Evolution of reciprocal altruism by copying observed behaviour

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To make decisions, animals frequently use information gained from observing other individuals. In some cases they simply copy observed behaviour. Using computer simulations, we here investigate the impact of copying on the evolution of reciprocal altruism. We show that in populations where individuals repeatedly interact within small groups, copying facilitates the evolution of cooperation even if the individuals do not take into account who is interacting. This mechanism, referred to as 'generalized indirect reciprocity' allows cooperation to evolve for organisms with limited cognitive capacities and when acquisition of personal and individual-specific information is costly. We discuss implications of copying on the emergence and maintenance of altruistic behaviour in animal populations and the human society.

Keywords: Agent-based simulations, copying, game theory, public information, reciprocal altruism.

Introduction

A COOPERATIVE or altruistic act is typically associated with costs for the cooperative individual, and is beneficial for someone else. Cooperative behaviour is common among humans and animals, and can be found even among microbes[1]. Humans, for example, engage in charity, while vampire bats, after a night of hunting, give excess blood to less successful con-specifics[2]. The evolution of cooperative behaviour seems to be a challenge for evolutionary biology. It has to be explained how selection of the fittest can favour individuals that perform acts that are associated with fitness costs. Several mechanisms for the evolution of cooperation have been identified[3,4].

The evolution of cooperation between unrelated individuals is frequently attributed to reciprocal altruism where a cooperative act increases the probability to benefit from cooperation in future interactions[5]. Mechanisms for the evolution of reciprocal altruism may rely on personal or socially acquired information about the behaviour of other individuals. This information may be individual-specific or unspecific (Figure 1). Personal information is individually acquired through direct interaction with the environment, i.e. through own experience. In contrast, socially acquired information is gained by observing the behaviour of others[6]. If information is gained about, and used towards, a specific individual, we refer to it as specific information. Unspecific information is not attributed to a particular individual – it is anonymous.

For direct reciprocity[7] personal, specific information is used. Cooperation may emerge if individuals reciprocate previous cooperation of their present partner. Thus, direct reciprocity is based on personal information of past interactions with the present partner. Therefore, direct reciprocity either requires that individuals interact with only one partner for some time or it requires cognitive abilities such as individual recognition and some memory to remember the outcome of past interactions with each potential partner.

Alexander introduced the term indirect reciprocity[8] for the possibility that altruistic behaviour towards an individual is returned by another individual. There are several mechanisms that may lead to cooperation in indirect reciprocity. These mechanisms differ on the type of information that is used to adjust cooperative behaviour[1,9].

Cooperation can also be favoured by evolution if individuals interact repeatedly within small groups and base their behaviour towards a partner on prior experience – irrespectively of the identity of the partner[10,11]. For such generalized reciprocity[11], or upstream reciprocity[10,12], individual recognition is not required. Only a single experience needs to be remembered.

In indirect reciprocity, measures of reputation such as image scoring[13] and standing[14–16] are based on socially acquired information. Individuals observe interactions between others and then decide about their behaviour towards the observed individuals on the basis of their observations. For image scoring, bystanders attribute an image score to the interacting individuals. Cooperative behaviour increases the image score, while non-cooperative behaviour reduces it. Cooperation can emerge and can be maintained in a population if individuals cooperate only with those individuals that have a high image score[13]. Image scoring, however, faces the problem that refusing cooperation to individuals with low image scores reduces the own image score. Thus, individuals may be left in the dilemma either to cooperate with a defector or

