningen).

The development of the theme proposal for TECT into a Call for Proposals also benefited from a workshop hosted by Peter Hammerstein (HU Berlin) in November 2005, with the participation of Louise Barrett (Liverpool), Robert Boyd (UCLA), Edward H. Hagen (Berlin), Laurent Keller (Lausanne), Ronald Noë (Strasbourg), Bettina Rockenbach (Erfurt), Eörs Szathmary (Budapest), Masanori Takezawa (Berlin), and Eric van Damme (Tilburg) and at a workshop in Brussels, December 2005, where representatives of the ESF Member Organisations and of other funding agencies discussed the theme development with Samuel Bowles (Santa Fe/Siena), Peter Hammerstein (Berlin), Ruth Mace (London), Ronald Noë (Strasbourg), Eörs Szathmary (Budapest) and Eric van Damme (Tilburg).

TECT Collaborative Research Projects (CRPs)

Cooperation in Mutualisms: contracts, markets, space and dispersal (BIOCONTRACT)

Naomi Pierce (Project Leader)

Overview

BIOCONTRACT aims to develop and test two lines of theory in order to explain cooperative associations between different species. First, the project applies micro-economic theory, especially the economics of information, to a variety of well-characterised mutualisms. Second, the project applies spatial game theory to two different symbioses, interactions between ants and plants, and interactions between plasmids and bacteria.

BIOCONTRACT integrates theory and empirical work, reaches across the interdisciplinary divide by applying the economics of information to mutualisms, and tests spatial game theory with real biological systems. The expected results will provide insights into the mechanisms that maintain cooperation in systems that lack recognition and memory, two features that characterise many mutualisms. The main features that make this project an advance on published work are the use of the economics of information, which is well developed in economics but almost unknown in biology, and the application of spatial game models to real mutualisms, which until now have remained a largely theoretical exercise. The project also investigates potential links between spatial game theory and micro-economics.

BIOCONTRACT aims at revealing general mechanisms that promote cooperation (and the forces breaking it down) in systems with bounded rationality, providing answers to the following kinds of questions: are there only a few, robust mechanisms that promote cooperation between species? Conversely, why are some mutualistic systems overrun with parasites or cheating? Are some types of mutualisms not feasible? Does cooperation evolve more readily under particular environmental conditions, and is ongoing habitat change eliminating those conditions? Has selection for cooperation promoted species diversification? What biological features confer greater power upon one partner over another, and can symbionts evolve to increase their power?

Evolutionary game theory can translate back into economics as learning games. It is expected, therefore, that economic theory will benefit from the work of BIOCONTRACT by allowing the study of partners on 'natural contracts' that have evolved between organisms with bounded rationality. Natural contracts can be compared with contracts that are reinforced by means of individual recognition and other complex psychological traits. The techniques developed here may thus be of use in the analysis of contracts between humans using an evolutionary perspective.

Contract theory and mutualisms

A good illustration of cooperation between species, or mutualism, is the interaction between blue butterflies (Lycaenidae) and ants. Lycaenid caterpillars provide food for ants in exchange for protection from parasites and predators. This example (and many others) suggests that we can think of mutualism as a form of economic trade, driven by the principle of comparative advantage. Nations that have a comparative advantage in the production of a certain good can benefit from specialising in the production of that good and trading the surplus for other goods. In the context of the butterfly–ant mutualism, caterpillars are better at extracting nutrients from plants than they are at defending themselves from predation, and ants are better at guarding and patrolling than they are at extracting food from plants. Trade between butterflies and ants should thus result in mutual benefit. How much benefit each species receives depends on the rate of exchange of the goods considered, which leads us to the first general question.

1. How do the partners in a mutualism distribute the surplus generated by specialisation?
Although both species in a mutualism benefit from the exchange of goods, ultimately they will reach a Pareto optimum situation in which one of the species will not be able to increase its benefits without decreasing the benefits to the other species. A set of distributions of goods that are Pareto optimum exists that leaves both species at least as well off as they were before trading. This set is known as the contract curve. Which optimum point on the contract curve for butterflies and ants is reached depends on features such as relative abundances and the asymmetry of power and information, among others. For example, if we assume that ant abundance is greater than that of butterflies, it is likely that the point of the contract curve reached is one in which ants contribute abundant protection, but butterflies contribute little food. A key difference between human transactions and mutualisms is that in economic transactions, the realised point on the contract curve is determined by negotiation between economic agents,

An *Azteca australis* queen colonising a *Cecropia* ant-plant sapling.

but in mutualisms, the realised point on the contract curve for butterflies and ants is determined by natural selection, which leads to the second general question.

2. Why do the partners in a mutualism abide by the contract that has evolved?
Most mutualisms involve some form of information asymmetry, which is one of the major reasons why potentially mutually enriching trade is invaded by cheaters. Economics of information can help to identify the mechanisms that are used to negotiate between agents in such cases. One way to model the bargaining process is with the framework known as the Principal-Agent (P-A) game. The principal proposes a contract, and the agent either accepts or rejects the contract. The P-A game is the base case studied in economic contract theory; the principal has all the bargaining power, and the contract is arranged so that the agent is on the margin of participating in the contract or rejecting it. In biological applications, such a one-sided allocation of power is not the only case observed. Fortunately, economic theory has been generalised in recent years to allow both sides to gain from the contract.

The questions posed by biologists about the evolution of mutualism in P-A terms can be reframed as follows: biologists have found ways in which hosts punish non-cooperative symbionts (or 'visitors'), which can be described as a kind of 'partner choice'. In P-A terms, the parallel problem is one of moral hazard: can principals articulate their contracts in terms of positive and negative incentives? Similarly, biologists have described ways in which mutualists associate preferentially with more mutualistic partner species from a wider set of potential symbionts, where some are cheaters. In economic terms, this is a problem of adverse selection, and we ask if principals can segment the market according to the existing types of agents.

Spatial game theory and mutualisms

The other focus of BIOCONTRACT is on the theory of spatial games. The classical theoretical framework for studying cooperation of unrelated individuals is the Prisoner's Dilemma Game, in which partners can choose either a defecting or a cooperating strategy. If both partners defect, they get a lower payoff than if both

cooperate, but a defector obtains the highest payoff if its opponent cooperates, leaving the cheated cooperator with the lowest payoff. Consequently, defection is the only evolutionary stable state in this model system, and cooperators cannot spread in a defecting population. However, cooperators are unsuccessful only when the model assumes well-mixed populations. In spatially structured populations where dispersal is limited, the peculiarities of each local subpopulation's demography dictate levels of defection/mutualism coexistence. Recent theoretical work emphasises the roles that spatial heterogeneity and environmental gradients play in stabilising mutualistic interactions in spatial games, and in promoting the diversity of species interactions.

Investigation of the role of spatial structure in promoting mutualism has been almost entirely theoretical, due in large part to the difficulty of measuring dispersal in natural biological systems. The project concentrates on applying spatial game models to two kinds of empirical systems for which we can either measure or manipulate dispersal: ant–plant and bacteria–plasmid mutualisms.

To summarise, the common thread running through all the models described above is that cooperation is maintained when cooperators interact more frequently than expected based on population abundances. The various mechanisms that have been proposed, including contracts and spatial games, can be seen as devices to bring about this association between cooperative members of different species.

Individual Projects (IPs)

Applying the economics of information to mutualisms

Naomi Pierce, **Drew Fudenberg** and **Jerry Green**, Harvard University (Principal Investigators)

Funding Agency: National Science Foundation (NSF), USA

In biology, a mutualism is an interaction between at least two species that results in mutually increased fitness. From a theoretical perspective, mutualisms raise two problems. One is how to distribute the benefits generated across the species, and the other is to identify the set of incentives that guarantees that each species will cooperate. To find answers to these questions we propose to adapt economic theory, which was developed for modelling transactions among humans, to model transactions among species.

BIOCONTRACT aims to:

- Establish a dialogue between economists and biologists.
- Model tractable biological mutualisms using principles from the economics of information.
- Act as one of the two theoretical foci for the overall consortium, with the goal of formalising information on empirical systems.
- Deepen our understanding of the evolution of co-

The internal structure of a *Ficus microcarpa syconium* (fig), showing flowers with long and short styles.

operation by allowing biologists to benefit from a substantial economic literature in the field.
- Provide insights for economists by conducting experiments with organisms that have bounded rationality and are free of complex psychological traits.

Naomi Pierce's research addresses insect/plant interactions, behavioural ecology and life history evolution. A long-term project in her laboratory has focused on the symbiosis between ants and larvae of the Lycaenidae (Lepidoptera) as a model system to understand species interactions and the evolution of life history traits. In analysing the evolution of these interactions, she has inferred the phylogeny of the Lycaenidae using molecular characters, and is comparing rates of evolution and correlated life history traits between species. Jerry Green is working on the robustness of economic mechanisms, on the strength of incentives that mechanisms provide, and the application of contract theory to problems with random participation constraints. Drew Fudenberg's research addresses game theory and its applications. The most closely related projects use evolutionary game theory to study the evolution of cooperation within a single species. His focus is to obtain analytical results for the long-run distribution of strategies in the population.

The adaptive dynamics of mutualism: spatial games, origins, and diversification

Ulf Dieckmann, IIASA, Laxenburg
(Principal Investigator)

Funding Agency: Austrian Science Fund (FWF), Austria

The adaptive evolution of mutualistic interactions is fraught with complexities. The main challenges are to explain the evolutionary origin of mutualisms and to understand their evolutionary stability with respect to the invasion of cheaters. While a suite of recently developed innovations for studying the evolution of cooperation are highly relevant for this project, any satisfactory explanation of mutualisms must account for the specific fact that such interactions always imply cooperation between two different species, which are characterised by separate, if coupled, evolutionary dynamics. Hence, co-evolutionary processes, as well as frequency- and density-dependent selection within each species, must be accounted for, if adequately realistic models of mutualism evolution are to be devised.

This project further develops the quantitative framework for studying the specific questions targeted in BIOCONTRACT, and, throughout this process, sustains a constructive interdisciplinary dialogue about the challenges involved in understanding mutualism evolution. It is believed that by bringing together the economic theory of contracts, evolutionary game theory, adaptive dynamics theory, life history evolution, and spatial evolutionary ecology under the umbrella of an integrative theoretical approach, traditional disciplinary confines can be transcended.

We will focus on three different, yet closely interfaced, lines of research: (1) analyse the effects of spatial structure on mutualism evolution; (2) study the interplay between mutualism and diversification; and (3) investigate whether, and if so how, adaptive evolution can lead to the gradual transformation into mutualisms of ecological interactions that start out as exploitative, or even as competitive.

Spatial games and mutualism between bacteria and their plasmids

Francisco Dionisio, University of Lisbon
(Principal Investigator)

Funding Agency: Foundation for Science and Technology (FCT), Portugal

This project studies how the evolution of social behaviour among bacteria affects the mutualism between bacteria and their accessory DNA elements, conjugative plasmids: how do bacteria evolve to manage public goods, here defined as any fitness-enhancing resource that is accessible to several individuals within a local group? Bacterial cells may have several evolutionary solutions to avoid the cost of free-riders. Some of these solutions may result in the termination of the contract between bacteria and their conjugative plasmids. Therefore, plasmids should evolve mechanisms to avoid these bacterial evolutionary solutions, hence maintaining a conflict of interest between the two partners.

Suppose that, facing the threat of a given antibiotic, bacterial cells survive by producing an enzyme to destroy antibiotic molecules. If the producer cell excretes the enzyme, the enzyme's activity could also be useful to surrounding cells, thus becoming a public good. Cells can, however, retain the enzyme in the vicinity of the cell by keeping it within the cell's own periplasm. In this way, the enzyme still destroys antibiotic molecules entering the enzyme-producing cell, but the enzyme's benefits are no longer available to competing neighbour cells.

A different strategy can occur when genes coding for the enzyme are located in mobile DNA elements, such as conjugative plasmids. By transferring such plasmids to neighbouring cells, producer cells can, in theory, force competing cells to produce the same public goods.

The project poses the following questions: which of these two strategies would be the best evolutionary response of enzyme-producing bacterial cells that are in competition with enzyme non-producers? Should producing cells retain the enzyme in the periplasm –hence avoiding its excretion – or should cells invest in forcing neighbouring cells to produce the same enzyme by transferring the appropriate conjugative plasmid?

Recently, it has been suggested that genes coding for public goods are more often located in mobile elements rather than in chromosomes, precisely to enable this kind of enforcement.

Therefore, if producer cells are able to retain these molecules in their vicinity, then it no longer constitutes a public good. In that case, one can expect chromosomes to recruit genes coding for the enzyme (and there are integrons and transposons that can mediate these recruitments). In such a scenario, costly conjugative plasmids could be discarded by the cell, so the mutualism between the plasmid and the bacterial cell would come to a halt.

Spatial games and mutualism between ants and plants

Jérôme Orivel, CNRS and University of Toulouse 3 (Principal Investigator)

Funding Agency: National Centre for Scientific Research (CNRS), France

Even though ant–plant symbioses are well-known examples of mutualisms, several examples of cheating are also known. In such cases, parasites of the mutualism either act without reciprocity (non-protective parasites) or prevent host reproduction, in order to favour vegetative growth (castration parasites). The understanding of the stabilising mechanisms that enable the persistence of mutualisms in the face of cheating is thus an important issue. Several models have been developed for particular systems, but no general theory exists to explain the factors promoting the evolution and persistence of mutualisms.

This project aims to provide empirical data on the strategies of exploitation versus cooperation between the partners involved in a particular ant–plant symbiosis, namely the relationship between the ant–plant *Hirtella physophora* and the ant *Allomerus decemarticulatus*. This system is characterised by an absence of competition between ant species, which provides a useful contrast with the *Cordia nodosa* system featured in Douglas Yu's Associated Project. All species of the ant genus *Allomerus* are plant specialists. The two species that have been studied so far have been found to be castration parasites. Plants reproduce either when some fortunate individuals are inhabited by truly mutualistic ant species (*Cordia nodosa*) or when the plant hides some flowers by senescing ant shelters (domatia) from the bases of old leaves (*H. myrmecophila*). However, neither of these solutions applies to the *H. physophora* association. The plant associates only with *Allomerus decemarticulatus*, and no tolerance strategies have been identified that counterbalance the cheating effect of its ant associate.

The three objectives of the project thus include documentation of castration behaviour by *A. decemarticulatus*, characterising dispersal strategies of the partners and spatial games and describing contracts between species. Both field and laboratory work will be performed in order to give a fully comprehensive view of the mechanisms involved in the maintenance of the cooperation between the species. Field experiments will be conducted in French Guyana where the host-plant is abundant in lowland forests and will concentrate on the documentation of castrating behaviour and the collection of samples for laboratory work.

Applying spatial games to empirical systems

Istvan Scheuring, Eötvös Loránd University (ELTE), Budapest (Principal Investigator)

Funding Agency: Hungarian Scientific Research Fund (OTKA), Hungary

Although numerous approaches have been suggested to explain cooperation within species, the mechanisms responsible for the evolutionary stability of cooperation between different species (mutualism) are much less understood. This project focuses on both strategic and specific models of the evolution of ant–plant and bacteria–plasmid mutualisms. One of the most surprising and widespread aspects of mutualism is that cheaters and mutualistic individuals can coexist.

In one of our two focal ant–plant systems, the ant genus *Allomerus* protects the host-plant *Cordia nodosa* from herbivores, but *Allomerus* also castrates the plant by destroying flowers. In the short term, castration is beneficial for the ant since it increases the growth of the colony, but over the long term, castration is detrimental because it prevents plants from reproducing and making more host-plants. Interestingly, a polymorphism in the intensity of castration has been detected: Castration is (nearly) complete where a substantial portion of the host-plant population is inhabited by the totally mutualistic *Azteca* ant genus, but castration is only partial where *Azteca* are rare.

The project addresses two questions: (1) Is it possible that local dispersal and spatial structure are responsible for incomplete castration? (2) What mecha-

nisms generate the equilibrium level of castration in the *Allomerus-Cordia* system? The answers to these questions are not simple since the situation seems to be akin to the tragedy of the commons phenomenon. A colony with perfect castration has a greater reproductive success than a colony with non-perfect castrators, but the perfect cheater takes advantage of the new saplings produced by the non-perfect cheaters (and by the true mutualists). It is hypothesised that the local dispersal of ant queens and plant seeds reduces the benefit of aggressive castration while increasing the success of non-perfect castrators.

