

Mechanistic constraints and the unlikely evolution of reciprocal cooperation

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Abstract

Social evolution theory faces a puzzle: a gap between theoretical and empirical results on reciprocity. On the one hand, models show that reciprocity should evolve easily in a wide range of circumstances. On the other hand, empirically, few clear instances of reciprocity (even in a broad sense) have been found in nonhuman animals. In this paper, I aim to suggest and evaluate a novel reason concurring to solve this puzzle. I propose that it is difficult for reciprocity to evolve because it raises an evolutionary problem of *bootstrapping*: it requires that two complementary functions: (i) the ability to cooperate and (ii) the ability to respond conditionally to the cooperation of others, arise together and reach a significant frequency, whereas neither of them can be favoured in the absence of the other. I develop analytical models and simulations showing that, for this reason, the evolutionary emergence of reciprocal cooperation is highly unlikely. I then discuss the consequences of this result for our understanding of cooperation.

Introduction

Cooperative interactions, in which one individual provides fitness benefits to another, have a major ecological impact and have been involved in most of the major evolutionary transitions (Maynard Smith & Szathmary 1995). In particular, the human ability to build up cooperative interactions with others based on the coordination and division of labour is arguably one of the main causes of our ecological success (Gurven *et al.*, 2000a,b; Hill, 2002; Gurven, 2004). When they are expressed towards genetically related partners, cooperative traits can be favoured by selection because of genetic relatedness, this is the principle of kin selection (Hamilton, 1964). But many cooperative traits, particularly in humans, are also expressed towards non-genetically related partners (Hill *et al.*, 2011), in which case they must benefit both the individual receiving them and the individual expressing them, that is, they must be *mutualistic* (West *et al.*, 2007c). The existence of mutualistic traits in living species raises the evolutionary question: through what mechanism(s) can

it be beneficial for an individual to increase the fitness of another?

One well-known potentially important mechanism of this kind is reciprocity (Trivers, 1971), which, taken in a broad sense, characterizes a diverse array of forms of social feedback, including the strictly reciprocal exchange of benefits (called direct reciprocity), the effect of reputation and the role of punishment. Reciprocity is powerful because it allows the benefits accrued by an individual to be (at least partially) redistributed to another, thereby allowing helping, or other forms of social investment, to be potentially beneficial to its provider. However, reciprocity is also the object of an apparent evolutionary paradox: a gap between theoretical predictions and empirical observations.

On the one hand, in line with work in game theory (Luce & Raiffa, 1957; Fudenberg & Maskin, 1986; Aumann & Shapley, 1994; Binmore & Samuelson, 1992), evolutionary modellers have shown that reciprocity can evolve relatively easily in a wide array of circumstances, including in agents endowed with extremely simple behavioural rules (Axelrod & Hamilton, 1981, and see also for example Nowak & Sigmund, 1992, 1993; Roberts & Sherratt, 1998; Lehmann & Keller, 2006; André & Day, 2007). The issue of the evolutionary *stability* of any given reciprocal strategy is debated (Selten, 1975 1983; Boyd & Lorberbaum, 1987;

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Lorberbaum, 1994; Lorberbaum *et al.*, 2002; André, 2010). It entails the maintenance of some form of phenotypic variability (due to mistakes, or pay-off uncertainty, see Selten, 1983; Leimar, 1997; Sherratt *et al.*, 2001; Ferriere *et al.*, 2002; McNamara *et al.*, 2004; McNamara & Leimar, 2010). However, at the very least, the *evolution* of reciprocal strategies themselves, from the initial state of pure defection, seems to pose no insurmountable difficulty, supporting the idea that reciprocity can play an important role in many different sorts of mutualistic interactions across the living world.