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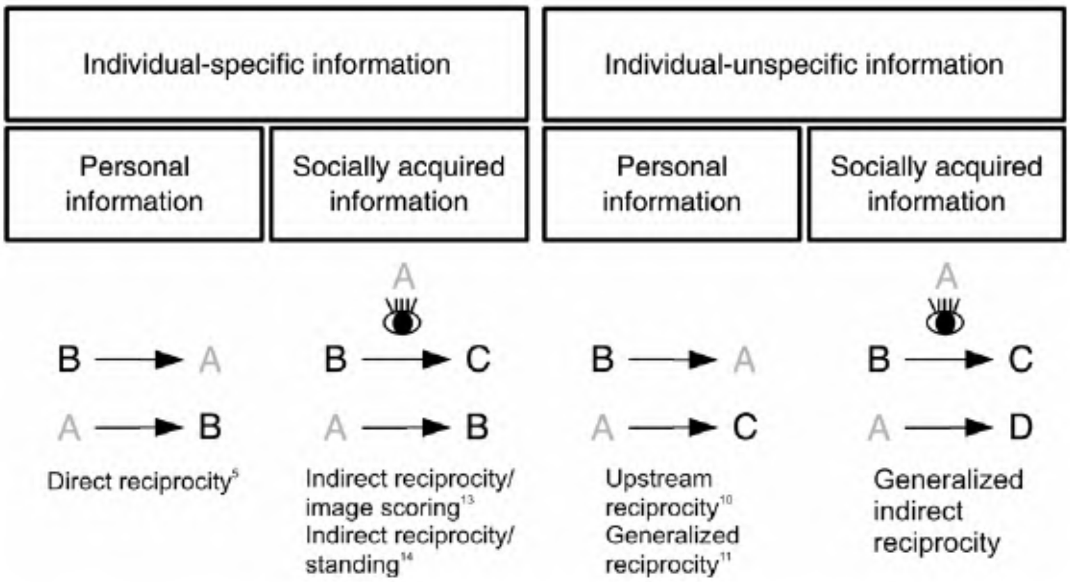

Figure 1. Cooperation may evolve through different mechanisms of reciprocal altruism that are based on different types of information. Direct reciprocity and mechanisms of indirect reciprocity such as standing and image scoring are based on specific information about the present partner that is either acquired by personal experience (personal information) or is socially acquired by observations (socially acquired information). Direct reciprocity: Individual A helps individual B, because B helped A before. Standing and image scoring: A observes that B helps C. Due to B's reputation resulting from this interaction, A helps B. Generalized reciprocity and indirect generalized reciprocity use individual-unspecific information that is acquired either by personal experience or by observation. Generalized reciprocity: A receives help from B and thus helps C. Generalized indirect reciprocity: A observed cooperation between B and C, and therefore helps D.

to defect and thus to reduce the own image score. A solution to this dilemma is provided by standing[14–16] and similar strategies[1]. The standing of an individual is similar to its image. Standing strategies, however, distinguish between 'justified' defection towards an individual in bad standing, and 'unjustified' defection towards an individual in good standing[14–16]. In contrast to image scoring, only 'unjustified' defection reduces the standing of an individual. Indirect reciprocity through image scoring or standing therefore requires individual recognition and significant memory capacities, and it requires the association of an individual's behaviour with its reputation. Compared to direct reciprocity, these strategies, however, have the advantage that information is not only gained from own experience but also from observed interactions. This advantage is of particular importance if repeated interactions between the same individuals are rare.

Based on computer simulations we here show that strategies can evolve that – similarly to image scoring and standing – base their behaviour on socially acquired information but do not require special cognitive abilities. Analogous to generalized reciprocity, we show that if individuals interact repeatedly within small groups it is sufficient for the evolution of cooperation to base behaviour on observed interactions, without identifying the interacting individuals. This mechanism for the evolution of cooperation is based on unspecific, socially acquired information, and is here referred to as generalized indirect reciprocity.