These questions lead up to a general problem to be studied: currently, two basic types of models are used to explain the evolution of mutualism, partner fidelity and partner choice. partner fidelity models refer to limited dispersal, while partner choice models are connected to biological markets or, in the language used in this CRP, to Principal-Agent (P-A) and other economics of information games. Earlier models had concentrated on the mechanisms that maintain either partner fidelity or partner choice; in fact, it seems as if these mechanisms frequently work together. Furthermore, partner fidelity maintains mutualism (or intra-specific cooperation) only under very specific circumstances, so it cannot be a general explanation. The aim here is to create a simple strategic model where these mechanisms can act together.

Associated Projects (APs)

Spatial games and mutualism between ants and plants

Douglas W. Yu, University of East Anglia, Norwich, UK (Associated Partner)

A key challenge in the study of mutualisms is to understand the mechanisms that prevent cheating. Several overlapping theories have been developed to explain the maintenance of cooperation in the face of selection to cheat. In some interactions, asymmetries in symbiotic relationships are caused by one partner 'coercing' the other into acting cooperatively, via sanctions or sensory traps. Other models rely on inherent tradeoffs that allow the stable coexistence of cheaters and cooperators, while other models invoke mechanisms that bring about the spatial correlation of cooperators via vertical transmission, partner selection or neighbourhood interactions.

A useful way of testing for these mechanisms is to examine systems in which the degree of parasitism varies; e.g. across individuals, populations, and/or species. Explaining variation in parasitism can shed light on its advantages and disadvantages and, thus, on stabilising mechanisms. Here, the project concentrates on ant–plant mutualisms. In most systems, host-plants provide ants with housing (domatia) in the form of hollow swellings (and sometimes, food), and in return ant-symbionts protect their host-plants from herbivores and competitors. Two kinds of cheater ants are known. The first are non-protectors, ant species that do not invest in the costly patrolling of plant parts. The second

The new shoot of a *Cordia nodosa* ant-plant, being patrolled by resident ants (*Allomerus*). The swelling is ant housing.

kind of cheaters are floral castration parasites. Workers do protect leaves, but also attack flowers, redirecting plant resources from reproduction to vegetative growth and maintenance, which benefits the ants. Explaining the persistence of ant–plant symbioses beset with castrators is a difficult problem.

The main objective of this project is to use indirect and direct genetic markers to test formally the key hypotheses that local co-dispersal is occurring in the ant *Allomerus* and the ant-plant *Cordia nodosa*, thus demonstrating the elements of a spatial game in nature. This work is part of a larger research programme in my group that is using population genetic measures to characterise 'meta-community' structure in *C. nodosa*; i.e. source-sink dynamics in a patchy system. Within this programme, our objectives are to contrast *Allomerus* dispersal with *Azteca* to test the idea that *Azteca* is a better long-distance disperser, to diagnose source-sink structure, which allows local mixing, and to test for local resource competition, in order to explain why *Azteca* has such low female investment.

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Cooperation in Corvids (COCOR)

Ronald Noë (Project Leader)

Overview

The core group of researchers in this project is formed by ethologists and cognitive psychologists working with birds belonging to the Corvidae family, i.e. crows, ravens, jackdaws, rooks, jays and their relatives. In addition, the project involves economists, artificial intelligence specialists and theoretical biologists working on different kinds of models of cooperative behaviour in organisms such as the corvids.

The project aims to tap the potential of studying corvids to deepen our understanding of cooperation in group-living organisms. Up to now, research on this topic has concentrated on the primates, both human and non-human. In order to tell unique 'historical accidents' apart from fundamental evolutionary principles, one needs extensive information on at least one more taxon that can rival the primates in its rich variation of social organisations. The European and North-American corvids are ideally suited to play this role; they are easily accessible for study and have a proven potential for an experimental approach. The COCOR consortium includes most of the European research groups working on these species.

COCOR strives to better understand the selective forces that resulted in the evolution of the mechanisms that play a role in cooperation. It also aims to unravel those mechanisms themselves at various levels, by investigating neuronal structures and endocrinological processes, by testing the basic cognitive abilities needed to cooperate and coordinate, by investigating the role of individual and social learning, and by separating the relative influence of genetic and environmental factors. Expected COCOR results would be easily comparable to those found for primates as the project copies key experiments and observational studies done with primates.

The field of comparative cognition has much to gain from a detailed comparison of these two groups: they provide an opportunity to identify which (if any) cognitive skills are common to cooperation and social living, irrespective of the phylogenetic route by which this state has been reached. In addition we hope to identify how selection has acted to produce cooperative solu-

Big flight of ravens in Russia.

tions unique to each taxon. The large family Corvidae (with over 120 species) is ideally suited to fulfil the role of a mirror group to the primates.

Evolved traits are rarely (if ever) the engineer's perfect solution for the problem at hand: evolution can tinker only with the material with which it is presented, rather than designing a solution afresh each time, so that all adaptations reveal their past history in their present form. In addition, they reflect the mechanistic constraints imposed by possessing a certain kind of anatomy. By studying how multiple species of corvids and primates, including humans, produce cognitive solutions to an array of similar problems, the project aims to identify typical 'primate' and 'corvid' solutions and investigate how these reflect the different constraints of morphology of both body and brain. In addition, the project aims to compare the animals' practical real-life solutions to such problems with those derived by game-theoretic analysis, neural networks and experiments with 'embodied artificially intelligent agents', i.e. robots.

An individual must solve a number of problems. More or less sophisticated ways of dealing with such problems can be expected depending on the frequency with which they are encountered by a given species and the degree to which solving such problems affects their fitness. Fortunately, a broad spectrum of social organisations can be found within the European members of the single genus *Corvus*: territorial breeding pairs (raven, *C. corax*); pair breeding and facultative cooperative breeding (carrion crow, *C. corone*); facultative colonial breeders (jackdaw, *C. monedula*) and obligate colonial breeders (rook, *C. frugilegus*). All four species show solitary, air-based and group foraging behaviour, and all show different degrees of cooperative behaviour.

Studying cooperative behaviour implies the study of the many building blocks that are necessary to identify and understand the cognitive strategies that underlie cooperation. Among other things, the project aims to discover:

- The natural history of cooperation, and related phenomena such as tolerance.
- Mechanisms that play a role: neurological substrate, communication, social learning.
- The strategic behaviour used in cooperation.

This approach is flanked by two fundamental different ways of modelling cooperation in group-living animals: first a group of economists construct models with the help of evolutionary game-theory and second, experts in artificial intelligence use 'embodied artificial agents' (robots) to emulate cooperation among living agents. The theoretical biologists in this project form the link between the theoretical and empirical approaches and ensure a feedback process between experimental results and the different types of models.

Individual Projects (IPs)

Cooperation and economic behaviour in rooks (*Corvus frugilegus*)

Ronald Noë, CNRS and University Louis Pasteur, Strasbourg (Principal Investigator)

Funding Agency: National Centre for Scientific Research (CNRS), France

This project studies a captive group of rooks (*Corvus frugilegus*) that were taken as nestlings from the colony on the campus of the laboratory in Strasbourg in May 2006. The birds were hand-raised for a few weeks and trained to take part in various experiments. The group is housed in a small outdoor aviary with an adjacent indoor room, which is divided into several smaller compartments. It is intended to build much larger aviaries that are better suited to rooks and will house two groups instead of one.

The central theme of the research in the framework of COCOR is cooperation. The main goal of this project is to test the biological market paradigm in these birds. Central to markets is the option to choose among different partners. Our experiments therefore aim to compare the investments and returns of individuals in dyadic cooperative tasks as compared to triadic setups. The research involves a number of smaller projects that are all linked to the central theme:

- **Ontogeny of gaze following**
  The birds are tested for 'heterospecific' gaze following. Such gaze following, i.e. looking in the same direction as another individual, has been described in several species notably ravens. The aim of the study is to determine at which age the birds started to follow the gaze of a human experimenter.
- **Lateralisation**
  The lateralisation experiment consisted in giving the birds small containers with food that could be reached through small holes in order to study asymmetries in leg and eye use.
- **Food sharing**
  By limiting the available food to a single feeder a situation was created in which the birds shared food with each other; either by active feeding of conspecifics or by tolerating conspecifics eating the same item. It turned out that these two forms of sharing were used in rather different social contexts.
- **Social learning**
  A pilot study tested if the rooks were able to 'imitate' a human model. The experimenter operated a small box containing food that could be opened in two different ways: either by pulling or pushing. The human model made these movements with his fingers; the birds could imitate these movements by using their


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Three juvenile rooks on a branch.

bill. Preliminary results showed that the rooks tended to use the same movement as the human demonstrator.

- **Cooperation and temperament**
  The topic of this study is the link between 'personality' or 'temperament' and the performance of individuals in cooperative tasks. The task involved pulling a string simultaneously in order to gain access to a food reward.

Cooperation and cognition in a variable social environment

Vittorio Baglione, University of Valladolid, Palencia (Principal Investigator)

Funding Agency: Ministry of Education and Science (MEC), Spain

Intelligence (i.e. the ability to solve problems) is mostly developed in species that live socially, such as primates, dolphins, parrots and crows. One of the most accepted theories to explain this association is that, in social groups, individuals that possess a 'Machiavellian mind' are better able to manage the social organisation of their group in order to obtain benefits. Therefore, animals whose lineage has a long history of social living have evolved higher cognitive abilities than species which members do not form groups.

However, the importance of 'social culture', i.e. the cultural transmission of knowledge and skills through generations, has been recently stressed to explain levels of intelligence observed in current species. Innovations critically depend on an individual's previous knowledge; i.e. the more an individual has learned in the past, the more likely it is to find new solutions to problems. In this context, sociality, where individuals interact continually and cooperate in certain tasks, may promote a higher cognitive capacity by exposing individuals to a large amount of cultural inputs and by 'switching on' their potential for social learning (ontogenetic level). In such a cultural environment, natural selection should also favour 'more competent students', i.e. those individuals with higher learning capacities, ultimately promoting species cleverness (evolutionary level).

The carrion crow *Corvus corone corone* offers a unique model to test the 'social culture' hypothesis through experiments in aviaries and in the field. In this corvid, social organisation varies geographically. Across Europe, crows breed in socially monogamous pairs, and their offspring disperse from the natal territory shortly after independence (4-6 weeks). In Northern Spain, conversely, crows breed in cooperative groups of three to nine individuals. Groups form through delayed offspring dispersal, and juveniles can associate with their parents on the natal territory for up to four years. Throughout this period, they cooperate with their parents in rearing new broods. In these family groups, parents are tolerant towards their offspring, and family members form a cohesive cooperative social unit for prolonged periods of time, providing a good background for cultural learning.

This project will test experimentally three main predictions derived from the 'social culture' hypothesis. One prediction is that crow juveniles that were exposed to different social backgrounds (cohesive family group versus unstable flock) are expected to differ in their abilities to learn tasks by observation of others' behaviour. Furthermore, social learning should improve when interactants are familiar. Second, the social context where individuals grew up generates differences in ability to solve novel problems. Third, among populations showing different social organisations, local adaptations may take place, where crows born in a complex cooperative society are expected to be 'genetically cleverer' than individuals born in a population where social living does not take place, due to selection for learning capability.

Affiliate relations and cooperation in ravens, *Corvus corax*

Thomas Bugnyar, University of Vienna and Konrad Lorenz Research Station (Principal Investigator)

Funding Agency: Austrian Science Fund (FWF), Austria

Observational evidence suggests that corvid flocks represent individualised societies with members selectively exchanging low- and high-risk behaviours such as preening and coalition formation. Moreover, recent studies emphasise a crucial role of affiliate relationships that may form between siblings but also between non-related individuals. What is not yet clear is to what

extent individuals make tactical use of their relations in cooperative interactions. The aim of the project is to: (1) test if ravens' affiliate relationships work as alliances in conflicts, leading to a system of dependent ranks both within and between sexes, (2) determine if, and how, individuals maintain affiliate relations when their partners are experimentally prevented from reciprocating social support and (3) examine the birds' willingness to share resources with 'reliable' and 'unreliable' partners.

Research rests on both natural occurrences of cooperation during and after fights and experimental manipulations, notably the presence and absence of affiliates as potential cooperation partners. The basic procedure consists of temporal removal of individuals (affiliates and as a control non-affiliates) at times of low and high social tension (e.g. before and during foraging at clumped food; before and after fights with and without coalitionary support). The reputation of partners is manipulated by consecutive removals of potential allies in socially tense conditions. Tests on food sharing consist of producer/scrounger experiments in which a partner's identity and experimental history are manipulated.

All tests involve both adult and juvenile birds to examine the effects of experience. Based on preliminary observations, it is expected that birds with affiliate relationships will consistently support each other in agonistic encounters with conspecifics, either actively by intervening in ongoing fights or passively by consoling the other after fights. Furthermore, the working hypothesis is that the amount and type of social support depends on the intensity of the relationship between individuals (indicated by the amount and equity of preening), the opponent's dominance status, and the number and identity of bystanders (and potential allies of the opponent). Reliability or the lack thereof, in the reciprocation of social support should affect the likelihood of sharing food between affiliated individuals. Overall, the birds' ability to control cooperation partners should be affected by age, with older birds being more responsive and quicker in their decisions to go on/refrain from further cooperation.

Modelling the biological and neurological basis of cooperation in birds with collective and evolutionary robotics techniques

Orazio Miglino, University of Naples Federico II (Principal Investigator)

Funding Agency: National Research Council (CNR), Italy

This project deals with evolving/training cooperative behaviours in small populations of robots. Particularly, small mobile robots such as Khepera and E-Puck are used. The robots are controlled by artificial neural networks and are trained/evolved to solve various kinds of collective and individual tasks. The modelling effort is founded on empirical work by the laboratory of animal cognition at Trieste and Teramo University, which study the neurological basis of cooperation in Eurasian jays (*Garrulus glandarius*), notably social recognition.

Social recognition is essential to all the mechanisms of biological cooperation and, if fully understood, it might be an exceptional mechanism to generate teams of robots displaying very sophisticated behaviours. The evolution of cooperation in small robot populations will be studied using an ethological approach, combining a physical cooperative robot simulation with a classic ethologic paradigm such as a cooperative task between two corvids/robots involved in a 'loose string's paradigm' task.

The main aim is to identify the neurobiological computational basis of how the cerebral hemispheres integrate their different competences in higher cognitive processes related to social recognition. The basic idea is to assume population level asymmetries as evolutionary stable strategies that maximise the benefits and minimise the costs associated with a number of social behaviours including social recognition. Previous studies in other classes of animals, such as fish, suggest that images of social partners seen on the right or the left side may evoke different types of social behaviour, probably because of differing modes of analysis of perceptual information carried out by the left and right sides of the brain. Comparative research in corvids on behavioural and cognitive tasks using the techniques of experimental psychology, behavioural biology and ethology will shed light on the different evolutionary, developmental and social aspects that may lead to this kind of specialisation.

The economics of cooperation in humans and crows: a comparative approach

Eric E.C. van Damme, Tilburg University (Principal Investigator)

Funding Agency: Netherlands Organisation for Scientific Research (NWO), Netherlands

The traditional approach in economics and game theory in general (and, hence, to cooperation in particular) is based on the twin assumptions of pure selfishness and fully rational behaviour. Humans, however, do not seem to make the fine distinctions the traditional theory assumes; after all, information processing is costly. At the same time, experiments cast doubt on the traditional assumption of pure selfishness. Recent, albeit

Rook on a tree.

somewhat fragmentary, literature does away with both traditional assumptions and, in line with this, adopts an evolutionary approach to equilibrium. This project will contribute to this literature by building on the empirical work of the other projects and on experiments with humans that will be conducted at the Tilburg experimental laboratory.

Four central topics will be studied:

1. The role of communication in establishing cooperation: communication tends to have a positive effect on cooperation. The question will be asked why this is so, and whether it can also have a negative effect.
2. Cooperation under time pressure: how do time constraints affect individual and group decision making? The relationship between time scarcity and fairness will be systematically investigated.
3. Reconciliation after breakdown of cooperation. The project examines how, after an individual betrays us, it is possible to reconcile and trust again. Since reconciliation is an important element in the biological literature, the project aims to increase our understanding of this topic by working with the other teams.
4. The effectiveness of punishment in sustaining cooperation: in the biological literature both harassment and punishment are considered as enforcement devices in cooperative situations. In contrast to punishment, harassment is not aimed at changing future behaviour but at changing the expected outcome of the interaction. The project aims to compare both devices and their effectiveness, in collaboration with other teams.

Associated Projects (APs)

Relationship intelligence and cooperative cognition in rooks and jackdaws

Nathan Emery and **Nicola Clayton**, University of Cambridge, UK (Associated Partners)

Like primates, members of the crow family form long-term, bonded relationships based on cooperation; however, the relationship is specific to the members of a pair. Partners build nests, help raise their offspring, find food and defend the nest against predators together. These partnerships are similar in many respects to the alliances of apes, but they are also very different. They form very early in development, often before sexual maturity, maybe between members of the same sex and the pair as a unit will be more dominant than individuals alone.