On the other hand, empirically, very few clear instances of reciprocity (even in a broad sense) are found in nonhuman animals. Worse, most of the instances of behaviours that had initially been thought of as examples of reciprocity have been shown to be, at the minimum, debatable (Connor, 1986, 1995a,b; Hammerstein, 2003; Bergmuller *et al.*, 2007; West *et al.*, 2007a; Clutton-Brock, 2009; Leimar & Hammerstein, 2010; Raihani *et al.*, 2012; for an example of debate, see Krams *et al.*, 2008; Russell & Wright, 2009; Wheatcroft *et al.*, 2009; Krama *et al.*, 2012; and for a recent review see Raihani & Bshary, 2011). Two main explanations have been proposed in the literature to resolve this apparent paradox, that is, to account for the rarity of reciprocity in spite of the apparent theoretical ease with which it should evolve. The first invokes cognitive constraints, claiming that reciprocity is too *complex* for nonhuman minds (Stevens & Hauser, 2004; Stevens *et al.*, 2005; Hauser *et al.*, 2009). The second invokes ecological constraints, stating that the reciprocal exchange of a resource can hardly be evolutionarily stable because it implies that the value of the resource changes through time for both individuals, and in opposite directions (Whitlock *et al.*, 2007). However, even though both hypotheses have significant merits, I believe that they are not sufficient to explain the rarity of reciprocal cooperation, an issue I will come back to in the discussion.

Here, I aim to suggest another plausible explanation for the relative rarity of all forms of reciprocity. Rather than cognitive or ecological constraints, I will consider the effect of *genetic* constraints. Imhof & Nowak (2010) and then Garcia & Traulsen (2012) have already shown that the structure of mutation, hence the genetic underpinnings of social strategies (i.e. genetic constraints), affects the evolution of cooperation. Garcia & Traulsen (2012) in particular recently showed that certain forms of genetic constraints significantly reduce the relative abundance of cooperation at a stationary distribution, in finite populations. However, the genetic constraints that these authors consider are not meant to be particularly realistic biologically, and most importantly, Garcia & Traulsen (2012) are interested in the evolution of cooperation in the very long run, whereas I am interested in the different problem of its emergence.

In this paper, I will show that, under realistic genetic constraints, reciprocal cooperation may be unable, or extremely unlikely, to *evolve* in spite of being evolutionarily stable. The reason is that reciprocity is a composite trait that entails (at least) two different biological functions: (i) the ability to provide benefits to others (i.e. to help) and (ii) the ability to detect (and respond to) the benefits provided by others. In mechanistic terms, these two functions bear no relationship to each other and must evolve independently, by different mutations. But neither is favoured in the absence of the other. Helping is counter-selected when others do not already respond to helping. Detecting and responding to helping makes no adaptive sense when others do not already help. This creates a chicken-and-egg problem and makes the eventual emergence of reciprocity very unlikely in general. The present analysis will be restricted to the simplest form of reciprocity, the direct exchange of help between a pair of partners, because this configuration captures the essential mechanism at work in all other cases of reciprocity in a simple form, but the arguments and results of the paper essentially apply to all forms of reciprocal exchanges.

The model

The social interaction

I consider a model in which individuals go through a pairwise repeated interaction lasting for a very long (infinite) number of rounds. In each round, each partner can either cooperate or defect (cooperation is all-or-nothing). For each unit of help offered in a given round, the actor pays a unitary fecundity cost c , and the receiver gains a benefit b (the main parameters of the model are presented in Table 1). Each individual is characterized by a social strategy s , with a resulting physiological cost $K(s)$ which captures the fact that conditional strategies are often more costly than constitutive ones. The genetic encoding of the strategies will depend on the precise genetic constraints considered (see sections ‘Traditional genetic constraints: the γ_c/γ_d model’ and ‘Mechanism-minded constraints: the γ/ρ

Table 1 Main parameters of the models.

u	Probability of mutation at each locus
k	Unitary cost of behavioural conditionality
q	Quantitative impact of social interactions on fecundity
b	Fecundity benefit of each unit of help received
c	Fecundity cost of each unit of help given
γ_c	Probability of cooperating after partner's cooperation (traditional genetic constraints)
γ_d	Probability of cooperating after partner's defection (traditional genetic constraints)
γ	Cooperative tendency (Mechanism-minded genetic constraints)
ρ	Conditional ability (Mechanism-minded genetic constraints)

model'). The social pay-off obtained by an individual playing strategy s_1 in an encounter with an individual playing strategy s_2 is given by

$$P(s_1, s_2) = bh(s_2, s_1) - ch(s_1, s_2) \quad (1)$$

where $h(s_1, s_2)$ is the average amount of cooperation expressed by an individual playing strategy s_1 in an interaction with a partner playing s_2 and depends on the genetic constraints considered. I now turn to the description of these constraints.