The model

Mathematical conditions for the evolution of generalized indirect reciprocity for a (infinitely) large number of repeated within-group interactions (i.e. low rate of death and between-group dispersal) can be derived and are analogous to those derived for generalized reciprocity[11]. Critical parameters for the emergence of cooperative behaviour are the cost/benefit ratio of cooperation, and the group size. Because it can be expected that, in comparison with generalized reciprocity, generalized indirect reciprocity is particularly favoured for a small number of repeated within-group interactions (see above), we here use agent-based simulations to investigate its evolution under more realistic conditions with high rates of between-group dispersal and death. In our simulations, the population consists of 10.000 individuals and is structured in groups of 5 individuals. Individuals reproduce locally, disperse and interact locally within their group: Two individuals of the same group are chosen randomly. One individual (donor) can choose between two options. It can perform a cooperative act in favour of another individual, or can refuse to do so. The latter option is referred to as defection. The other individual (recipient) has no choice but benefits from the cooperative act. To cooperate in such an interaction is assumed to be costly for the donor, but beneficial for the recipient. If the donor cooperates, the recipient gains a payoff of b, while the donor gains nothing. If the donor defects, it gains a payoff $c < b$ that is equivalent to the cost of cooperation, while the recipient gains nothing. This payoff structure is one of the simplest possible formulations of an altruistic interaction and is equivalent to the example of vampire bats sharing excess blood with less successful con-specifics[2]. We use a payoff of $c = 1$, and $b = 3$ in all simulations. Two of these interactions played simultaneously give the well-studied Prisoner's Dilemma[1]. Our payoff values correspond to the payoff of $S = 0$, $P = 1$, $R = 3$ and $T = 4$ that is typically used in studies on the Prisoner's Dilemma. Individuals participate in a finite number of interactions within their life. Dispersal is simulated by choosing two random individuals from the population that swap their group. Local reproduction and death are simulated by choosing two random individuals from the same group, one of which reproduces while the other dies. The probability for an individual to replace the other are $f1/(f1 + f2)$ and $f2/(f1 + f2)$ respectively, where $f1$ and $f2$ are the average payoff values of the individuals over their entire life. Individuals that never interacted are assumed to have a fitness of zero. Relations to other update rules have been described previously[17].

We study competition between three strategies, namely AllD, AllC and COPY-TFT. AllD always defects, AllC always cooperates. COPY-TFT cooperates if the last observed interaction was cooperation, and defects if the last observed interaction was defection, i.e. it simply copies the observed behaviour. Similar to TFT in direct reciprocity, COPY-TFT chooses cooperation if it is in the donor position before having observed any interaction. All simulations start with a population of unconditional defectors (AllD). The mutation rate (from any strategy into any strategy) is 10^{-3} in all simulations. Further parameters are given in the legend of Figure 2.

Results

Typical simulations are shown in Figure 2. The simulations illustrate that COPY-TFT can invade a non-cooperative (AllD) population and can establish cooperation. The dynamics is similar to analogous simulations of competition between AllD, AllC and TFT in direct[18] and in generalized reciprocity[11]. Initially, COPY-TFT has a small disadvantage against AllD. However, because this disadvantage is comparably small, mutations lead to an increase of COPY-TFT. Once COPY-TFT has reached a sufficiently high level, it can spread in a defective population. After COPY-TFT has taken over the population and has established cooperation, AllC is neutral and can drift into the population. If AllC reaches sufficiently high levels, AllD can invade again. The population therefore fluctuates around a composition with a high fraction of COPY-TFT players, a considerable fraction of unconditional cooperators, and a few unconditional defectors.

The similarity of the dynamics of competition between AllC, AllD and COPY-TFT in generalized indirect reciprocity to the dynamics of competition between the analogous strategies in direct and in generalized reciprocity arises from a similar outcome of pair-wise competition. AllC can be invaded and replaced by AllD. If rare, COPY-TFT is nearly neutral in a population of AllD. This is because as soon as it observes defection, COPY-TFT becomes non-cooperative, offering no advantage to unconditional defectors in the group. The only disadvantage of COPY-TFT arises from the initial move of naïve individuals that did not have a chance to observe defection in their group. Such disadvantageous moves can be expected to decrease in frequency with increasing group size and with an increasing number of interactions within a group. Once present at a sufficient frequency, such that groups are formed which consist only of COPY-TFT players, cooperation can be maintained in these groups and results in benefits of COPY-TFT over AllD. Therefore, COPY-TFT can replace AllD if present at a sufficient initial frequency. High local relatedness decreases this initial frequency. Once COPY-TFT has established cooperation, AllC is neutral and can drift into the population.

Discussion

Our results demonstrate that if individuals interact repeatedly within small groups, cooperation can emerge through strategies that base their behaviour on the outcome of the last interaction observed in the group – without including information about the interacting individuals. Thus, generalized indirect reciprocity represents an alternative mechanism for the evolution of reciprocal altruism that involves the use of unspecific and socially acquired information.