Individuals within a pair selectively feed and preen their partner, often demonstrating reciprocity in the amount and type of commodities given and received. Food offering appears to be essential for the formation of partnerships, but preening and social support are more important for maintaining the relationship. Rooks will also 'console' their partner if they were the victim or aggressor of a fight. Jackdaws can locate hidden food in a cooperative object-choice task, but using information provided only by their social partner.

Although cooperation in wild corvids has been studied, very little is known about their cooperative tendencies in an experimental context. Recently, it was found that rooks spontaneously cooperate on a rope-pulling task previously used to test chimpanzees. Although rooks are very tolerant of their helper (even if it is not their social partner), they did not appear to understand that they needed a partner to help them with the task when this required them to delay responding until a helper entered the test arena. The project will pursue these studies in the laboratory and field to determine whether rooks will delay responding if they can choose who can help them, or they can control the release of a helper. The project will also investigate whether rooks and jackdaws can calculate the reward contingencies inherent in the Ultimatum Game, and at what level of reward they will stop cooperating.

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Dynamic Complexity of Cooperation-Based Self-Organising Networks in the First Global Age (DynCoopNet)

Ana Crespo Solana and **J. B. "Jack" Owens**
(Co-Project Leaders)

Overview

The DynCoopNet collaborative research community will transform research in several disciplines in order to understand, through the perspective of geographically integrated history, the striking role of cooperation in the development of the commercial networks of the global economy, 1400-1800. In order to reach this ambitious goal, DynCoopNet confronts one of the major research challenges of world history: understanding the dynamic, non-linear world economic system of the First Global Age, 1400-1800. In this system, cooperation was much more strikingly important than in the world economy that would follow. Because it was a different complex system from the world economy that followed, DynCoopNet's research on the First Global Age will provide new insights into how cooperative relationships are established and maintained.

DynCoopNet will contribute to the TECT Programme through an examination of the evolution of cooperation within self-organising commercial networks of merchants and other groups on which the first world economy depended. Through a convergence of methods unusual in the historical social sciences, the Collaboratove Research Proposal will reveal the mechanisms of cooperation that permitted merchants and others to establish and sustain the often long-distance

Wikipedia

This 1587 "planisphere" or world map by Rumold Mercator (1545-1599) shows that by the late sixteenth century, Europeans and their collaborators could grasp the broad outlines of the world's regions. Rumold was the son of the Flemish cartographer Gerardus Mercator (1512-1594), whose name continues to be associated with a particular type of map projection.

trading networks of the period. Internally, DynCoopNet constitutes an integrated research project, governed by a mutually agreed upon protocol for data sharing and joint publication. As part of its effort to build necessary research infrastructure, DynCoopNet is petitioning major national and international history organisations to adopt its protocol as part of their professional standards.

DynCoopNet pays particular attention to the global domains of Iberian monarchies: During a crucial period, 1580-1640, the crowns of Aragon, Castile, and Portugal were united under a common Habsburg dynasty, on whose far-flung domains the sun never set. Somehow during the First Global Age, without being coerced to do so, merchants and others came together and cooperated to establish often spatially extensive networks through which they moved products and information over great distances. In this sense, these were self-organising networks because they were formed and maintained by the interactions of the participants themselves, creating a global economic environment well beyond the capacity of any governmental or other hierarchy of that time to establish or control. After defining the characteristics and roles of cooperation in the early centuries of the First Global Age, the CRP will identify and analyse the emergence of new forms of commercial relationships in order to understand the system's transformation to a second world economy. In this second world economy, cooperation was marginalised as a means to sustain networked connections between locations. Through the collaborative efforts of historians, geographic information systems (GIS) and cartographic visualisation professionals, and mathematical modellers in economics and geography, DynCoopNet will produce new spatiotemporal data models that can be queried and new forms of visualising the evolving trading relationships at different scales.

The DynCoopNet collaborative research community employs GIS technology and geographic information science (GIScience) methodologies to manage, analyse and model geospatial, temporal and historical components of cooperative trading information. GIS technology enables georeferencing information based on associated locations and contextualising the information geographically. GIS offers a data integration engine and visualisation tool to bring together layers of information necessary to understand the high levels of cooperation and the transformation of the world economic system at the end of the First Global Age. At the conceptual and computational levels, GIScience methodologies offer ontological and semantic approaches to define entities of interest and discern their cooperative relationships.

In the world regions covered by DynCoopNet there were significant variations in cooperative behaviour, and these were shaped by cultural information and institutions specific to place and by the geographic position of a place within the webs of circuits used by commercial networks. Through the development of geocomputational models (such as agent-based modelling, multi-level modelling, or geospatial evolutionary algorithms), the dynamic and complex mechanisms of cooperative trading can be revealed. While the current GIS technology has only limited capabilities in handling temporal data, much research progress has been made in representing events and processes in GIS databases. DynCoopNet proposes to make heavy use of geovisualisation methods in the form of statistics, animation and visual analytics to explore spatial and temporal distributions and relationships among trading groups and trading locations. Spatial analysis techniques will be used to assess the similarity of the social and economic settings of locations. Based on the similarity assessment, these techniques will be employed to investigate how geographic relationships among locations related to the institutional and cultural environments of these places and how the relationships promoted or hampered cooperative trading. Models of dynamic social networks will be evaluated for their appropriateness in modelling trade cooperation, and revisions of these dynamic social networks will be incorporated into DynCoopNet's temporal GIS component to examine the mechanisms by which cooperative relationships were established and maintained. Through DynCoopNet's innovative research, a temporal GIS will be developed to handle the historical processes of a complex system.

Mathematics can model domain knowledge from research disciplines. Current GIS software is static, whereas history is about change over time. DynCoopNet will combine the work of mathematical modellers in economics and geography with research in GIScience to create a temporal GIS adequate for the needs of researchers in the historical social sciences. Spatial statistics and mathematical modelling will be used to compensate for incomplete data because of the fragmentary survival of sources and in order to discern the possible impact of layers of interaction of which there are few surviving traces. The world economy is conceptualised as a complex, dynamic, non-linear system within which cooperation-based commercial networks functioned as self-organising ones. Therefore, DynCoopNet will also use various types of mathematical modelling to explore the emergence of new forms and cause-and-effect relationships, to validate or corroborate hypotheses about cooperation, and to identify unexpected tendencies or trends. The mathematical expressions developed for these purposes will form the basis for the creation of an open-source, temporal GIS.

Rather than employ mathematical models derived by analogy from models in physics, DynCoopNet will develop and employ explicitly economic models, particularly those developed to deal with the evolution of complexity.

Ever since the 1990s, some economists have placed an emphasis on the importance of understanding self-organising networks, necessary in their view in order to grasp economic complexity. Some consensus has also been reached on the need to build into models the characteristics of the individual actors. However, as yet no satisfactory way has been proposed to achieve this twofold aim, especially in cases where research must take into account different individual motivations and often strikingly different perspectives about the world (in reference to both spatial and temporal ontologies). DynCoopNet focuses on the development of a scheme for modelling the complexity of this type of networked interaction within a spatially large, ultimately global geographic area and over long periods of time. This scheme will be employed to build a GIS for data organisation and visualisation. Therefore, DynCoopNet is expected to make a substantial contribution to several disciplines through its research in mathematical modelling.

DynCoopNet founds its approach to geographically integrated history on three interrelated assumptions: the world economy of the First Global Age was an open, complex, dynamic, non-linear system; the history of any place cannot be understood without understanding how it has been connected to other places; a place is part of an ultimately global system that influences the history of all places all of the time. In the social science literature, it is often asserted that greater human cooperation in trading became possible with the increasing effectiveness of the state or similar institutions. However, these cooperation-based networks of the First Global Age were characterised by a diffusion of authority and frequently by-passed the segmented political hierarchies characteristic of the period's governments. Moreover, these networks served as the source of the creativity and innovation necessary to respond in a flexible manner to the era's endemic disruptions to information, transportation and capital flows. In order to understand cooperation in this earlier, quite different world economy, the DynCoopNet collaborative research community focuses on a series of interrelated questions that tie their work to the overall TECT Programme:

- Did the spatial organisation of the trading networks, the level of risk, the exercise of power or division of labour in more complex organisational schemes influence the patterns of cooperation among actors?
- Within their social and cultural environments, how did merchants maintain 'creditworthiness' (reputation, trust), and was reputation really necessary for such a remarkable degree of cooperation often over great distances and with people they sometimes did not know? Were there brokers?
- How were the rules of the market sites and long-distance interactions set and maintained?
- How did information flow through commercial networks and of what kinds?
- Under what circumstances did cooperation in trading activity break down or fail to develop?
- What sorts of behaviour undermined the 'trust' among parties engaged in trading activity?
- Did new forms of communication in the First Global Age, particularly cartography and the printed book, contribute to the emergence of new forms of human cooperation?
- Did the emergence of cooperative commercial activity constitute a historical process that contributed to greater tolerance and conflict reduction in any part of the global economy?
- Did the patterns of cooperation characteristic of the behaviour of some groups provide them with some comparative advantage? If so, in what circumstances?
- Was there something about cooperation in self-organising networks that gave participants the energy, time and knowledge necessary for innovation to gain a comparative advantage over groups and networks where cooperation was less frequent?
- What were the historical pathways by which within-group and between-group patterns of cooperation and trade emerged in the First Global Age?
- Were the places characterised by cooperation in trading activities also communities within which high levels of other forms of cooperation were evident (e.g. social mechanisms reducing factional conflict, investment in common religious devotions, communal farming and herding)?
- Did the cooperation characteristic of self-organising commercial networks of the First Global Age emerge from behaviour that had developed earlier for other reasons?
- Were the evolutionary processes of commercial cooperation in the First Global Age ones that can be linked to longer evolutionary-historical sequences, or was the First Global Age itself the product of some major systemic transformation (bifurcation)?

Individual Projects (IPs)

Ana Crespo Solana, Superior Council for Scientific Research (CSIC), Madrid, Spain
(Principal Investigator)

Funding Agency: Ministry of Education and Science (MEC), Spain

Crespo serves as Co-Project Leader of DynCoopNet and facilitates communications among European members coordinating, in particular the team of Spanish researchers, who analyse cooperation among merchants, financiers and government officials from the 15th to the early 19th century and the impact of this cooperation on the development of trading networks (see below: Alonso, Álvarez Nogal, Casado Alonso, Gelabert, Montojo). This group will prepare georeferenced ethnographic and quantitative data sets which will be deposited in public digital archives that support DynCoopNet's protocol about data sharing and joint publication. Crespo's research concentrates on merchant communities and the role of their interactions in the development of European socio-economic integration, with particular emphasis on the 18th century. She will investigate and compare the cases of Amsterdam, Cadiz, Hamburg and London, with a special emphasis on their relations with the Caribbean (both islands and mainland regions).

Crespo will focus on merchant groups of Dutch origin settled in the commercial cities of the Atlantic seaboard and the 'crossroads' between the North and the Baltic Seas, emphasising the networked relationships among those outside the Netherlands and the mercantile elite of Amsterdam. She will explore the relationships between the phenomena of migration, the formation of commercial societies, and the evolution and spatial integration of different areas of Europe by these commercial networks. From her data, she will develop empirical generalisations that can be employed for further research on mercantile communities in general, on their roles in the interconnection between European economic zones, and on their influence and impact on the political and diplomatic relations among governments.

Miguel Ángel Bernabé Poveda, Technical University of Madrid (Principal Investigator)

Funding Agency: Ministry of Education and Science (MEC), Spain

In collaboration with Monica Wachowicz and PhD students in their university's doctoral programme in geo-information for government and society, Bernabé is developing the GIS for the organisation and visualisation of the CRP's geospatial historical data. He deals with the problems of digitising historical maps and making them available as part of the CRP's online, shared data archive.

The GIS projects serve the CRP as its major data integration engine. Once the data are integrated in a GIS, the CRP will use the results along the lines outlined by the US University Consortium for Geographic Information Science (UCGIS) which has identified four 'emerging themes' of research, and two of these particularly interest the DynCoopNet CRP: (1) Geospatial data mining and knowledge discovery; (2) Geographic visualisation, which is Bernabé's specialty. Through the collaborative efforts of historians, GIS and cartographic design professionals, and mathematical modellers, the CRP will produce new spatiotemporal data models that can be queried and new forms of visualising evolving trading relationships on different scales. The objective is to be better able to compare patterns and processes of cooperation in these self-organising commercial networks with those discovered by other TECT CRPs. The spatiotemporal GIS will be developed over the course of interactions between the assembly of data sets of cooperative commercial interactions and the mathematical modelling of the dynamic complex system within which the self-organising trading networks were embedded. The continuously enlarged, updated and improved GIS data set will permit researchers to discern, query and interpret patterns, relationships, events and actions, and will allow users to drill down to the unaggregated data sets on which the visual representations of such phenomena are based. For some of this work, the CRP enjoys the collaboration of the software firm IVER and the gvSIG project of the regional government of Valencia (www.gvsig.gva.es), which work together to develop open source GIS software.

In conjunction with Owens and Antoni Picazo (see below), Bernabé will also respond to one of the CRP's questions: did new forms of communication in the First Global Age, particularly cartography and the printed book, contribute to the emergence of new forms of human cooperation? Through a careful examination of the period's maps and related documents, they explore how merchants and others in the First Global Age understood spatial relationships.

David Alonso García, Complutense University of Madrid (Principal Investigator)

Funding Agency: Ministry of Education and Science (MEC), Spain

Alonso investigates the merchants and other financiers (often called tax farmers) who used their capital to bid for the right to collect certain royal revenues in the 16th century. These men had to form companies and use their networked relations to mobilise capital in ways that sustained the Hispanic monarchy. In order to arrive at a better understanding of the Castilian fiscal system, and the connections of merchant fiscal activities with their highly diversified trading, GIS visualisations will help to analyse the evolution of these merchant groups in Castile and of their interactions with other geographic areas (for example, Rome, Lisbon and Flanders). He focuses on their interactions with officials of the royal treasury and on the internal organisation of these merchant groups as a means of analysing these important self-organising commercial networks in terms of the degree of cooperation and conflict in business relationships.

In doing so, Alonso expects to be able to elucidate three processes: (1) the routes of financial communication in Castile, where money travelled because of the fiscal system; (2) a database of prosopographical and other information about financiers, which will permit him to study the personal development of each one as a financial actor; and (3) the relationships between the tax system and commercial world in Spain and elsewhere in Europe, because tax farmers were important international merchants as well as investors in the Crown's fiscal system.

Castilian Merchant Juan López Gallo. Merchants adapted to the cultural norms of their time, as in the case of Juan López Gallo and his family, who were resident in the Flemish city of Bruges. Much of the cloth industry of the Low Countries depended on the massive importation of Castilian wool, and this trade formed the basis of a dense web of collaborative relationships among merchants throughout western and central Europe.

Vicente Montojo Montojo, General Archive of the Region of Murcia (Principal Investigator)

Funding Agency: Ministry of Education and Science (MEC), Spain

Montojo will examine the involvement in the commerce of southeastern ports of Alicante (Valencia) and Cartagena (Castile) of merchants from Atlantic and northern merchant centres (German, Flemish, French, Dutch, English, Irish and Portuguese) and from the central Mediterranean in the First Global Age. He will focus on their degree of cooperation among themselves and with merchants and officials based in the kingdoms of Castile and Valencia. He examines the integration of the northern European merchants through research on partner choice, social structure, reactions to political authorities, and connections to their countries of origin and to Madrid and other financial centres. His preliminary investigations have exposed a surprising degree of cooperation among merchants from these two ports, which were then in different countries, when one would have supposed that Alicante and Cartagena were competitors. His work will centre on a number of archival collections in Barcelona, Madrid and Valladolid, and on the notarial registers of Alicante.

Antoni Picazo Muntaner, University of the Balearic Islands, Arta (Principal Investigator)

Funding Agency: Ministry of Education and Science (MEC), Spain

Picazo investigates the evolution of concepts of geographic space in relation to the expansion of self-organising commercial networks. In particular, he continues his research on the commerce of Pacific Oceania and its multiple connections with the domains and markets of the global Hispanic monarchy and the markets and products of East and Southeast Asia. He analyses the impact of cartography on the way in which those networks' participants understood the world and their cooperative relationships in spatial terms. His work will contribute novel information to DynCoopNet's response to the question: did new forms of communication in the First Global Age, particularly cartography and the printed book, contribute to the emergence of new forms of human cooperation?'