Traditional genetic constraints: the γ_c/γ_d model

Essentially two sorts of assumptions have been made in evolutionary models regarding the genetic underpinnings of social strategies. Some consider that all possible strategies are related by a mutation matrix, most typically with uniform mutation rates (e.g. Axelrod, 1984, 1997). Others decompose strategies into several traits which evolve separately, either in a continuous or in a discrete trait space (e.g. Nowak & Sigmund, 1992). Imhof & Nowak (2010) and then Garcia & Traulsen (2012) show that choices regarding the effects and rates of mutation have important consequences, with weak mutation effects and 'multilocus' approaches being the least favourable to the evolution of cooperation.

In both versions of the model, here I take the multilocus approach, encoding strategies into a set of genetic loci which mutate independently. In the first version of the model, I consider a form of genetic constraints used in classic models in the literature (see e.g. Nowak & Sigmund, 1992; or more recently Barta *et al.*, 2011). This will not yield original results but is needed for comparison with the alternative approach (section 'Mechanism-minded constraints: the γ/ρ model'). I assume that social strategies are encoded by two genetic loci: (i) a first locus codes for the individuals' willingness to cooperate after their partner has just cooperated, called here γ_c , and (ii) a second locus codes for the individuals' willingness to cooperate after their partner has just defected, called here γ_d . Each γ_x is either equal to 0 (defection) or 1 (cooperation). For instance, an individual with $\gamma_c = 1$ and $\gamma_d = 0$ is a reciprocator, an individual with $\gamma_c = 1$ and $\gamma_d = 1$ is an unconditional cooperator, etc. The cognitive cost of behavioural conditionality is assumed proportional to the difference between γ_c and γ_d , hence $K(s) = k \cdot |\gamma_c - \gamma_d|$.

All individuals are assumed to begin every social interaction with at least one instance of cooperation. Eventually, in the course of interaction, players then reach a stationary level of cooperation, which depends on their social strategy. Interactions are then assumed to last for a very long time, such that the average level of cooperation expressed by players during the entire interaction only depends on this stationary level, which can be calculated for each pair of partners as shown in Table 2.

Table 2 Average cooperation in the γ_c/γ_d model.

(γ_c, γ_d)	(0,0)	(1,0)	(0,1)	(1,1)
(0,0)	0	0	0	0
(1,0)	0	1	$\frac{1}{2}$	1
(0,1)	1	$\frac{1}{2}$	$\frac{1}{2}$	0
(1,1)	1	1	1	1

Average cooperation expressed by the row player during an interaction with the column player.

Mechanism-minded constraints: the γ/ρ model

The above genetic constraints are based on the premise that willingness to cooperate after cooperation (γ_c) and willingness to cooperate after defection (γ_d) are two independent, genetically transmitted traits. In consequence, a constitutive defector ($\gamma_c = 0, \gamma_d = 0$) can become a conditional cooperator with a single random mutation ($\gamma_c = 0 \rightarrow \gamma_c = 1$), whereas becoming a constitutive cooperator requires two mutations ($\gamma_c = 0 \rightarrow \gamma_c = 1$ and $\gamma_d = 0 \rightarrow \gamma_d = 1$).

Biologically, however, this premise is somewhat surprising. First, there is likely to be a functional relationship between γ_c and γ_d , as both features entail the ability to cooperate *in general*. Second, from the initial state of constitutive defection, more modifications should be required to reach conditional than constitutive cooperation, as the former involves two novel functions: (i) the ability to cooperate and (ii) the ability to be conditional (i.e. measure and respond to partners' cooperation), both of which are absent in pure defectors.