Advantages of generalized indirect reciprocity arise from the use of socially acquired information. Socially acquired information can be used if personal information is costly or not available. Costs of acquiring personal information arise from the risk of being cheated by a partner. It is clearly of advantage to observe non-cooperative behaviour rather than experiencing it. On the other hand, the capability of observing the behaviour of other individuals may be associated with costly cognitive capabilities. Therefore, using socially acquired information is particularly advantageous in social settings in which repeated interactions among the same individuals are rare, making each interaction and thus its observation valuable.

In the recent past, behavioural studies showed that animals frequently use public information in addition to personal information to decide how to behave in the future (for reviews see references[6,19,20]). Public information is defined as inadvertent social information on a feature

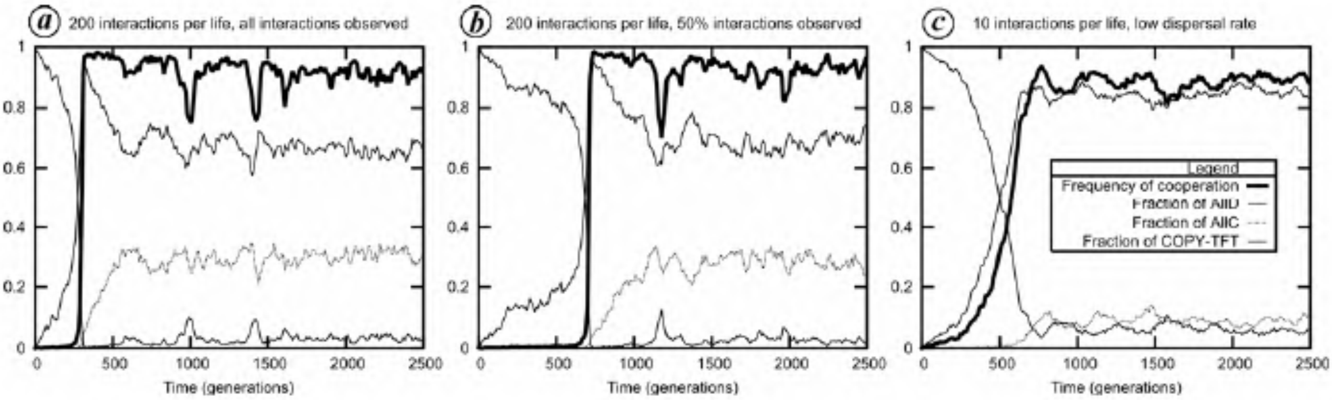

Figure 2. Evolution of generalized indirect reciprocity. ***a***, Within their life, the individuals participate in about 200 interactions, i.e. they act about 100 times as donor and recipient, respectively. The individuals observe all interactions within their group. The dispersal rate is equal to the death rate, i.e. individuals change their group on average once in their life. The simulation starts with a population of AllD (dotted line). COPY-TFT (thin line) initially accumulates due to mutations. If present at a sufficient frequency, COPY-TFT spreads and establishes a high frequency of cooperation (thick line) in the population. Once cooperation is established, AllC (dashed line) can drift into the population. If AllC has drifted to sufficiently high level, AllD can spread. As a consequence, the three strategies drift around a stochastic equilibrium with a high fraction of COPY-TFT, a medium fraction of AllC and a small fraction of AllD. ***b***, Individuals observe only half of the interactions. All other parameters are the same as in the simulation shown in Figure 1 A. Although the individuals base their behaviour on incomplete information, COPY-TFT can spread in the population. Compared to the simulation where all observations are observed, more time is required for COPY-TFT to establish cooperation. The three strategies reach similar levels as in the simulations shown in Figure 1 A. ***c***, Low dispersal rates facilitate the emergence of cooperation. Individuals change their group at a frequency of only 0.1 per life. They are assumed to participate in 10 interactions per life. The simulations show that at low dispersal rates, COPY-TFT can establish cooperation even if interactions are rare. This is because if reproduction is local, low dispersal rates lead to clustering in the population. Many groups consist of individuals with identical strategies. This is equivalent to a high within-group relatedness and favours the evolution of COPY-TFT. Not only the cooperating individual, but also its offspring benefit from reciprocity. Note that although there is a high relatedness within the groups, unconditional cooperation (AllC) cannot invade a population of unconditional defectors (AllD), because both the cooperative interactions and competition for reproduction are within the group, i.e. are at the same local scale. Therefore, the benefits of unconditional cooperation that arise from a high relatedness are exactly balanced by the high competition between relatives for reproduction within the group[38].