J. B. Owens, Idaho State University, Pocatello (Principal Investigator)

Funding Agency: National Science Foundation (NSF), USA

Co-Project Leader Owens is the intellectual author of DynCoopNet. Owens' geographically-integrated history laboratory at ISU, with the assistance of four graduate research assistants and several undergraduate interns, is producing data sets, with a heavy current concentration on the 18th century, with which the project's mathematical modellers can work to identify the most productive techniques for analysis and the expressions of complexity and non-linear dynamics most serviceable for temporal GIS.

The laboratory is also preparing Sara T. Nalle's database (see below) on Castilian and Portuguese family organisation and partner choice for spatial analysis. Along with Ciolek (see below), Owens coordinates communications among the members of the DynCoopNet collaborative research community.

Owens' research focuses on cooperation in the organisation of 16th century smuggling networks operating along the border between the domains of the crown of Castile and the neighbouring kingdom of Valencia. He is particularly interested in the relationship between the cooperation required for successful smuggling operations and the development in the region of Murcia of a cohesive governing oligarchy of collaborating families, who had earlier been engaged in violent factional conflict. This project emerged from Owens' earlier research on the need for collaboration among political leaders of various levels within Castile's segmented, hierarchical system of authority.

Amélia Polónia da Silva, University of Porto (Principal Investigator)

Funding Agency: Foundation for Science and Technology (FCT), Portugal

Polónia leads a multidisciplinary Portuguese team, involving geographers and historians, who will systematise and interpret a massive body of documentary, archival data. This data will be used to identify mercantile agents and administrators, as well as the financial mechanisms and political interactions, which must be known in order to understand the conception and operation of cooperation-based, self-organising commercial networks. They will employ GIS to organise this data in a georeferenced form in order to employ spatial statistics and to reconstruct and represent cartographically the webs, networks, and interdependencies that are identified.

Porto, in Northern Portugal, was a major Atlantic port in the first global age. Here is the oldest known image of Porto, taken from an atlas prepared in 1634 for the Habsburg ruler of the global Hispanic Monarchy, Philip III of Portugal (Philip IV of Castile), by Pedro Teixeira.

Second, the team, in collaboration with Casado Alonso (see below) will digitise one of the most important surviving personal archives of a major 16th-century merchant, that of the Castilian New Christian (of Jewish ancestry) Simón Ruis (1525-1597), which is now housed in the Provincial Archive of Valladolid (Spain) on the basis of his correspondence and letters of credit, the network of merchants and business negotiations of which he was the centre, will emerge. This will shed light on the evolution of self-organising networks in Ibero-American commerce, especially that involving the key products of the First Global Age: precious metals, slaves and sugar. From this body of information, the team will formulate an empirically based model, susceptible to mathematical analysis, which will permit the explanation and comprehension of the historical mechanisms that are identified.

Associated Projects (APs)

Carlos Álvarez Nogal, Carlos III University, Madrid, Spain (Associated Partner)

Álvarez Nogal's work investigates the way that those involved in commerce created the financial institutions of Castile, the Hispanic monarchy, and Europe during the 16th and 17th centuries while never giving up trading: how did merchant-financiers generate the confidence of others in their 'creditworthiness' and how did they obtain and handle the information crucial to their business negotiations? Álvarez attempts to evaluate the degree to which differences in organisation among financiers and merchants can be explained less on the basis of their country of origin and customs and more on their ability to obtain and make use of information. In particular, he is concentrating on Genoese bankers, their companies, and the networks of which they were a part. For this work, he will employ the theory of transaction costs, game theory and models of entrepreneurial organisation.

Contrary to the claims about the weaknesses of Castilian financial institutions made by many who have written on the period, Álvarez hypothesises that financial institutions played a decisive role in the Castilian economy and that Castile and the Hispanic monarchy in general had a very developed and competitive financial system for the period, capable of offering quite a variety of services to the Crown and to individuals. The presence of a number of foreigners was merely an indication of Castile's broad connections with the financial world of the First Global Age. Because much of the debate over these financial institutions suffers from a grave lack of data, he will develop a database about Madrid as one of Europe's most important financial markets between 1550 and 1650, especially after it became the site of the royal household and court (in 1561) and after Castile's ruler also took the Crown of Portugal in 1580.

Hilario Casado Alonso, University of Valladolid, Spain (Associated Partner)

Casado, in cooperation with the Portuguese IP, studies consumption and the commercial cloth networks linking Castile and Portugal and their respective domains during the First Global Age. His research on the flow of information among merchants and financiers in the Hispanic monarchy from the 15th to the 17th century links up to many other subprojects of this CRP: how did they handle risk, especially through maritime insurance? What were the roles of public and private institutions in the resolution of conflicts? The latter subject relates directly to the concern in cooperation research about what is done to restrain 'cheaters and defectors'.

T. Matthew Ciolek, The Australian National University, Canberra, Australia (Associated Partner)

Ciolek provides guidance to CRP members about how to establish the collaborative, interoperating online databases and digital archives at the basis of the DynCoopNet Project, a website, and a wiki to keep track of links, notes and commentaries of individual participants. His research focuses on creating and maintaining a central online database/catalogue of all the land and maritime transportation and communication routes in Europe (1400-1800) and on determining travel times and speeds of movement between the nodes of the most important routes. Because so much of his past research has focused on Asian and Pacific routes, Ciolek is particularly able to support aspects of the research of PI Picazo (see above) and APs Rila Mukherjee and Benigna Zimba (see below). With Owens and other interested DynCoopNet members, Ciolek will write a manual about organising a collaborative, multidisciplinary, multinational research project of this type, and he will collaborate on papers on the routes used by the self-organising commercial networks studied by DynCoopNet.

Emery A. Coppola Jr, NOAH L.L.C., New Jersey, USA (Associated Partner)

Coppola employs his expertise in the combination of artificial intelligence with other modelling methodologies to explore the self-organising networks of the First Global Age. In particular, he is adapting the system of artificial neural networks (ANNs) that he has developed to deal with water resources management problems and energy trading to the modelling demands of DynCoopNet. Because of their powerful non-linear modelling capability, ANNs can accurately model highly non-linear and complex phenomena and expose the emergence of new forms. With the application of these methods to historic data, Coppola aims to expand his ability to use ANNs to model highly dynamic systems, where states are continuously evolving in response to stresses. He argues that ANNs have the power to identify important cause-and-effect relationships.

Beyond developing an understanding of the use of ANNs to enhance understanding of complex commercial networks, Coppola is working on the integration of ANN technology with GIS, not only for assimilating and feeding data for ANN development and testing, but also for visually representing the results effectively. Because of the number of factors that are being addressed – economic, ecological, etc. – integration of these technologies has potentially wide-spread applications to many different fields of study.

Wikipedia

Detail of a 1634 painting by Francisco de Zurburán (1598-1664) depicting the English attack on the port of Cádiz in 1596. DynCoopNet hypothesizes that the cooperation-based trading networks of the first global ages provided merchants with needed flexibility to respond to the frequent disruptions of commercial circuits by war, weather, epidemic disease, and other problems. The original is in the Prado National Museum, Spain.

Juan Gelabert González, University of Cantabria, Spain (Associated Partner)

Gelabert's work challenges directly widely employed theses about the inevitability of shifts in economic prominence among European countries (in the North-West and the Iberian Peninsula) in the 16th and 17th centuries. In redirecting attention to the impact of political decisions on the economic vitality of countries, his project seeks to establish the degree to which, in an interconnected world, government action can affect the economic future of a country relative to other countries. Gelabert explores the commercial and political interactions among countries along Europe's Atlantic seaboard during the years of military confrontation and diplomatic shifts (1585-1621) among the main political powers (Spain, England, France, Portugal, the Dutch Republic) of the area. He is particularly interested in how the resort to trade embargoes by the Hispanic monarchy and certain diplomatic arrangements among some of these countries created internal tensions among commercial communities based on the Channel coast of France (Rouen, Le Havre etc.) which, in turn, affected trade passing through them to and from the Mediterranean and the Baltic. He will learn how the diplomatic, religious and political confrontations of the era led to the development of alternative strategies of trade, particularly those involving contraband and colonial expansion. Gelabert elaborates a history of highly dynamic breaks and openings of commercial circuits, which allows CRP researchers to consider what elements of cooperation-based commercial networks permitted some groups to respond more flexibly and successfully to the difficulties and opportunities that were presented.

Rila Mukherjee, University of Hyderabad, Gachibowli, India (Associated Partner)

Mukherjee's research focuses on the pre-colonial South Asian economy, notably on the interactions among various groups of European merchants and those of the eastern Indian Ocean. She is currently involved in research on the high levels of cooperation between the people of the Andaman Islands in the Bay of Bengal

and merchants using the shipping routes of the region. She is also connected to a GIS-based project studying the impact of environmental changes in river deltas of Bengal.

Sara T. Nall, William Patterson University of New Jersey, USA (Associated Partner)

Nalle is in the process of assembling, on the basis of her work in Portuguese and Spanish archives, a database of material on partner choice and the organisation of families among different groups in the Iberian Peninsula. She is trying to understand how authority was exercised within different categories of family and how differences shaped the formation of values and cultural perspectives about reputation and trust that sustained or damaged cooperation among kin, members of ethnic groups, and merchants or members of other economic groups. Social and economic change, the result of Spain's rapid rise as the world's first global power, forced families to contend with an unusual array of problems, which may be seen in changing notions of patriarchal authority, differing strategies of assimilation, changes in the household division of labour, and increased competition in the marriage market as emigration and war turned men into a scarce commodity. To the extent that families formed an important basis for cooperation-based self-organising commercial networks, exploring these changes is important for the DynCoopNet CRP. To manipulate her rich fount of information, Nalle employs the powerful data mining and statistical analysis software SPSS. With the help of graduate students of Owens' geographically-integrated history laboratory (see above), she is georeferencing the places associated with the individuals in her database so that she can use spatial analysis for understanding how partner choice and family organisation facilitated cooperation and at what levels, in terms of the degree of social networking and extent of spatial dispersion.

Tönu Puu, Centre for Regional Science (CERUM), Umeå University, Sweden (Associated Partner)

Puu is widely recognised for his work on geographical spatial organisation modelling and non-linear dynamic economic processes. Of particular value to the CRP is his modelling of evolution in an economy where one does not study the growth within a given set of human artifacts within a system, but the change of the set itself through increased diversity and emergence of new artifacts (innovation). This approach may permit modelling along similar lines of the establishment of new trade relations. Puu also works on the development of economic and cultural complexity by the modelling of increasing complexity through an analogy to the development tree modelled through catastrophe theory. The DynCoopNet challenge will be to connect these spatial models of non-linear dynamics to empirical generalisations about the evolution of cooperation-based commercial networks in the First Global Age and to integrate the models into a spatiotemporal GIS that is useful for information management, analysis and visualisation.

Michael Sonis, Bar-Ilan University, Israel (Associated Partner)

Sonis brings to the DynCoopNet project his research on complication (evolution of complexity) mathematical models, which are inspired by empirical regularities of the spatial socio-economic and behavioural sciences. Sonis is studying complexity and complication in historical socio-economic and socio-ecological dynamics, especially where these involve innovation diffusion (especially of innovative ideologies that lead to 'aggressive intolerance'), migration, elite competition and the socio-ecology of individual choice in collectives. Finally, he models basic spatial theories of human cooperation, which are important for understanding cooperation-based self-organising networks (innovation diffusion theory, central places theory, theory of migrations, transportation networks and spatial linear economic systems).

His modelling efforts will contribute to dealing with DynCoopNet's most ambitious research questions: e.g., whether the cooperation characteristic of self-organising commercial networks of the First Global Age emerged from behaviour that had developed earlier for other reasons; with defining the historical pathways by which within-group and between-group patterns of cooperation and trade emerged; whether the patterns of cooperation characteristic of the behaviour of some groups provided them with some comparative advantage and, if so, in what circumstances; or whether there were evolutionary processes of commercial cooperation in the First Global Age that can be linked to longer evolutionary historical sequences. Within a more specifically geographic framework, he will contribute to DynCoopNet's attempts to understand if the network patterns created by cooperative trading activity helped define the central places within the global economy, or if this sort of collaboration was marginal to the major economic centres.

Shahriar Yousefi, Centre for Advanced Research in Nature and Society (CARINAS), Aarhus, Denmark (Associated Partner)

Yousefi's expertise is in the area of spatial analysis and spatial statistics, particularly for the understanding of complex economic dynamics. He employs artificial intelligence and neural networks as an integrated element in the battery of quantitative methods, which will be used to examine the self-organising networks of the First Global Age. These methodologies have a remarkable potential for providing reliable insight in cases in which the specification of causal relations is difficult (or very uncertain) as well as providing powerful tools for obtaining precise predictions and reliable inference by using the available information.

Yousefi helps direct a multiperspective analysis, involving the application of quantitative methods and modelling efforts, of data about cooperation-based self-organising commercial networks in the First Global Age. Given the complex features of these trade networks and the fact we know very little about them, Yousefi suggests that (as a minimum) we rely on the six approaches or directions listed below.

1. The temporal changes in the networks (in other words, dealing with the dynamic properties).
2. The spatial changes in the networks (in other words, dealing with the neighbouring effects and statistical homogeneity etc.).
3. The spatiotemporal evolution of the networks (in other words, dealing with the spill-over effects and diffusion phenomena).
4. The presence of complex feedback mechanisms in the networks.
5. The application of artificial intelligence and neural networks (in conjunction with Coppola).
6. Pattern recognition through wavelet analysis.

This allows an opportunity for devising more robust models, which can replicate the real networks, a larger base for interpretive approaches is provided; and a mechanism for the interaction of complementary competences is maintained.

May Yuan, University of Oklahoma, USA (Associated Partner)

Yuan's research interest is in geographic representation, spatiotemporal information modelling, and applications of geographic information technologies to dynamic systems, such as the world economy of the First Global Age. She is a leading expert on geospatial data mining and knowledge discovery to support high-level information computing and spatiotemporal analysis (of phenomena such as events, processes and change analysis). Yuan's, cooperation is primarily with Bernabé's team (see above) on: spatiotemporal analysis and modelling; spatiotemporal visual analytics; spatiotemporal data mining; spatiotemporal reasoning; and spatiotemporal ontologies.

Benigna Zimba, the Higher Institute of International Relations, Eduardo Mondlane University, Mozambique (Associated Partner)

Zimba's research will focus on the impact of gender relations and changing market conditions on the ways in which African merchants cooperated with those from Europe who operated within the Portuguese zone. Zimba's projects focus on women's roles in land control, herding, crop production and cloth-making in shaping commercial interactions linking Mozambique to the global economy. In particular, she focuses on the routes of the slave trade. Her work ties in with that of PI Polónia and AP Mukherjee (see above).

Wikipedia

Portuguese merchants appearing before the King of Kongo. Unlike in the Americas, where the arrival of Afroeurasian diseases decimated the indigenous population and made possible the European conquest of vast territories, Europeans had to show their respect to African and Asian authorities, as depicted in this picture of Portuguese appearing before the King of Kongo. Therefore, European merchants often had to cooperate with non-European traders and producers.

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DynCoopNet
Ethical Guidelines for the Use of Shared, Distributed Data, Collaborative Research and Joint Publication

Preface

With the new information technologies and means of communication available, the ability of historical researchers to share data and engage in collaborative research has been greatly expanded. Such sharing and collaboration are fundamental to research on world history and on the history of spatially large entities such as the global Hispanic monarchy or the domains of some of its constituent Crown governments (for example, Castile or Portugal). But many of those who might participate in such projects come from disciplines such as history and, unlike colleagues in some other disciplines, are completely untrained in the ethical protocols for the use of shared, distributed data, collaborative research and joint publication. In the absence of training, experience and guidelines in this area, many historians are reluctant to share data or participate in collaborative projects. Therefore, the DynCoopNet collaborative research community will be governed by the policy presented in this document, which will be posted on the DynCoopNet website. If their national and international disciplinary organisations lack such a policy as part of their professional standards (as is the case with most history organisations), DynCoopNet members will present the community's policy statement for adoption by the professional standards committees of these organisations.

J.B. Owens

Register of documents maintained by a notary in the major commercial center of Toledo (Castile) in 1565. Most DynCoopNet data about cooperation in trading activities must be extracted from sources such as this. This register is in exceptionally good condition.

Data Policy

The following policy has been adopted in order to encourage historical researchers to make available the underlying data on which their papers, articles and books are based for long-term access, to archive their data in approved data centres, and to recognise in their publications the valuable role of the researchers who collect and prepare important data for use by the global historical research community.

1. Members of the DynCoopNet collaborative research community should make available the data on which their articles and books are based. To ensure public access and long-term availability of the data they must be permanently archived in a data centre or centres that meet the following three conditions:
   (a) Open to researchers throughout the world
   (b) Committed to archiving data sets indefinitely
   (c) Provide services at reasonable costs.