Based on the above considerations, I propose an alternative form of genetic constraints. Individuals are also characterized by two independent loci, but they are (i) a general ability $\gamma \in \{0,1\}$ to help, and (ii) an ability $\rho \in \{0,1\}$ for this help to be offered conditionally. For instance, an individual with $\gamma = 0$ and $\rho = 0$ is a plain defector, an individual with $\gamma = 1$ and $\rho = 1$ is a reciprocator, an individual with $\gamma = 1$ and $\rho = 0$ is an unconditional cooperator, etc. As in the first model, conditionality (here measured by ρ) is assumed to have a linear fecundity cost, given by $K(s) = k\rho$. Under these genetic constraints, and under the same assumptions as in the previous model (all individuals start every social interaction with one instance of cooperation, and interactions are assumed to last for a very long time), the average amount of cooperation expressed in the 16 possible pairs of partners can be derived and is given in Table 3.

Evolutionary analyses

Here, I describe the methods employed to study the evolution of social strategies, these analyses being performed identically under both forms of genetic constraints.

Table 3 Average cooperation in the γ/ρ model.

(γ, ρ)	(0,0)	(1,0)	(0,1)	(1,1)
(0,0)	0	0	0	0
(1,0)	1	1	1	1
(0,1)	0	0	0	0
(1,1)	0	1	0	1

Average cooperation expressed by the row player during an interaction with the column player.

I consider a population of finite size N evolving under the Moran process. Every individual is assumed to meet an infinite number of partners. The fecundity of a focal individual with strategy s . is written

$$F(s_{\bullet}) = e^{-k(s_{\bullet})} e^{q \cdot \sum_s f(s) P(s_{\bullet}, s)} \quad (2)$$

where $f(s)$ is the frequency of the strategy s in the population, and q measures the quantitative impact of the considered social interactions on the individual's total fecundity.

In each time step, one random individual dies and is replaced by the offspring of another individual chosen with a probability proportional to its fecundity. Under the approximation of vanishingly rare mutations, the population is almost always fixed for a single strategy and evolution can be approximated as a random walk from one homogeneous state to another. Under this approximation, Fudenberg & Imhof (2006) show that the transition probability from a state fixed with strategy i to a state fixed with strategy j is given by the product $u_{ij} p_{ij}$, where u_{ij} is the probability of mutation between strategies i and j , and p_{ij} is the probability of fixation of a single mutant playing j in a population where every other individual plays i . Note that, under this approximation, recombination between the two loci need not be taken into account, as there is never more than one locus segregating in the population.

The probabilities of mutation between strategies, u_{ij} , depend on the genetic constraints chosen (section 'Traditional genetic constraints: the γ_c/γ_d model' or 'Mechanism-minded constraints: the γ/ρ model'). In either case, mutation probability is assumed to be identical on both loci and given by u , and the probability of double mutations is neglected because it is a second-order term in mutation probability. The exact fixation probabilities in the Moran process, p_{ij} , are given by Karlin & Taylor (1975):

$$p_{ij} = \left(1 + \sum_{k=1}^{N-1} \prod_{n=1}^k \frac{F(i, j, N-n)}{F(j, i, n)} \right)^{-1} \quad (3)$$

where $F(j, i, n)$ is the fecundity of an individual playing strategy j in a population containing n individuals playing j and $N-n$ individuals playing i and is given by equation (2). With exponential fecundity as in the equation (2), Traulsen *et al.* (2006) show that the

fixation probabilities can even be expressed in a closed form, which is used here (see section 4 in the Supporting information for details on this derivation).

Under both types of genetic constraints, starting in a state in which all individuals are plain defectors ($\gamma_c = \gamma_d = 0$ or $\gamma = \rho = 0$), the aim of the analysis is to derive the expected time for the population to first reach a state in which all individuals are reciprocators ($\gamma_c = 1$ and $\gamma_d = 0$, or $\gamma = \rho = 1$). This is calculated from the fundamental matrix of the simplified Markov process, considering the reciprocator state as absorbing (see section 5 in Supporting information). From this expected time T , the probability of emergence of reciprocal cooperation per generation is calculated as NT^{-1} , where N is the population size. This probability of emergence is, by definition, linear in mutation probability u . The analysis is completed with Monte Carlo simulations, in which recombination can occur between the two loci. With a probability $r = 0.5$, each time an individual is chosen to reproduce, another individual is chosen with probability also proportional to fitness, and the offspring is a recombinant of the two.