that enables the observer to obtain an estimate of its characteristics (e.g. the richness of a food patch, the aggressiveness of an opponent, the dangerousness of a predator, the quality of a mate[6]). Individuals may simply copy the observed behaviour of a con-specific. For example, guppy females and sailfin molly males mate with the same individual a con-specific had chosen before[21,22]. Such copying can evolve when individuals have the opportunity to observe the mate choice of others and when mate choice is costly. The physiology of an eavesdropper may also change as has been shown in a cichlid fish that increased hormone (androgen) levels when observing other fish fighting[23]. This might result in a general change of behaviour that is not confined to a specific individual or dyad.

The use of unspecific rather than individual-specific information in generalized indirect reciprocity offers advantages similar to those associated with generalized reciprocity and upstream reciprocity. Acquiring and storing information about each potential partner is costly. Costs arise from the development and maintenance of a cognitive machinery. Stevens and Hauser identified a list of psychological constraints that may impede the evolution of cooperation based on individual-specific information[24]. For the evolution of cooperation through generalized indirect reciprocity, however, cognitive capabilities such as individual recognition, numerical discrimination and significant memory are not required. It is sufficient that individuals are capable of simply copying observed behaviour. Given that social learning is frequent in different contexts of animal behaviour[25], copying might be easy to evolve in the context of cooperative behaviour, and it might be associated with comparably low fitness costs.

In an experimental study on cooperative behaviour it was shown that social experience influences the propensity to cooperate in rats in an unspecific way[26]. Physiological mechanisms exist that may enable individuals to react to experienced behaviour. It has been demonstrated experimentally that primates and rats exposed to socio-positive or -negative experience show significant hormonal changes[27,28]. Recently, oxytocin was shown to influence human pro-social behaviour[29]; it might also mediate the benefits of positive social interactions in non-human animals[30]. Such hormonal changes may critically affect the tendency to cooperate specifically in an individual-unspecific context. Hormonal levels may store social experience and influence future cooperative behaviour, but do not reflect individual-specific information. Similar processes might also influence an animal's hormonal release when it observes (rather than experiences) co-operation or defection. Hormonal systems may be seen as information-processing systems with low memory compared to neural information procession. They may therefore, be systems sufficient for processing individual-unspecific information and may offer the advantage of being associated with comparably low costs.

A number of behavioural mechanisms have been proposed that are based on socially acquired information and are beyond the context of reciprocal altruism. For example, animals might use their anonymous previous cooperative experience as information about the cooperativeness within a social environment to make decisions about moving between groups[31]. Lotem and co-workers[32], and Zahavi[33] proposed that cooperation could evolve if individuals gain signalling benefits from behaving altruistically. Such unconditional cooperation, however, requires that altruistic acts are costly signals of individual quality (i.e. a handicap[33]) and are used by spectators as an indicator of an individual's quality.

An interesting aspect of cooperative behaviour based on socially acquired and unspecific information is the possibility of cooperative or exploitive behaviour to spread in a population through observation. Strategies such as COPY-TFT, therefore, open the way for cultural transmission of observable behaviour. The behavioural trait of a con-specific, either directed towards oneself, or towards other individuals, is acquired and performed towards any partner. It has been suggested that individuals may acquire cooperative or exploitative behaviour from others and that the disproportionate exposure to one of these behaviours increases the likelihood that it will be acquired[34].