   Other data centres, though chartered for specific lengths of time, may also be acceptable as an archive for this material if there is a commitment and coherent plan to migrate data to a permanent archive when the centre ceases operation.
2. Data sets that are available only from the author, through miscellaneous public network services, or academic, government or commercial institutions not chartered specifically for archiving data, should be cited with care by DynCoopNet members. This type of data set availability is judged to be equivalent to material in the grey literature. If such data sets are essential to the paper or book, authors should treat their mention just as they would a personal communication. These mentions will appear in the body of the paper, article or book but not in the reference list.
3. To assist reviewers and other researchers in accessing the data sets, authors are encouraged to include a brief data section in their papers, articles and books. This section should contain the key elements of the metadata and the information needed to obtain the data set being cited.
4. The format for a reference will follow that required by the publisher's style policy. However, the following elements must be included in the reference: author(s), title of data set, access number or code, data centre, location including city, state, and country, and date.
5. Full Dublin Core (DC) metadata must be provided for each data set, and if the data is geospatial, ISO 19115 metadata must be provided as well.

The characteristics of the ideal data archive are:

- Permanent archive: Committed to maintaining and providing long-term access to the data sets.
- Platform independent: The format of such data sets and graphics files shall be platform-neutral to allow the widest possible availability.
- Future portability: Formats for archiving data and graphics files must be in a generic, preferably non-proprietary format consistent with conversion to future open standards if necessary.
- Ease of management: Files shall not require significant pre-processing or reformatting for administrators in order to archive the data.
- Usability: Compression techniques used for data sets should be available on multiple platforms, such as zip utility.
- Flexibility: The guidelines and their recommended standards should be sufficiently flexible to allow for future incorporation of technological advances, and to allow for future user input gained from practical experience.

Joint Publication Standards

1. Only individuals who have significantly contributed to the research and preparation of the paper, article or book and who share responsibility and accountability for the work should be listed as co-authors. All of the listed authors must have seen the final version of the paper, article or book and agreed to its submission.
2. The corresponding author accepts the responsibility of having included as authors all persons who meet these criteria for authorship and none who do not. The corresponding author also attests that all living co-authors have seen the final version of the paper, article or book, agree with the major conclusions, and have agreed to its submission for publication.
3. The first author or authors listed should be those who wrote the paper, article or book.
4. Additional authors would be any other senior researchers, post-doctoral researchers, graduate or other students, and the research advisers of these students who prepared and analysed data, solved research problems, suggested interpretations of data etc., or assisted the 'first author' in performing these tasks.
5. If a graduate student or graduate students write a paper, article or book, the graduate adviser should be listed as the final author.
6. Deceased persons who meet the criteria for inclusion as co-authors should be so included, with a footnote reporting date of death.
7. If the writers of the paper, article or book have made use of shared, distributed data sets prepared by others, these data set creators should be shown the paper, article or book and offered the opportunity to be listed as co-authors if they agree to share responsibility and accountability for the work.
8. Other contributors who do not meet the authorship criteria should be appropriately acknowledged in the paper, article or book. Those acknowledged might include those who provided major administrative assistance.
9. Contributions by those who do not wish to accept responsibility for the paper, article or book should be acknowledged in a note or special Acknowledgments section.
10. If there is any question about whether a researcher's contribution is substantial enough, the person should be offered co-authorship.
11. All of the co-authors will be included in lists of works cited at the end of journal articles, but the citations within the text will generally follow the form (Goss et al. 1999), unless it is clear from the description of authorship in the article that the first two or three co-authors played equal roles in writing the text.

The disciplines of atmospheric science and oceanography both deal with open systems covering large geographic spaces, and publication in these fields depends on access by scientists to data sets prepared as a result of research done by others. Therefore, these fields have been taken as models for the DynCoopNet data and authorship policies. In particular, sections have been adapted from the Ethical Guidelines to Publication of Chemical Research of the American Chemical Society (ACS) [pubs.acs.org/instruct/ethic.html], the Guidelines to Publication of Geophysical Research of the American Geophysical Union (AGU) [www.agu.org/pubs/pubs_guidelines.html], and the Policy on Referencing Data in and Archiving Data for AGU Publications [www.agu.org/pubs/data_policy.html].

Dr. Lisa Goss, Associate Professor of Atmospheric Chemistry at Idaho State University suggested these documents as guides to what should be included in this policy statement, and she provided a concise description of what these disciplinary guidelines usually mean in practice. To formulate her practical suggestions, she consulted with more senior researchers and journal editors in her field and shared her own experience as a graduate student and researcher. The DynCoopNet collaborative research community expresses its thanks to Dr. Goss for her assistance.

Sustaining Eco-economic Norms for a Sustainable Environment (SENSE)

Simon Levin (Project Leader)

Overview

We live in a global commons, in which actions we take affect the general welfare, for good or for bad, but in which the costs and benefits realised by individual agents do not reflect fully those broader elements. Individual agents, whether these be people or institutions or nations, act in their own self-interest, often at cost to societies, the biosphere, and hence the global community and future generations. This was the lesson Garrett Hardin tried to convey when he first adapted Lloyd's concept of the global commons into the environmental literature; but it is a lesson that humanity has largely ignored, at its peril. The view that all interactions among nations involve zero-sum games ignores the reality that there are win-win possibilities, and prevents innovative solutions to our common dilemma.

Hardin's conclusion that avoiding the tragedy of the commons requires 'mutual coercion, mutually agreed upon' suggests that although scientific and technological advances will be important in addressing (and in some cases causing) problems of the commons, solutions are impossible without addressing human behaviour. Evolutionary theory provides deep insights into how cooperation and collective action can emerge.

Animal societies are typically held together by one of the following 'social glues': (1) altruism directed towards kin; (2) reciprocal altruism and mutualism among non-relatives; and (3) coercion. Alone or in concert these relationships lead to collective action that benefits all members of societies as long as they are small, the network of relationships is small and interactions among members are largely direct. How these forces scale up to larger collectives where relationships are weak, especially when connections become indirect, is less well understood.

Even less explored is the extent to which 'mutual coercion, mutually agreed upon,' can arise through natural and cultural evolution, and what lessons we might derive from an evolutionary perspective. The overarching aim of SENSE is to bring together a team of scientists with theoretical and empirical expertise on how particular social glues foster altruistic and cooperative behaviour in animal and human societies, in order to determine how those glues together can produce mutually agreed-upon coercion that leads to greater social good in large, complex and structured societies.

SENSE builds upon several diverse literatures: the evolution of cooperation in non-human systems, the emergence of cooperation in human societies, in social and economic systems, models of social norm dynamics, and cultural evolution, as well as the dynamics of complex adaptive systems. Through a framework of modelling and empirical work, SENSE aims to unify these, developing a theory that crosses scales and crosses systems.

Collective decisions – from individuals to groups, from groups to nations, from nations to the global biospheric population – create a framework that is central to our ability to achieve mutual benefits from mutual action. Patterns of consumption are driven by individual interactions and imitation, and indeed how happy humans are is determined to large extent by their economic standing relative to others Thus, there is a profound social component to the problems of the commons, and social norms can be the source of global environmental problems. On the other hand, the potential for the propagation and maintenance of social norms through interactions among individuals is also the source of hope for addressing these very problems. Ecological and socio-economic systems alike are complex adaptive systems, integrating phenomena across multiple scales of space, time and organisational complexity. In such systems macroscopic phenomena to a large extent emerge from, and in turn influence, the individual and collective dynamics of individual agents that are pursuing their own selfish agendas.

SENSE is based on this essential insight, developing theoretical and empirical approaches to understanding the interplay between collective phenomena and individual actions. In particular, it explores the development of cooperative behaviour, and how it can be enhanced in dealing with global environmental problems. The overall objectives are to identify conditions, strategies and policies that foster mutual coercion, mutually agreed upon for sustainable use of the global commons.

Building on the expertise of a team of animal behaviourists, ecologists, evolutionists, economists and game theorists, the three subprojects provide the foundation for a synthetic theory of how mutual coercion can be mutually agreed upon among large collectives nested in even larger collectives. Combining theoretical and empirical approaches, the Austrian IP will examine how punishment can enhance the spread of altruistic acts through large diffuse societies. In a similarly integrated theoretical and empirical approach, the US IP will examine how altruism and cooperation are affected by the evolution of punishment, social norms and the structure of societies. The Dutch IP will apply these insights to

Pastoral people (*Laikipia Maasai*) herding cattle. They herd cattle and like most herders, add more livestock to the landscape than it can support, which leads to the tragedy of the commons.

explore cooperation in achieving agreement on global management at the national and international level.

Overall, our objective is to have strong integration among the three component parts of the CRP.

Cooperation among genetically unrelated individuals is common in human societies. The relationships that maintain it are often reciprocal, but need not be so. Mutualisms and coercion can also be involved.

In general, these relationships are diffuse, and influenced both by the actions of others and by normative standards of behaviour that often change only over much longer time scales. Interactions require tradeoffs and are often embedded in complex social networks. Over our cultural history such social norms have arisen and been sustained in small groups, often however increasing conflict among groups as a consequence. In recent times, at least in many societies, our tribal history has been replaced by one in which those tribes have been bound together into nations, held together by common rules of conduct and systems of morality and justice. This may be for the good, except that it means that intertribal conflicts have been replaced by international ones so that not only the benefits but also the costs are much greater in scale.

A fundamental question, then, which requires close examination, is whether the link between cooperation at one level and competition at higher levels can be broken. Groups form in part to provide collective benefits in competition with other groups. This interplay can cascade up the hierarchy, as formerly competitive groups join together to form coalitions that compete in turn with other such groups or coalitions. In the limit of the total global population, however, if cooperation cannot arise without competition, then global solutions become impossible. SENSE uses a variety of empirical and theoretical investigations to explore whether and how cooperation can arise without higher-level competition. The project studies group formation to un-

derstand the distribution of group sizes, and explores how coalitions form and how social norms arise and are maintained.

The central issues that form the basis of SENSE are:

- How do the details of collective behaviour change across taxa, as we move from bacteria to invertebrates to vertebrates, culminating in humans? What is the interplay between genetically based evolution and cultural change in shaping cooperative behaviour?
- Where does 'mutual coercion, mutually agreed upon,' arise? Can we draw from examples of policing among other vertebrates, especially primates, to derive lessons for human societies?
- How does punishment arise, and how does it interact with the emergence of voluntary, societally beneficial actions?
- How do social norms arise and spread? Do computational and other constraints explain why individuals engage in apparently irrational behaviours in particular situations, because their behaviours reflect syndromes that have evolved in different contexts, or as generalised solutions to classes of problems?
- Does cooperation at one level entail competition at the next, or can we achieve cooperation even at the highest level of aggregation?
- More generally, how do networks of interaction arise, and how do their topologies feed back to influence individual behaviours? What is the role of the flow of information within these networks?

Individual Projects (IPs)

Altruistic punishment

Karl Sigmund, University of Vienna
(Principal Investigator)

Funding Agency: Austrian Science Fund (FWF), Austria

Within the last decade, coercion has emerged as one of the major factors upholding a high level of contributions to joint undertakings. Experiments have shown that in the absence of sanctioning institutions, individuals are ready to 'take the law into their own hands' and punish wrong-doers, even at a cost to themselves. Such costly punishment is applied even if it cannot possibly be recouped in later interactions. Anthropological experiments have shown that all human populations are willing to use costly punishment, to a varying degree, and that this willingness to punish correlates with the propensity for altruistic contributions. Altruistic punishment is a human universal, and recent experiments using brain-imaging have found the corresponding specialised regions in the human brain.

In a public goods interaction, free-riders who do not contribute but exploit the efforts of others fare better than those who contribute. If one assumes that successful strategies spread – genetically or culturally – defectors should take over, and the joint effort should collapse. This 'social dilemma' can be overcome by punishment directed towards the defectors, which reduces their payoff. But since it is costly, it also reduces the punisher's payoff. In fact, if the penalised players are allowed to retaliate, both parties will suffer to a comparable degree. This raises the so called 'second order social dilemma'; individuals who contribute, but do not punish, will be better off than the punishers. The frequency of punishers will decline and the defectors will return.

If punishers punish not only the defectors, but also those who do not punish the defectors, this introduces a 'second order punishment' which, if prevalent, will increase the tendency to 'first-order punish' the non-contributors. However, this holds only once these norms are established. It is difficult to conceive how costly punishment can invade society. Initially, it is bound to be rare, and would have to incur large costs by having to relentlessly punish left and right.

A recent model by Fowler has suggested a solution. If individuals have the option not to participate in the public good game, but to chose an autarkic income rather than engage in a joint enterprise, then punishers will be able to invade and go to fixation. However, the deterministic model is so fraught with structural instabilities that it is inadvisable to draw any conclusions from

it. Preliminary individual-based simulations suggest that for a wide range of parameters, the conclusion is right. The project aims to analyse these computer simulations statistically, for a wide range of parameters, and to apply recent methods of stochastic game dynamics that use well-known stochastic models from population genetics. Finally, the project also envisages economic experiments. It is easy to conceive several variations of the public goods game with punishment, some with volunteers (players can abstain from participating in the game), some without (players are obliged to take part).

The roles of social structure and social norms on the evolution of cooperation

Simon Levin (Project Leader), Daniel Rubenstein, Princeton University (Principal Investigator)

Funding Agency: National Science Foundation (NSF), USA [grant not awarded]

Frequent cooperation between genetically unrelated individuals makes human societies an anomaly in nature. Although some altruistic acts fit Trivers' notion of direct reciprocity, many more altruistic acts are committed by donors who have no expectation of future rewards from recipients, often because there is no expectation of subsequent interactions between the same pair of individuals.

Donors often cooperate via 'indirect reciprocity' with individuals who are likely to help other members of the group. This concept may rely on the individual's reputation and patterns of punishment within a group and the availability of such information to the members of the group. However, the emergence of cooperation may actually call for this information to be 'noisy'. Recent work on social norms has further attempted to explain the evolution of the complex forms of cooperation observed in humans. Public goods experiments have demonstrated that individuals often enforce social norms through sanctions, at a cost to themselves, thereby ensuring the persistence of cooperation in the system. However, it is necessary to explain the initiation, spread and maintenance of norms, in order to explain the nature of cooperation arising from them. Since social norms vary greatly among and within cultural groups, the nature and degree of cooperation observed in a society may depend on the mechanisms that shaped its structure, which are likely to include issues of status and the shape of the social network.

This project will explore how the nature of structure and norms affect the ways reciprocity, mutualism and coercion operate and generate actions that cross organisational levels to sustain cooperation and even altruism. In particular, the project investigates the role of social status in cooperation, and models the development and spread of opinions and social norms in populations. Further, the project links social norms to game-theoretic approaches in the study of cooperation, and investigates emergence and influence of higher-order structure (such as emerging network topologies, metapopulations or hierarchical organisations) on development and evolution of cooperation. Methodologically, this project will meld theoretical investigations with role-playing experiments. A case study will explore relationships between nation states and multinational corporations, mutually tied to each other as they draw upon resources to provide services to citizens. In particular, the project focuses on problems associated with achieving social cooperation for greenhouse mitigation strategies.

Signing of the Treaty of Rome – Rome, 25 March 1957.

Cooperation at national and international levels

Aart de Zeeuw, Tilburg University (Principal Investigator)

Funding Agency: Netherlands Organisation for Scientific Research (NWO), Netherlands

The most pressing environmental problems of our time are either global in nature (such as climate change) or global in treatment (such as waste disposal). The international issue is the central theme of this project: how can cooperation at the highest level be achieved? In economic theory, different decision levels (individuals/firms, states, IEAs) are usually analysed separately. The novelty of this project is to study the effect of the interaction between these different decision levels.

The starting point is a group of agents called countries. In each country there is another group of agents called firms or harvesters. These agents harvest a global environmental resource. This could be the global climate, which is 'harvested' through CO_2 emissions, or a renewable resource such as an open sea international

Air pollution

fishery. There are regulators or policy makers at two levels. At the international level there exists some international structure (e.g. EU, WTO, Kyoto Protocol) that negotiates a global policy regarding the resource. This policy prescribes certain norms or obligations for each country, which could be implemented through certain instruments (standards, taxes, tradable quotas). Within the country, the government acts as a regulator and introduces a policy that is levied on the agents within the country so that the regulated country conforms to its norms or obligations set at the higher level. This policy could, for example, be the National Allocation Plan for CO_2 emissions of the EU countries. Policies and instruments at the country level need not be the same across countries.

On the one hand, countries decide about their policy on the basis of the outcome of the negotiations at the international level, considering, at the same time, how they expect the individuals within the country to react to their policy. The way that agreed policies are implemented and the impact of different types of uncertainty (e.g. scientific and model uncertainty, uncertainty regarding consequences of actions) may play an important role here. On the other hand, countries determine their position in the negotiations at the international level.