As a complementary analysis, a deterministic multilocus approach based on the same social interaction and strategies is also developed. This model is described in the Supporting information (section 7). The important difference from the stochastic model is that, like in the simulations, recombination is taken into account. This occurs with probability r per individual per generation.

Results and interpretation

In the stochastic analysis, under realistic values for the cost of conditionality (k) and the effects of cooperation (b , c and q), the probability of emergence of reciprocity per generation is at least 10 times lower in the γ/ρ model than the γ_c/γ_d model and becomes orders of magnitude lower in fairly large populations and/or with a significant cost for conditionality (Fig. 1). Hence, the evolutionary emergence of reciprocity is orders of magnitude slower when it entails two independent functions than a single one. Increasing the net benefit of cooperation ($b-c$) has a strongly positive effect on the evolution of reciprocity in the γ_c/γ_d model, but not in the γ/ρ model (Fig. 2; increasing q has the same effect, not shown).

In addition to results that are also seen in the stochastic model, the deterministic analysis also makes it possible to examine the effect of recombination (Fig. 3). Recombination is shown to have a negative effect on the evolution of cooperation in the γ/ρ model, especially when the recombination rate is very low, but it has no effect in the γ_c/γ_d model.

To understand these results, it is useful to recall the mechanism allowing the emergence of reciprocity. In a population containing a majority of defectors, rare reciprocators pay a constant cost for having a complex

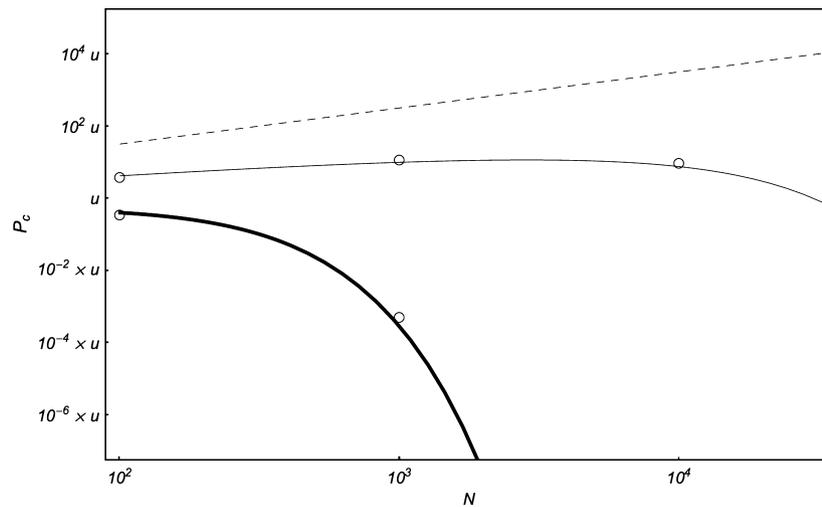


Fig. 1 Probability of emergence of reciprocal cooperation, per generation, in the Moran process, as a function of population size (N). Lines show the results of the analytical model, and empty circles show estimates obtained from simulations. The benefit and cost of cooperation are $b = 5$ and $c = 1$, respectively. The cost of conditionality is $k = 10^{-2}$, and the quantitative impact of the social interaction is $q = 0.1$. The thick line presents results obtained with the genetic constraints γ_c/ρ . The thin line presents results obtained with the genetic constraints γ_c/γ_d . For the sake of comparison, the dotted line presents results for the case of a plain adaptive mutation with the same benefit as reciprocal cooperation $-k + q(b-c)$.