Our model for the evolution of generalized indirect reciprocity does only take into account the behaviour between two anonymous individuals. However, generalized indirect reciprocity may also be a mechanism for the evolution of cooperation based on marks that are (inadvertently) left in the environments from cooperative or non-cooperative actions. In an untidy place, for example, people may tend to care less to deposit waste in the waste bin than they do in a clean place. Such behaviour might be adaptive because it is not advantageous to invest in cooperative actions where it is unlikely that the investment will be reciprocated. Marks are pieces of socially acquired information that cannot be associated with a specific individual. In contrast to other forms of reciprocal altruism, generalized indirect reciprocity provides a mechanism for the evolution of cooperation based on marks. We, therefore, believe that cooperative traits that are influenced by environmental marks might be a valuable topic for future investigations.

Marks that indicate a cooperative or uncooperative environment might help to judge the probability to receive help in the future. The 'broken windows policy'[35] applied by the New York police to reduce crime is based on the hypothesis that when small damages (e.g. on houses, cars) are not repaired, soon more will follow and the likelihood of stealing from the damaged properties increases. It has been argued that by repairing damages immediately the incidence of serious crimes in New York were lowered significantly[36], although it is difficult to obtain evidence for a causal effect.

Even if, in contrast to the above scenario, individual-specific information is available, it is unclear whether it is always used. Although typically capable of processing complex, socially acquired, individual-specific information, humans often use their experience in an unspecific way. Moreover, humans observe the behaviour of others to interfere about social norms. To behave in the way other individuals behave appears to be a simple and risk-free strategy to comply with social norms. As our results indicate, such a strategy allows for the spread and maintenance of altruistic behaviour. However, copying also has negative aspects. If behaviour is copied without being evaluated for its adaptive value, copying may become disadvantageous. If the predominant behaviour is not optimal, individuals that deviate from it may have a selective advantage. Moreover, copying may also lead to a rapid break-down of cooperation in a group. Mistakes in behaviour or a single defector that enters a group due to migration or mutation is sufficient to turn a cooperative group into a defective one. Thus, copying is a cheap but dangerous alternative to more elaborate strategies such as 'standing' within the framework of indirect reciprocity.

The question of how often humans use unspecific rather than individual-specific information is of high relevance for human society. Problems related to crime or education are closely linked to the processing of social information. Findings, for example, that relate violent video games with decreased pro-social behaviour in children suggest that social experience carries over from one social context to another[37]. We propose that further studies should attempt to analyse under which conditions cooperative behaviour in humans and non-human animals is based on generalized indirect reciprocity rather than more complex strategies that include individual-specific information.

Role of society in science: the Branco Weiss Fellowship

Society in Science supports interdisciplinary research at the intersection between science and the society. Game theory and its applications to societal processes might be a prime example for such research. A major objective of game theory is to understand optimal behaviour in situations where individuals have the choice between different actions, and the outcome (costs and benefits) depend on the own action as well as the actions of the others. A particularly interesting and important example is cooperative behaviour and the tragedy of the commons. Here, individuals have the choice between selfish behaviour that gives rise to individual benefits, and cooperative behaviour that is costly for the individual but beneficial for a larger group or a common good. Situations analogous to the tragedies of the commons arise for many interactions within human society, some of which are crucial for the future of mankind, such as the protection of the global climate. Here, game theory provides means to resolve conflicts between individual interests and interests of larger groups or the human society as a whole.

Game theory is a highly interdisciplinary research discipline. It has roots in economics, applied mathematics, evolutionary biology and psychology, and has become an increasingly popular toolkit in both the social sciences and the life sciences. Performing research in such a discipline is not without risks for young researchers. Research projects are often located outside of established research fields, where they may face limited opportunities for funding or publishing. The conditions offered by the Branco Weiss Fellowship are ideal for overcoming the problems associated with unconventional and risky projects. A time horizon of five years allows overcoming initial barriers and establishing novel research directions. Fellows are free in their choice of location and research group, which strengthens their independence and allows them to join the most promising institutions for their projects. The intense exchange of ideas between the fellows and the scientific board members of Society in Science generates an excellent breeding ground for innovative research projects.

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