The final outcome regarding the total harvesting of the global commons depends on the chain of reactions at the different decision levels. It will be interesting to see if the usually grim picture regarding international coordination changes if all these interactions and signals are taken into account. It may be important to explicitly consider a possibility of irrevocable commitment at certain stages of the process such as investment in green technology. It may also be important to explicitly consider positive externalities of cooperation such as sharing the costs of technological change. The final purpose is to see if full cooperation at the international level is possible and what is important or needed to reach that goal.

People in SENSE

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The Social and Mental Dynamics of Cooperation (SOCCOP)

Herbert Gintis (Project Leader)

Overview

Despite the fact that human cooperation has been a central concern of biology and the human behavioural sciences since Adam Smith and Charles Darwin, there is currently no accepted model of how the cognitive capacities and motivational predispositions of humans interact to support cooperation and how these unique human traits evolved. Contemporary evidence from neuroscience, behavioural genetics, and behavioural game theory suggests that while the behavioural disciplines (biology, economics, anthropology, psychology and sociology) have made major contributions to understanding cooperation, each discipline ignores a key part of the overall picture. The nature of cooperation is such that it does not break down into independent parts susceptible to isolated analysis by specific disciplines. The SOCCOP project is a novel and uncompromisingly transdisciplinary strategy for understanding human cooperation. We anticipate a number of specific scientific breakthroughs that promise to have a practical application to problems of organisational governance, conflict resolution and the promotion of intergroup tolerance.

Simply bringing researchers together from different disciplines to work jointly will not suffice to meet the challenge of understanding cooperation. This is because the various disciplines have incompatible core models of human behaviour. However, there has been considerable progress in overcoming the disciplinary hurdles in the past decade through an intense dialogue between empirical and theoretical studies using such transdisciplinary tools such as behavioural and evolutionary game theory, agent-based modelling and neuroscience. This experience is the backdrop of Gintis' suggested framework for the unification of behavioural research. Our TECT proposal is the first comprehensive transdisciplinary research project fully informed by this framework. Relying on past experience and an innovative methodology, we expect a degree of cross-disciplinary coordination and interaction well beyond anything that has hitherto proved possible.

Specifically, SOCCOP aims to:

- Develop consistent and stable behavioural measures that can be used in other studies.
- Perform behavioural studies on a group of >600 individuals.
- Evaluate the empirical plausibility of distinct models of the evolution of human cooperation.

Accident, Sweden.

- Combine game theory and behavioural genetics to understand the genetic basis of phenotypic behavioural heterogeneity in humans.
- Locate genetic correlates of behaviour in strategic interaction, with behavioural evidence from behavioural game theory.
- Identify both the pro-social and anti-social aspects of human cooperative tendencies.
- Develop a new approach to organisational governance, public policy and economic incentives taking into account the cooperative nature of humans.
- Publish results in high-impact journals and international meetings.

SOCCOP's research strategy rests on shared theoretical assumptions that establish the common framework of the proposed research activities. These assumptions are the following:

- Human society is the product of an evolutionary dynamic. While our species is by far the most advanced among the variety of social species to have evolved, it is subject to the same deep evolutionary principles. This means that the proximate mechanisms of human behaviour are likely to be the product of ultimate evolutionary mechanisms, and are likely to be revealed by a thorough analysis of both the continuity and the rupture of human behaviour in comparison with that of other species.
- Human society is a complex adaptive system. This means that it is likely to be understood not by one overarching model, but by a variety of interrelated models, some highly analytical and mathematical, others agent-based, and still others historical and ethnographic.
- Human society is the product of gene-culture co-evolution, culture not only being the *differentia specifica* of humanity, but also the central environmental dimension accounting for the unique ensemble of genetically based capacities for cognition, communication, emotion and even aesthetics.
- In place of the rational actor model, we will adopt the more general beliefs, preferences and constraints (BPC) approach, both because of the centrality of the socially produced nature of beliefs and preferences (overlooked in classical game theory) and because the term 'rational' is irremediably saddled with misleading connotations to which we do not ascribe.

The following are the main points in the proposed framework for unifying the behavioural sciences. Two major categories: (1) evolution; and (2) game theory, cover ultimate and proximate causality. Under each are subcategories that relate to overlapping interests of two or more behavioural disciplines:

1. Evolutionary perspective

Evolutionary biology underlies all behavioural disciplines because *Homo sapiens* is an evolved species whose characteristics are the product of its particular evolutionary history.

1a. Society as a complex adaptive system:
Understanding human society requires a combination of analytical model building and testing, agent-based modelling and testing, and such non-analytical scientific endeavours as ethnographic, cultural and biographical research. To capture correctly the interplay of analytical and synthetic studies, we must recognise that human society is, quite literally, a complex adaptive system. A complex system consists of a large population of similar entities (in our case human individuals) who interact through regularised channels (e.g. networks, markets, social institutions) with significant stochastic elements, without a system of centralised organisation and control (i.e. if there is a state, it controls only a small fraction of all social interactions and itself is a complex system). A complex system is adaptive if it evolves through some evolutionary (e.g. genetic, cultural, agent-based silicon) process of hereditary reproduction, mutation and selection. To characterise a system as 'complex adaptive' does not explain its operation and does not solve any problems. However, it suggests that a wide variety of research tools, often considered as antithetical to one another, are likely to be jointly effective. Such novel research tools are needed because a complex adaptive system generally has emergent properties that cannot be analytically derived from its component parts. The complex adaptive nature of human society explains why the PIs are concerned with agent-based models of cooperation and communication and why anthropological evidence is prominent in many accounts.

1b. Gene-culture co-evolution:
The centrality of culture and complex social organisation to the evolutionary success of *Homo sapiens* implies that individual fitness in humans will depend on the structure of cultural life. Obviously, since culture is influenced by human genetic propensities, it follows that human cognitive, affective and moral capacities are the product of a unique dynamic known as gene-culture co-evolution. This co-evolutionary process has endowed us with preferences that go beyond the self-regarding concerns emphasised in traditional economic and biological theory, and embrace such other-regarding values as a taste for cooperation, fairness and retribution, the capacity to empathise, and the ability to value such constitutive behaviours as honesty, hard work, toleration of diversity, and loyalty to one's reference group.

1c. Imitation and conformist transmission:
Cultural transmission generally takes the form of conformism: individuals accept the dominant cultural forms, ostensibly because it is fitness-enhancing to do so. While adopting the beliefs, techniques and cultural practices of successful individuals is a major mechanism of cultural transmission, there is constant cultural mutation and individuals may adopt new cultural forms when they appear to better serve their interests. One might expect that the analytical apparatus for understanding cultural transmission, including the evolution, diffusion and extinction of cultural forms, might come from sociology or anthropology, the disciplines that focus on cultural life, but such is not the case. Both fields treat culture in a static manner that belies its dynamic and evolutionary character. By recognising the common nature of genes and culture as forms of information that are transmitted intergenerationally, biology offers an accurate analytical basis for understanding cultural transmission.

1d. Internalisation of norms:
In sharp contrast with other species, human preferences are socially programmable. Culture thus takes the form not only of information allowing superior control over nature, but also of norms and values that are incorporated into individual preference functions through the sociological mechanism known as socialisation and the psychological mechanism known as the internalisation of norms. Surprisingly, the internalisation of norms, which is perhaps the most singularly characteristic feature of the human mind and central to understanding cooperation and conflict in human society, is ignored or misrepresented in the other behavioural disciplines, anthropology aside.

2. Game theory

The analysis of living systems includes one concept that does not occur in the non-living world, and is not analytically represented in the natural sciences. This is the notion of a strategic interaction, in which the behaviour of agents is derived by assuming that each is choosing a fitness-relevant response to the actions of other agents. The study of systems in which agents choose fitness-relevant responses and in which such responses evolve dynamically, is called evolutionary game theory. Game theory provides a transdisciplinary conceptual basis for analysing choice in the presence of strategic interaction. However, the classical game-theory assumption that agents are self-regarding must be abandoned except in specific situations (e.g. anonymous market interactions), and many characteristics that classical game theorists have considered deductions from the principles of rational behaviour, including the use of backward induction, are in fact not implied by rationality. Evolutionary game theory, whose equilibrium concept is that of a stable stationary point of a dynamical system, must thus replace classical game theory, which erroneously favours subgame perfection and sequentiality as equilibrium concepts. I will interact with the other PIs to bring out the game-theoretic casting of their projects and results.

2a. The brain as a decision-making organ:
In any organism with a central nervous system, the brain evolved because centralised information processing entailed enhanced decision-making capacity, the fitness benefits more than offsetting its metabolic and other costs. Therefore, decision making must be the central organising principle of psychology. This is not to say that learning (the focus of behavioural psychology) and information processing (the focus of cognitive psychology) are not of supreme importance, but rather that principles of learning and information processing make sense only in the context of the decision-making role of the brain.

2b. The rational actor model:
General evolutionary principles suggest that individual decision making can be modelled as optimising a preference function subject to informational and material constraints. Natural selection leads the content of preferences to reflect biological fitness. The principle of expected utility extends this optimisation to stochastic outcomes. The resulting model is called the 'rational actor' model in economics, but I will generally refer to this as the beliefs, preferences and constraints (BPC) model to avoid the often misleading connotations attached to the term 'rational'.

While accepting that the above framework may entail substantive reworking of basic theory in a particular discipline, it is expected that much research will be relatively unaffected by this reworking. For instance, a psychologist working on visual processing, or an economist working on futures markets, or an anthropologist tracking food-sharing practices across social groups, or a sociologist gauging the effect of dual parenting on children's educational attainment, might gain little from knowing that a unified model of decision making underlay all the behavioural disciplines. But, it is suggested that in critical areas such as the relationship between corruption and economic growth, community organisation and substance abuse, taxation and public support for the welfare state, and the dynamics of criminality, researchers in one discipline are likely to benefit greatly from interacting with sister disciplines in developing valid and useful models.

Individual Projects (IPs)

A framework for the unification of behavioural sciences

Herbert Gintis, Central European University (CEU), Budapest (Principal Investigator)

Funding Agency: Hungarian Scientific Research Fund (OTKA), Hungary

The various behavioural disciplines, including economics, biology, anthropology, sociology, psychology and political science, model human behaviour in distinct and incompatible ways. Among the characteristic incompatibilities are the treatment of the individual as rational and self-interested in economics and biology, and the treatment of human social institutions as mechanisms fostering efficient cooperation among self-interested individuals. This contrasts sharply with the view of the individual in social psychology, sociology and anthropology as a repository of cultural values, and the treatment of cooperation in society as a product of the internalisation of cultural norms. Another major incompatibility, cutting across disciplinary lines in the same way, is the use of game theory and decision theory in economics and biology to explain human behaviour, and the virtually complete rejection of these tools in the other disciplines.

These incompatibilities can be described as a failure of the behavioural sciences, not because discrepancies exist, but because behavioural scientists have failed to address and adjudicate their differences. This project aims at eliminating some of these interdisciplinary contradictions and at permitting a more seamless integration of interdisciplinary research, applying some of the conclusions of the Project Leader's previous work. The expected result of the project would be a book on the topic of the unification of the behavioural sciences, with contributions by authors in different fields, including neuroscience, anthropology and cognitive psychology.

Institutional niche construction and the evolution of a cooperative species

Samuel Bowles, Santa Fe Institute (Principal Investigator)

Funding Agency: National Science Foundation (NSF), USA

This project focuses on explaining how distinctive human institutions (within group reproductive levelling and between group lethal competition) may have facilitated the evolution of (within-group) altruism and cooperation among early humans as well as out-group hostility. The project also explores the implications of recent advances in behavioural economics and cognitive psychology for improving the governance of cooperative and trading relationships in firms, neighbourhoods and nations.

Evolutionary game theory and agent-based simulations as well as empirical sources are used to model two of the ways that humans have created niches allowing for the evolution of social preferences. The first are strong insider/outsider distinctions and frequent intergroup conflict, and the second are systems of within-group reproductive levelling by means of resource sharing (and related variance reduction practices). Taken together these institutions represent a constructed niche facilitating the evolution of the social preferences supporting within-group cooperative behaviours. The analytical methods will follow the gene-culture co-evolution framework outlined by Herbert Gintis.

These models will be subjected to empirical tests for plausibility using what is known from archaeological, climatic, genetic, linguistic and other data about conditions during the late Pleistocene. The approach will model the co-evolution of group-level traits (the institutions in question) and individual traits (altruistic punishment and other social preferences). The work is important because while the essential role of these institutions in human evolutionary processes is recognised, their emergence, persistence and proliferation are not well understood. Further, the project explores the implications of the cooperative nature of our species for the design of public policies and institutions. Policies and institutions that are designed to work well if citizens and economic actors are entirely self- interested will not generally be the best institutions for a heterogeneous population in which significant numbers are motivated by strong reciprocity motives, inequality aversion or other social preferences.

Proximate explanations for human and animal cooperation

Cristiano Castelfranchi, Institute of Cognitive Sciences and Technologies, CNR, Rome (Principal Investigator)

Funding Agency: National Research Council (CNR), Italy

This project unites an interdisciplinary group of cognitive and social scientists from cognitive psychology and distributed artificial intelligence who study the psychological mechanisms behind cooperative behaviour both in non-human and human primates.

In non-human primates, reciprocal altruism may be based more on the triggering of 'positive' emotions by

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Grooming in wild bearded capuchin monkeys (*Cebus libidinosus*) in Boa Vista, Piauì, Brazil.

the receipt of altruistic behaviours than on any mechanism of book-keeping. This hypothesis has rarely been explicitly tested and then only in dyadic contexts. This project will test this in larger groups in more natural settings in which partner choice plays a significant role. Experiments in this area will be complemented by ethological captivity and field studies. In humans, reputation and its transmission, for instance via gossip, allow people to use indirect informational reciprocity in partner selection and social control in large open non-kin settlements, where agents can be preceded by their reputation. This project will explore how this critical type of knowledge is processed in the agents' minds, how social structures and infrastructures are related to it, and consequently how it affects agents' behaviour.

Further, the project explores the 'psychology of norm compliance' by unravelling the cognitive prerequisites to comply with a norm. Thus, for instance, it will be studied how 'respect for authority' can function as a cognitive process leading to the adoption of a particular course of action and how blaming functions in order to enforce conformity. Two strategies of blaming (direct and indirect forms of blaming) will be modelled and their effects disentangled.

Finally, the project explores several possible hypotheses about the evolutionary origins of the human cooperative mind with its sophisticated cognitive abilities. In particular, it investigates (1) the possible co-evolution of authority and subject psychologies underlying norm issuing and norm compliance; (2) the role of deontic teaching in cultural transmission; and (3) the peculiar role of the human fertilisation system in the evolution of human mechanisms for complex cooperation.

High-level neuronal architectures for cooperation and communication

Michel Kerszberg, Pierre et Marie Curie University, Paris (Principal Investigator)

Funding Agency: National Centre for Scientific Research (CNRS), France

This project aims to discover, by the combination of rational and evolutionary design of neuronal networks, what kinds of neural network properties allow the emergence of cognitive/computational capacities that underlie various forms of cooperation and communication among simulated agents.

For cooperation, the project asks whether, under appropriate selective conditions, and with appropriate neural and populational pre-adaptations such as planning and decisional abilities, the emerging architectures are capable of recognising individuals (from behaviour or other external features) and that the agents become genetically biased towards strong altruism.

The project posits that the architectures emerging from this co-evolution of genes and culture are the proximate causes for the altruistic behaviour, while the necessary reciprocity would imply the existence of appropriate niches where the behaviour becomes a norm. The project aims to show that a highly coordinated, synergistic collaborative task such as cooperative hunting, leads to agents with shared attention/intentionality and that without emerging communication the task cannot be fulfilled as efficiently. The semantic content of the communication, constrained by the cooperative situation, is expected to lead to not only symbolic reference but also to at least rudimentary syntax. Reverse engineering of the emerging architectures can lead to testable propositions about the human condition.

The way in which biological, and in particular neural architectures, are related to information-processing abilities is subtle. It has been shown that, contrary to what is sometimes glibly asserted, the coding capacity of the genetic system is huge, leaving open the question of why certain abilities are 'innate' while others 'need' to be 'learned', sometimes with input from congeners, pedagogy, work sharing and cooperation. In spite of much work, little progress has been achieved. In part this is due to the excessive cost of building actual robots to perform the work, when the necessary environment can much more cheaply be simulated. This project builds on Michel Kerszberg's framework, within which the interactions between intrinsic brain developmental factors and environmental stimulatory factors (including congener behaviour) will be studied.