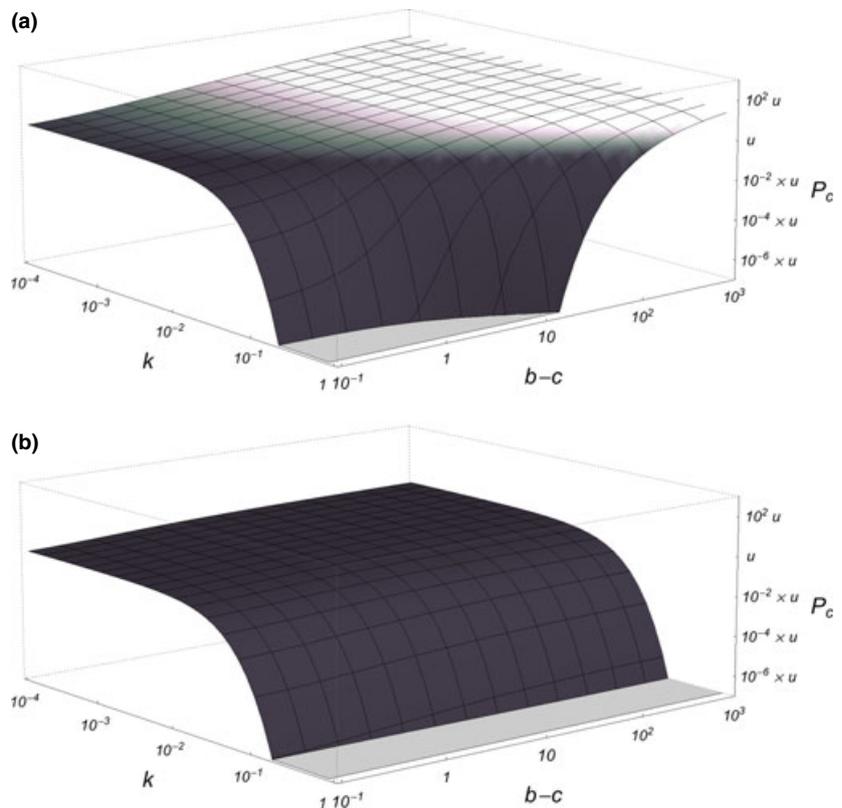


Fig. 2 Probability of emergence of reciprocal cooperation, per generation, in the Moran process, as a function of the cost of conditionality (k) and the net benefit of cooperation ($b-c$), with the genetic constraints γ_c/γ_d (a) and the genetic constraints γ_c/ρ (b). Population size is $N = 100$, the cost of cooperation is $c = 1$, and the quantitative impact of the social interaction is $q = 0.1$.

conditional ability, and they get a benefit only when they interact with other reciprocators like them. Hence reciprocity can become favoured provided its initial

frequency is sufficiently high, that is, it must overcome an *invasion barrier* (a threshold frequency given by $k/q(b-1)$ in the present model). In an infinite

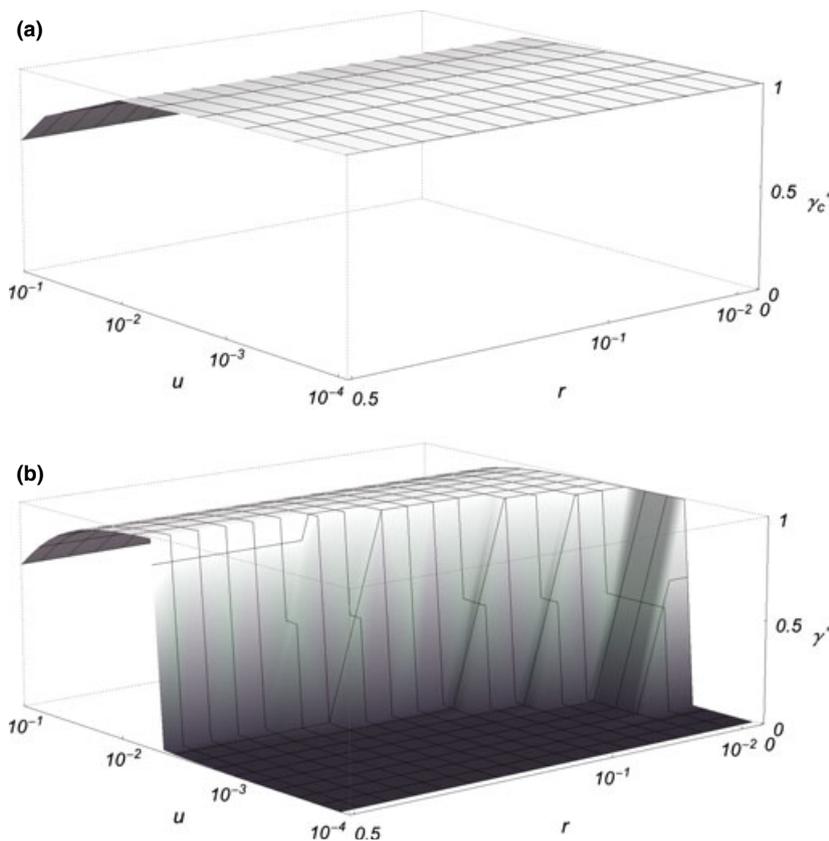


Fig. 3 The average amount of cooperation at equilibrium in the deterministic model, as a function of mutation probability (u) and recombination rate (r), with the genetic constraints γ_c/γ_d (a) and the genetic constraints γ/ρ (b). The stability of equilibrium points is tested by calculating the eigenvalues of the Jacobian matrix around each point. In cases in which two stable equilibrium points are found, only the point with the lowest level of cooperation is shown, because it corresponds to the equilibrium reached when reciprocal cooperation is initially absent. The cost of conditionality is $k = 10^{-2}$, and the quantitative impact of the social interaction is $q = 1$.

population, the invasion barrier required for the emergence of reciprocity can be crossed owing to recurrent mutation. In a finite population, the invasion barrier can also be crossed owing to demographic stochasticity.

The need to overcome an invasion barrier generally constitutes a constraint on the evolution of reciprocity, but in traditional models, this constraint is relatively moderate, due to a specific assumption: reciprocity is assumed to be only one mutation away from pure defection. This assumption has two favourable consequences. First, reciprocator mutants are relatively likely to appear by mutation. Second, when reciprocators and defectors segregate in the population, recombination does not destroy the reciprocator phenotype. In contrast, under an alternative model in which reciprocity is assumed to be a composite trait, two mutations away from pure defection, these two favourable properties vanish. First, the probability of appearance of reciprocators in a population of defectors becomes dramatically lower (approximately the square of the mutation probability), making it extremely unlikely for the invasion barrier to be crossed. Second, because reciprocity is now an *association* of two traits, it is destroyed by recombination, yielding intermediate, maladaptive, strategies.

Moreover, when reciprocity is a simple trait, the same mutants (i) pay the cost of conditionality and (ii)

benefit from cooperation. Hence, a large cost of conditionality can be compensated if cooperation is strongly beneficial (Fig. 2a). In contrast, when reciprocity is a composite trait, the first mutants to arise pay the cost of conditionality but do not benefit from cooperation (they have $\rho = 1$ but $\gamma = 0$). As a result, a large cost for conditionality cannot be compensated by a larger net benefit of cooperation (Fig. 2b).

Complementary analysis

Even though the emergence of cooperation is strongly impeded in the γ/ρ model, it can still occur with non-negligible probability in small populations when the cost of conditionality k is low (see Fig. 1). In this case, conditionality ($\rho = 1$) can drift neutrally to fixation, paving the way for the eventual emergence of helping (a scenario similar to some models of the evolution of mate choice; Kirkpatrick, 1982). Hence, the assumption that conditionality carries a significant cost is an important element in the present results.

Biologically, however, there is another reason why conditionality is unlikely to arise through drift alone, beyond its cost. Complex biological functions generally do not emerge in the absence of directional selection in their favour. This is not primarily a consequence of their cost, however, but rather of the fact that they

entail an accumulation of several mutations that is implausible in the absence of selection. In the present case, therefore, I wanted to know what happens if conditionality is in fact a complex biological aptitude in itself, requiring several mutations to build up.

To this end, I modified the simulation procedure in the following way: (i) Conditionality is assumed to have no cost at all ($k = 0$). (ii) Individuals are characterized by a discrete genetic trait $l \in [0, L]$ which yields a quantitative degree of conditionality $\rho = l/L$. (iii) The probability for an individual with genotype l to mutate to $l+1$ is u , but the probability to mutate to $l-1$ is $l \times u$. Hence, the mutation structure contains an asymmetry, capturing the fact that random mutations are more likely to damage than improve an existing conditional ability. (iv) To introduce a selective pressure in favour of conditionality, a simple form of uncertainty is introduced: with a given probability ε , a player is totally unable to cooperate irrespective of genotype.