The behavioural genetics of trade and cooperation

Arcadi Navarro, Pompeu Fabra University, Barcelona (Principal Investigator)

Funding Agency: Ministry for Education and Science (MEC), Spain

Intricate cooperative behaviours and the ability to develop complex trade systems have been key to the ability of humans to adapt to many different environments and changing circumstances along our evolutionary history. The project asks whether genetic factors contribute to diversity in these traits. It explores how these interact with each other and with environmental factors. How do these factors differentiate humans from other primates? The central goal of this project is to provide the first genome-wide scan of genetic factors influencing cooperative and trade behaviour.

There is an increasing amount of compelling evidence that behavioural differences between humans could be, in part, the outcome of genetic variation, just as it is the case for many other complex traits. The evidence coming from humans is reinforced with much more detailed knowledge about the genetic basis of animal behaviour. There are, however, many other examples, including cases in which the behaviour of an individual within a group depends on its genotype. Detailed knowledge of the genetic factors underlying standard behavioural variability within a species is not available for humans. This is paradoxical, not only because humans are the species for which behavioural studies are more abundant and detailed, but also because the study of the genetic architecture of complex traits has registered enormous advances over the last decade.

The project intends to run a genome-wide reach for genetic markers associated to human behavioural variability. Behavioural experiments, sample collection and genetic analysis will be performed in close collaboration with Ernst Fehr's laboratory in Zürich (Switzerland). The project will measure complex behavioural traits in detail in a sample of around 600 or more individuals. Exhaustive questionnaires will be used to register self-reported behavioural measures of traits such as altruism, empathy, nurturance or aggression. In addition, laboratory experiments including standard games such as the ultimatum game or the prisoner's dilemma will provide direct measures of an individual's behaviour under controlled circumstances. The project will generate a baseline of candidate regions where genes linked to human behaviour lie. These genes will be subject to further functional and comparative genomics studies.

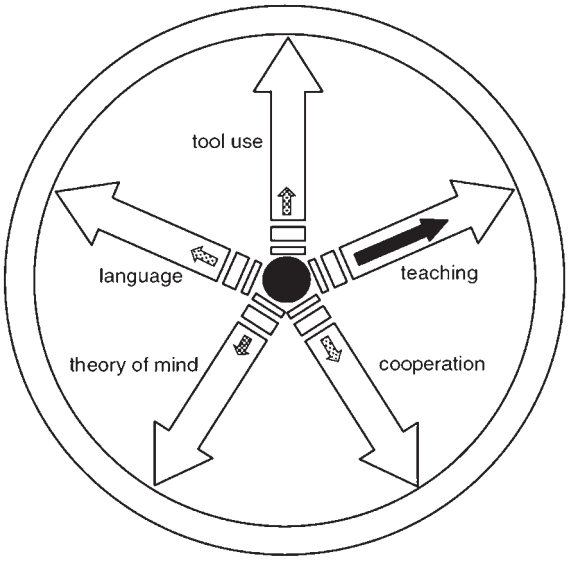
In silico evolution of cooperation and communication

Eörs Szathmáry, Eötvös Loránd University (ELTE), Budapest (Principal Investigator)

Funding Agency: Hungarian Scientific Research Fund (OTKA), Hungary

At the heart of this project lies the question of how neuronal networks can be determined by relatively few genes so that complex cognitive traits show significant heritability. This project takes an in silico approach to the problem with the aid of the Evolutionary Neurogenetic Algorithm (ENGA) that allows the selection of neuronal agents embedded in a simple or complex simulated physical and social environment. The project will identify scenarios according to which complex communication or strong cooperation emerges, and will analyse the correlated neuronal and genetic changes in the successful agents. It will seek synergies between levels in forms of cooperation and forms of communications.

The goal of the project is to reverse-engineer the emerging networks. Since complex communication and complex cooperation go hand in hand, cooperative, simulated situations will be encased in a game-theoretical framework. Since the communicating neuronal



The co-evolutionary wheel and the human adaptive suite. In this example, direct selection on genetic variation is on teaching/docility (black arrow) but this gives some improvement, to varying degrees, in other dimensions (patterned arrows) as well. Szathmáry, E. 2007. Towards and understanding of language origins. In M. Barbieri (ed.), Codes of Life, Springer-Verlag, pp. 283-313.

agents will not only learn but also their learning capacity will undergo genetic evolution, this project is an eminent case of simulated gene-culture co-evolution. A major challenge is the study of the emergence of language which has been identified as the last major genetic transition. Language is a novel inheritance system with indefinitely large hereditary potential in humans. The question is how a transition from protolanguage to language is possible in a society of evolving agents.

This project contributes to the development of a new neurogenetic system based on genetic algorithms and neuronal networks that allows co-evolution of motor and communication behaviour and the neural architecture of the agents and an object-oriented software framework to provide the required flexibility. This system offers researchers a fine control over biological detail in their simulations. This model is a recombinant of evolutionary robotics and the evolutionary approach to neuronal networks with indirect encoding, with some key new elements, such as topographical network architecture.

Associated Projects (APs)

The behavioural genetics of risk, time and social preferences

Ernst Fehr, University of Zürich, Switzerland (Associated Partner)

Genetic factors appear to play a decisive role in behaviour. There is evidence that the correlation of behaviours among homozygous twins is much larger, suggesting a significant role for genetic factors in risk, time and social preferences. This project collaborates with Arcadi Navarro's team, whose interests also cover the genetic and evolutionary backgrounds of basic human behaviours.

Much work in behavioural genetics is not based on observed behaviour but on reported behaviour, i.e. on behaviour reported in questionnaires. In contrast to this approach, this project intends to measure risk, time and social preferences directly in laboratory experiments. Experimental economics and experimental psychology provides a rich and fertile menu of behavioural tasks, enabling the measurement of this important dimension of behaviour.

The project envisages running experiments with about 600 people. Saliva samples will be collected in order to determine associations between genes and behaviours. A subsample of heterozygous and homozygous twins will also be included in the experiments.

The first task is to define stable behavioural phenotypes in terms of risk, time and social preferences. This task will be solved using behavioural experiments that measure a variety of behaviours of the same subjects across time and across different experiments. Then, after the stable phenotypes are assessed, experiments on risk, time and social preferences with 600 subjects will be conducted. The DNA of 300 subjects will be analysed on a large scale. Based on the results from this sample – in terms of correlations between specific genes or gene clusters with the measured behaviours – it is predicted that similar correlations will hold in the whole sample and in the second part of the sample. If this turns out to be true, the project will have found strong evidence that the observed correlations are not spurious. Finally, based on the specific genetic findings, e.g. an involvement of the dopaminergic and the serotonergic system in risk, time or social preferences, it is planned to conduct pharmacological experiments with the relevant agonists and antagonists.

A meeting led by pastoral elders (*Laikipia Maasai*), central Kenya.

Metacognition and decision making under risk: individuals and groups

Alex Kacelnik, University of Oxford, UK (Associated Partner)

This project focuses on theoretical and empirical analysis of individual and group decision making under risk, with an emphasis on the role of subject-generated uncertainty. Dealing with metacognition in the context of risk has the attraction of being strongly multidisciplinary: ideas from economics, evolutionary theory, behavioural ecology and psychology contribute to define the problem and to generate the experimental approach. Adding the supra-individual dimension associated the problem with the functional analysis of cooperative behaviour and group functioning.

Although initially the ability of thinking about cognitive dimensions was assumed to be an exclusively human feature, decision-making research involving metacognition acquired new momentum when researchers brought the problem to non-human subjects. Dealing with non-human subjects makes a big difference because it calls for methods of assessing metacognitive information without self-reporting and without extrapolating from observed choices (as the goal is to establish the relationship between both). Inspired by experimental protocols developed in animal research on metacognition, this project returns to humans, integrating metacognition into issues related to risky decision making.

A further dimension of the problem refers to supra-individual decision making. In many situations (e.g. grant allocation by committees), groups combine knowledge and utility functions to take joint decisions. In doing this, there is a collective cooperative evaluation and weighting of group members' expertise, and individual members (ideally) regulate the forcefulness of their arguments according to metacognitive judgments. The aim of the project is to quantify this process by employing our software in experiments involving groups and in situations where several subjects contribute knowledge and one decides (many-to-one), as well as situations where one subject produces information and several reach a decision (one-to-many). Sharing information and decision power is likely to have been a major issue in the development of cooperation in animal and human groups. This project proposes to examine rather precisely how this sharing operates.

The development of cooperative norms

Ruth Mace, University College London, UK (Associated Partner)

This project analyses the ecological variation between communities belonging to the same cultural group, in order to tease apart the extent to which individual or population level differences influence the development of prosocial norms. Through these analyses the project will throw light on the mechanisms of cultural evolution, which help assess the ecological plausibility of models developed in this project. Key questions are: do properties associated with social organisation (e.g. distribution and accessibility of resources, degree of immigration/emigration, population size) affect the norms adopted by a group? Does the behaviour of individuals in economic games reflect a dispositional or context specific strategy? What are the processes that drive 'cultural evolution' of prosocial behaviour? What are the time scales over which they occur? Does the degree of cooperative clustering in a social group affect networking and information flow, which may in turn feed back into the nature and degree of cooperation?

The effect of group size is of key interest as many evolutionary models assume that large group size inevitably weakens cooperative behaviour whereas many economists do not make that prediction and one model predicts that cooperation can emerge more easily in large groups. This project aims to identify how group size and migration patterns influences cooperative norms in an Indian population comprising many subcommunities of varying sizes.

Individuals have different costs and benefits associated with cooperation that are likely to be influenced by such variables as their relatedness to the rest of the group. The project examines determinants of individual variation responses to ultimatum and other games to determine the relative importance of group properties discussed above versus individual costs and benefits.

New immigrants into a group, such as women moving into the community to marry, may behave according to the norms of their natal village or their new village,

or this may be a function of the length of time in which they have inhabited the new village. First and second generation immigrants into a community will also be compared for temporal differences in prosocial norms.

Network analyses will be used to identify important attributes of the social structure of communities and whether these account for any of the observed variation between communities. We will use economic games, primarily the ultimatum game and public goods games, to measure prosocial behaviour in different communities belonging to the same ethnic group.

The evolution of moral behaviour

Robert Rowthorn, Cambridge University, UK (Associated Partner)

This project, conducted in cooperation with Rodriguez-Sickert and Ricardo Guzman (Chile) has two components: one theoretical and the other experimental. In current models, group size is exogenous. The puzzle of cooperation in large groups is unlikely to be solved until group size itself is allowed to co-evolve along with cooperation. People get together for a reason: to seize the gains of cooperation and specialisation. Large groups benefit from scale economies. They command larger armies than small groups and allow greater degrees of specialisation. However, there are forces operating against larger groups. The increasing advantage of free-riding (due to monitoring problems) is one such force. Another is the increasing difficulty of coordination in a large society. Is the emergence of hierarchies a solution that human societies have found to cope with these problems?

Migration gives rise to problems which are often similar to those large groups size. Benefits deriving from cultural diversity, such as innovation, may be outweighed by communication difficulties and parochial loyalties that obstruct group level collective action. For this reason, intergroup competition may confer an advantage upon groups that limit diversity by severely restricting immigration from other groups, or else by promoting the rapid assimilation of immigrants. The evolution of such social mechanisms may have genetic counterparts in the form of a high propensity to conform or a high propensity towards xenophobia.

The project asks the question: how do social learning and social structure co-evolve? A growing experimental body of evidence points to how alternative forms of social learning are used to obtain information from an environment detached from social interaction. However, how these mechanisms co-evolve in an environment in which individual decisions involve strategic interaction with others has not been explored. This project aims to set up experimental micro-societies that play the societal game under different information conditions concerning: (1) information about role model payoff: at the end of every round each player is informed about the payoff of a randomly selected role model; and (2) information about behavioural frequencies: at the end of every round all players are informed of the frequencies of each kind of behaviour.

People in SOCCOP

Project Leader

Herbert Gintis, Central European University (CEU), Budapest, Hungary

Principal Investigators

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Cristiano Castelfranchi, Institute of Cognitive Sciences and Technologies, CNR, Rome, Italy
Michel Kerszberg, Pierre et Marie Curie University, Paris, France
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TECT Networking Activities

TECT Networking Activities

Launch Conference EUROCORES Programme TECT (The Evolution of Cooperation and Trading) Collegium Budapest, Budapest (HU), 4-7 July 2007

[Convenors: **Eörs Szathmary/Rüdiger Klein**]

The EUROCORES Programme TECT (The Evolution of Cooperation and Trading) held its launch conference in July 2007. Collegium Budapest, one of the select groups of European Institutes for Advanced Study, provided a welcoming and stimulating environment for the wide-ranging, interdisciplinary interactions during the four-day conference.

EUROCORES programmes coordinated by the humanities have established the highly successful practice of organising launch conferences in order to stimulate, early on in the process of programme building, the emergence of networking activities between the often strongly interdisciplinary Collaborative Research Projects (CRPs). In this case, CRPs presented included: Cooperation in Mutualisms: contracts, markets, space, and dispersal; Cooperation in Corvids, The Social and Mental Dynamics of Cooperation; Dynamic Complexity of Cooperation-Based Self-Organising Networks in the First Global Age; and Sustaining Eco-economic Norms for a Sustainable Environment.

TECT is the third EUROCORES programme, after BOREAS and CNCC, to include among the participating funding agencies the National Science Foundation of the USA (NSF). Given that TECT researchers are based in all five continents (Europe, America, Asia, Africa, Australia) the need for an initial opportunity for all researchers from all teams to meet and interact was so much appreciated that the request was made for such general meetings to take place on a regular basis. The conference programme is witness to the wide range of topics treated under this EUROCORES programme. The conference succeeded in triggering a series of follow-up meetings, which are listed below.

The launch conference also laid the foundation for sustained collaboration of TECT with a number of large-scale initiatives funded under the European Commission's Sixth Framework Programme (FP6), notably GEBACO (a NEST Pathfinder Initiative entitled: 'The genetic basis for cooperation') and INCORE ('Integrating Cooperation Research across Europe –- Coordination Action'), which will lend added impact to the TECT research agenda.

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Reciprocal altruism using the swing.

"Studying Challenges of the Global Commons" TECT workshop hosted by The Beijer International Institute of Ecological Economics, Stockholm (SE), 5-7 September 2007

[Convenors: **Daniel Rubenstein/Aart De Zeeuw**]

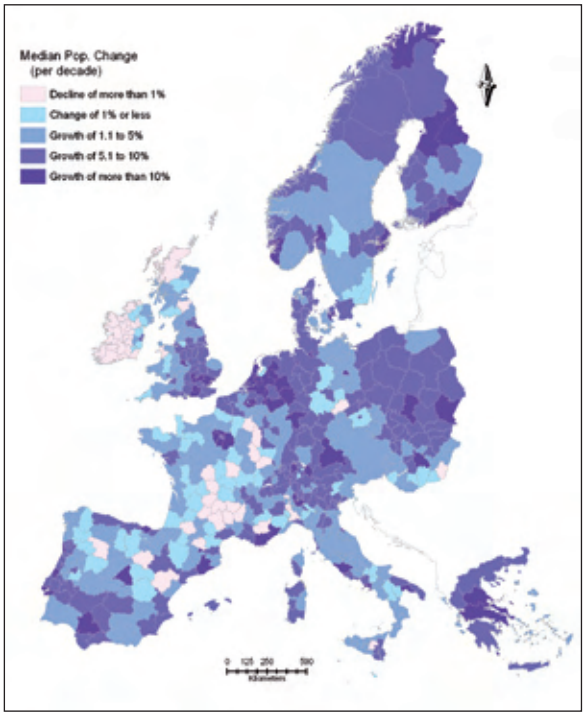
TECT researchers and others debated ideas on the evolution of cooperation in relation to problems of managing the global commons. Two TECT Collaborative Research Projects (SENSE, led by Simon Levin and Daniel Rubenstein, Princeton, and SOCCOP, led by Herbert Gintis, Budapest) focus on unravelling the rules that govern the evolution of human cooperative behaviour. The work of DynCoopNet, a team composed of researchers from the Iberian Peninsula, India, Mozambique, Australia and the USA, provided a stronger historical dimension, focusing on the development of norms, their enforcement, and what distinguishes situations in which trust and cooperation build from those in which cooperation breaks down or never develops.

Other TECT-related projects, such as REPSOCBIOL (The Role of Reputations in Human Cooperation: bridging social and biological approaches), also gave presentations. The workshop allowed members of the teams to interact with researchers based at the Beijer Institute who focus on global commons governance thereby enabling them to expose their proposed modelling and empirical studies to high-level critique. The aim

was to identify strategies that would enhance cooperation and help attenuate 'tragedies of the commons' on the local, regional and global scale.

The SENSE project, led by Simon Levin, states: 'We live in a global commons in which the actions we take affect the general welfare, for good or for bad, but in which the costs and benefits realised by individual agents do not reflect fully those broader elements. Individual agents, whether these be people or institutions or nations, act in their own self-interest, often at cost to societies, the biosphere, and hence to the global community and future generations… Evolutionary theory provides deep insights into how cooperation and collective action can emerge. Animal societies are typically held together by one of the following 'social glues': altruism directed towards kin, reciprocal altruism and mutualism among non-relatives; and coercion. Alone or in concert these relationships lead to collective action that benefits all members of societies as long as they [the societies] are small, the network of relationships is small and interactions among members are largely direct. How these forces scale up for larger collectives where relationships are weak, especially when connections become indirect, is less well understood. Even less explored is the extent to which "mutual coercion, mutually agreed upon" can arise through natural and cultural evolution.'

There is scope for collaboration and exchange on the theme of 'commons' with another humanities-led EUROCORES programme, "Inventing Europe: technology and the making of Europe (1850 to the present)", which had included a recommended proposal, "Inventing and Governing Transnational Commons in Europe".



European population change, 1870-2000.

"A Place in Europe": A tri-EUROCORES meeting launches a strategic initiative on time-enabled geographical information systems (H-GIS)
Barcelona (ES), 30 November–2 December 2007

[Convenors: **Jordi Marti-Henneberg/Rüdiger Klein**]

Researchers from three EUROCORES programmes in the humanities – Inventing Europe, TECT and BOREAS – met in Barcelona with other networks funded by FP6 and other European as well as US-American, Canadian and Russian initiatives to discuss a strategy for the development of historical GIS in the context of transnational research infrastructures. The meeting was convened by ESF and a Spanish-led Collaborative Research Project in the EUROCORES programme "Inventing Europe" under Project Leader Jordi Marti-Henneberg, University of Lleida.

Geographers, ecologists, demographers and many others whose data are (or can be) spatially referenced have come to rely on GIS as a powerful analytical and communication tool. Transport and populations historians recognised early on that time-enabled applications allow compelling visualisations of highly structured, quantitative data. Environmental historians can use data thus mapped for example to analyse multiple factors contributing to changing fishing and food patterns throughout history or to the multifarious histories of river courses.

All presentations during the workshop concurred on the assessment that possibilities to develop and use versatile H-GIS (or historical GIS) tools would enhance collaborative (and often comparative) research such as is envisaged in most European and other international frameworks. Jack Owens of the University of Idaho, Principal Investigator in TECT writes: 'GIS offers historians who specialise in the histories of different places and chronological periods an effective vehicle for collaborative research among themselves and for involving researchers from other disciplines' (*ArcNews*, XXIX, 2). It is against this background that this tri-EUROCORES meeting decided to launch a strategic initiative to argue the case for strengthening coordinated, transnational investment in and work on time-enabled geographical information systems.

A working group will continue canvassing the communities and the researchers will reconvene during conferences and workshops in Lancaster (UK) and Lisbon (PT) in the course of 2008 to refine their project, in order to gather support for a document that can serve as a basis for a science policy briefing.

"Towards a Unifying Theory of Cooperation and Mutualism", TECT workshop Oeiras (PT), 8-11 January 2008 (co-sponsored by the Gulbenkian Foundation)

[Convenor: **Francisco Dionisio**]

TECT, through its research and networking funding, offers opportunities for building closer links between empirical, theoretical and modelling work in cooperation research.

This workshop started from the statement that cooperative interactions occur in both sentient and non-sentient organisms. Typically, different sets of models are used to explain cooperation in each domain. Workshop participants set out to explore how the concept of 'partner choice' can be applied to cooperation across the gradient of sentience.

Hitherto, it has been the case that the explanations of cooperation between sentient organisms and cooperation between non-sentient organisms have been largely independent scientific pursuits, even if studies are limited to interactions between non-kin. In sentient organisms, the leading explanations for cooperation involve memory and recognition, in which the probability of future cooperative interactions depends on having demonstrated cooperativeness in previous interactions, either directly to the prospective partners (direct reciprocity) or to third parties visible to the prospective partners (indirect reciprocity). The prospect of losing cooperative partners in the future helps to enforce cooperation in current interactions. Workshop contributions collected these kinds of mechanisms under the general term 'partner choice'.

The Collaborative Research Project COCOR (Cooperation in Corvids) CRP uses corvids (crows, ravens, jackdaws, rooks, jays etc.) as their model system for studying the contribution of cognitive processes to cooperative behaviour. While it was emphasised that cognition-based strategies are not necessarily different from non-cognition-based strategies at the conceptual level, the underlying mechanisms are very different and give rise to more inter- and intra-individual variation than can be expected in non-sentient organisms. COCOR emphasises aspects such as attention to the partner's behaviour, gaze following, deception, in dyadic cooperative interactions as well as in interactions in which the subjects can exert partner choice. These cognitive aspects of cooperation are studied in spontaneously occurring forms of cooperation, such as food sharing and coalition formation, as well as cooperation experiments.

The robotics team in COCOR takes a complementary approach to modelling by trying to create embodied agents using artificial intelligence techniques. Interactions between this group and both the economists and the empirical biologists are important in order to develop robotics as a central module in TECT, which can provide a stepping stone between computer models and living subjects.

In contrast, the Collaborative Research Project BIOCONTRACT (Cooperation in Mutualisms: contracts, markets, space, and dispersal) studies cooperation between (primarily) non-sentient organisms belonging to different species; i.e. mutualisms in the terminology of ecology. There is, by definition, no possibility of memory and recognition, and thus no possibility of demonstrating or ascertaining cooperativeness before an interaction takes place, such as is thought to occur in corvids. Moreover, many mutualistic interactions take place only once, or outcomes cannot be monitored, such as in seed dispersal or pollination. In such cases, do mutualistic hosts, typically plants, bias visitation toward more beneficial visitors? This would be a form of partner choice. In other mutualistic interactions, it is known that hosts can indeed monitor the outcomes of symbiont behaviour and punish or reward on the basis of that behaviour. This is also partner choice, albeit of a different kind.

This cross-CRP meeting helped to share different concepts of partner choice and to understand how the different versions are applied to corvids and to mutualisms. It was found that it would be useful to consider if the many versions of partner choice can be unified, so producing a bridge between the two kinds of cooperation. Such an exchange was facilitated by the fact that both BIOCONTRACT and COCOR emphasise the use of economic models in the study of biological systems. It was found useful for economists in both groups to meet at an early stage of CRP formation in order to coordinate their approaches.

"Trust, Reputation, Defectors, and Sustaining Social Norms: studying spatially complex cooperative relationships", TECT Workshop, Porto (PT), 26-29 March 2008

[Convenors: **Amelia Maria Polonia da Silva/Jack Owens**]

Multidisciplinary collaboration has the potential to generate radically new scientific ideas, and the DynCoopNet project offers TECT CRPs research approaches that

are not well represented in other TECT projects. In general, there is a lack of dynamic, non-linear models of cooperation in commercial relationships, which are multilateral and spatial. DynCoopNet brings to TECT: (1) a large body of ethnographic, historic data about cooperation; (2) economists and geographers who are experts in non-linear dynamics and spatial modeling; and (3) geographic information scientists working to reconceptualise Geographic Information Systems (GIS) in order to organise and analyse dynamic spatial data. At the same time, other TECT projects hold greater expertise in various forms of game theory and modelling based on the results of experiments with games; institutions and cognitive psychology; group ecology; and evolutionary theory in biology.

This workshop aims to build the bases for collaboration between different TECT projects by concentrating on common concerns, such as reputation, the maintenance of social norms, partner choice, networks, information distribution and complex adaptive systems. Several of the workshop's central themes have been crafted to develop joint publications involving scientists from different TECT projects, including a CRP that had been recommended, but did not receive any funding (REPSOCBIOL). The two themes expected to provide a basis for one or more joint publications each are: reputation, group augmentation, network flexibility and cheaters and defectors in global trading networks.

The workshop will also help to better inform participants about DynCoopNet research which it is hoped will shape future collaboration and joint publications: (1) Reputation and Social Norms: letter-writing and information distribution (about research on two rare types of source, which provide valuable insights into the perspectives of people living within a system different from our own); (2) Modelling from Economic and Ecological Data from the First Global Age; Temporal GIS, Space-Time Representation of Cooperation Networks, Spaciotemporal Analysis, and Data Mining; and (3) Maps as Sources of Historic Data.

"The Social and Psychological Dynamics of Cooperation and Punishment", TECT workshop, Barcelona (ES), 25-27 April 2008 (co-sponsored by UAB's Social Brain Chair and the PRBB)

[Convenor: **Arcadi Navarro/Herbert Gintis**]

This workshop brought together TECT and local researchers interested in temporal aspects of social and mental dynamics of cooperation. Participants focused on determining and studying cooperation-related time-extensive regularities over human history. Members of the SOCCOP and DynCoopNet teams and others presented ideas on the evolution of cooperation over time, from the late Pleistocene and early Holocene up to the present time. The SOCCOP groups focuses on unravelling rules that govern the evolution of human cooperative behaviour together with their social and genetic causes, while DynCoopNet focuses on self-organising, cooperative trade networks in the First Global Age (1400-1800).

The DynCoopNet team focuses on issues about the measurement and analysis of cooperation mechanisms to study their enforcement, and what distinguishes situations in which trust and cooperation build from those in which cooperation breaks down or never develops. The workshop is intended as a catalyst for research on the temporal evolution of cooperation and trade.

SOCCOP researchers presented results on modelling social norm development in early humans/hominids and on current measures of social norms in current populations (mostly based on behavioural economics experiments and including Western and other societies). DynCoopNet presented data obtained from historical documentation and the methods and criteria that they are following to determine the appropriate variables to measure economic and social parameters in a space-time comprehensive framework.

The aim of the workshop is to exchange practical information in order to establish comparative parameters to measure social structure in a time-extensive framework. To do so, samples of all behaviour measures in relation to cooperation and trade (cooperation, trust, risk-taking, trade etc.) were examined and selected from different social contexts and historical times. It is intended to establish comparative parameters and methods to measure cooperation and trade behaviours in a time-extensive framework (towards joint models of social evolution).

"Tools of the Trade in Cooperation Research", TECT Summer School, Obernai (FR), 30 August–6 September 2008 (co-sponsored by INCORE)

[Convenor: **Ronald Noë**]

This week-long summer school is aimed primarily at PhD students and those who have recently taken up post-doctoral positions. With a focus on theoretical and methodological approaches, it is designed both for those who specialise in human and those who specialise in non-human forms of cooperation, from molecular biologists to economists and political scientists.

Workshops will be led by specialists from across Europe and there will be an emphasis on improving ongoing projects and facilitating exchange between teachers and students from different disciplines.

The workshop will be open to TECT early career scholars, but others can also apply. Teachers include some of the top-European researchers in the field, such as Eörs Szathmary, Karl Sigmund, and Simon Gaechter.

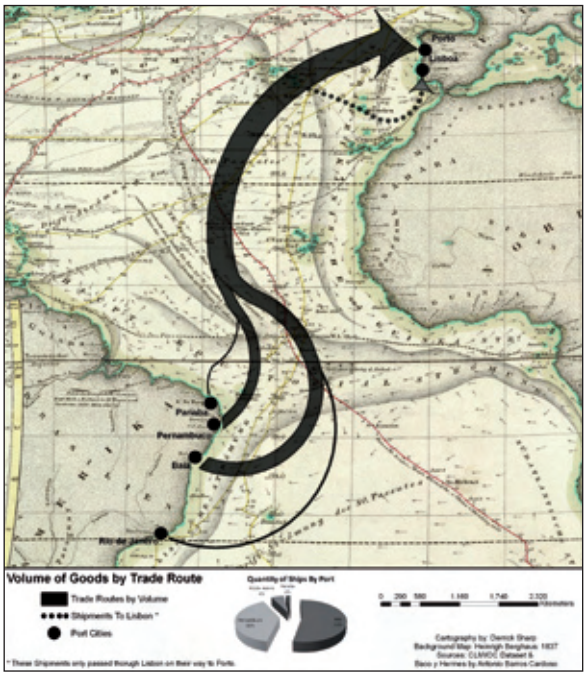
"Visualisation and Space-Time Representation of Dynamic, Non-linear, Spatial Data in DynCoopNet and Other TECT Projects", TECT Strategic Workshop, Madrid (ES), 25-26 September 2008

[Convenors: **Ana Crespo Solana/Jack Owens**]

This strategic workshop aims to strengthen and build collaborative relationships among the TECT projects, all of which will be represented. Participants will be able to enhance their technical abilities to carry out their individual research. A group of world-class experts on various geotechnology and cartographic visualisation fields will present ideas about how to envisage space-time representation within Geographic Information Systems (GIS). Therefore, the workshop will advance all modelling and visualisation within the TECT Programme.

Through this workshop, the specificity of the DynCoopNet project potentially becomes an asset to TECT as a whole, by providing a forum for discussion about space, time and mobility of self-organising cooperation networks of the First Global Age based on different perspectives from geographic information scientists, historical geographers, cartographers, geomatics engineers and computer scientists. As part of its research programme, DynCoopNet places special emphasis on the use of historic cartography as a data source about cognitive understandings of space and their relationship to cooperation in trading activity. Embedded in all of these concerns is DynCoopNet's determination to understand a complex, dynamic, non-linear system and what eventually drove it to instability and transformation. The main research topics are (but not limited to):

- visualisation of network dynamics
- space-time representations and reasoning
- modelling ecological, ethnographic and historical evidence in digital maps
- fractal geometry and non-linear models
- georeferencing and conflation of geometric content of historical maps
- use of GIS for management and analysis of historical data of map libraries.



Brazilian trade: Cartographic representation of imports into Porto from Brazil during the first half of the eighteenth century.

"Money, Altruism and Genes: exploring the genetic basis of cooperative and commercial behaviours", TECT Symposium Barcelona (ES), 20-23 November 2008, includes the workshop "Genetic Basis of Coalition Formation in Non-Human Primates" (with co-sponsorship from GEBACO, INCORE and local sources)

[Convenors: **Arcadi Navarro/Ronald Noë**]

The symposium will bring together most TECT Collaborative Research Projects and other networks studying the genetics of behaviours related to cooperation and trade in Europe and elsewhere (notably: GEBACO and INCORE). Participants will be a select group of experts in genomics, experimental economics, game theory, primatology and ethology. The meeting aims to serve as a catalyst for research in the genetic basis of cooperation and trade. At the TECT launch conference in Budapest, it became clear that better coordination is needed between the initiatives investigating the genetic basis of social behaviours (cooperation, trust, risk-taking, trade etc.) in Europe and elsewhere. Also, many other TECT projects dealing with complex, dynamic, non-linear systems and societies (DynCoopNet, BIOCONTRACT, SENSE) would benefit from the knowledge generated by the study of the genetic architecture of cooperative traits in humans and other primates. Within this broad symposium theme, a workshop will be held on the genetic basis of coalition formation in primates.

The symposium intends to update all participants

on the state of both ideas and ongoing research in the genetic basis of social behaviours under diverse points of views: from classical twin studies, to whole genome scans, including candidate gene approaches, gene expression analysis and theoretical modelling of social behaviours. At a more practical level, participants will be given an opportunity to discuss and exchange practical information, such as sample sizes, recruiting procedures, instruments of measure of behaviour, ethical issues involved etc. It is expected that questions and experimental protocols can be shared as well as, crucially, the design of replicate experiments to confirm and validate extant results. The symposium will emphasise the need for identifying behavioural traits that are: (1) essential for participation in cooperation and trading; and (2) could be quantified either in natural or experimental settings in such a way that a link to genetic variation could be made.

A specific workshop will bring together leading experts on aspects of the genetic basis of behaviour with the aim of establishing an ambitious interdisciplinary research programme on the study of the genetics basis of coalition formation in male primates. The current state of information on male coalition data from long-term baboon and macaque field sites will be established. The workshop will also discuss new field sites, the most viable [genetic] techniques and need for protocols that will facilitate cooperation across laboratories and countries. An issue at stake is the need for a standardised behavioural protocol that can be used to compare sites and species and that can therefore be linked to the relevant genetic analyses. Given the wide-ranging focus of the symposium (planned for 50 to 60 people) and the specificity of the workshop (planned for 15 to 20 participants), the meeting will be an historically unique and timely forum for discussion on the genetic architecture of behavioural traits. As part of its research programme, the whole of TECT will benefit from its results, while it is also hoped that profitable avenues of research for the immediate and long-term future (perhaps the next decade) will be defined.

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