Simulations show that the probability that cooperation will emerge decreases exponentially with the number of mutations required to build up conditionality (Fig. 4). Even in a small population with no cost of conditionality, the emergence of reciprocity becomes extremely unlikely if conditionality requires more than a couple of mutations to build up. On the one hand, helping cannot arise unless conditionality is already high. On the other hand, even though conditionality could build up gradually by a series of mutations, this could occur only if it were under positive selection, which is impossible unless helping is already present.

Discussion

Reciprocal cooperation entails an important component of coordination: it is adaptive to cooperate reciprocally when others also do so; otherwise defection is generally

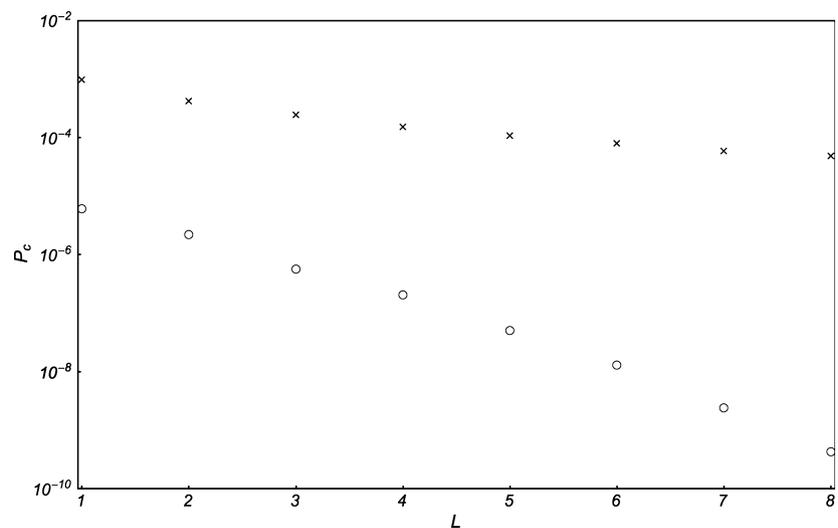
a better strategy. In other words, reciprocity is an adaptation to itself. Hence, it is not favoured when very rare in a population of defectors, and it may only become favoured if it manages to reach a threshold frequency, an *invasion barrier*, which must occur for nonselective reasons.

In traditional models, reciprocity is seen as a *simple* trait, triggered by a single random mutation which transforms defectors into reciprocal cooperators. In such a case, mutations and/or demographic stochasticity can lead to the appearance of a significant subpopulation of reciprocator mutants, and hence, it can relatively easily lead to the overcoming of the invasion barrier (Nowak & Sigmund, 1992; Nowak *et al.*, 2004; and section 'Traditional genetic constraints: the γ_c/γ_a model' above).

In reality, however, there is no reason why reciprocity should be such a simple trait. Quite to the contrary, the ability to cooperate reciprocally, like any biological function, is likely to be a composite trait entailing several subfunctions (see Stevens & Hauser, 2004; Stevens *et al.*, 2005). In particular, reciprocity does entail at least two different functions: (i) the behavioural ability to provide benefits to others (i.e. to help) and (ii) the cognitive ability to detect (and respond to) the benefits provided by others. These two functions have no general reason to be caused by the same mechanistic properties of organisms. Indeed, if one were to build a machine that was able to perform a given form of helping, it would be very unlikely to have the ability to detect others' helping as an automatic by-product.

In this paper, I have shown that, if reciprocity is really such a *composite* trait, triggered by several independent mutations, then the overcoming of the invasion barrier becomes dramatically less likely. This can be understood intuitively. In evolution, composite functions are usually shaped by the enduring effect of directional selection, which yields a gradual *accumulation* of

Fig. 4 Probability of emergence of reciprocal cooperation, per generation, in individual-based simulations, plotted as a function of the number of mutations needed to reach perfect conditionality ($\rho = 1$), under the genetic constraints γ/ρ (empty circles). The mutation probability is $u = 10^{-5}$. The benefit and cost of cooperation are $b = 5$ and $c = 1$, respectively. The cost of conditionality is $k = 0$, and the quantitative impact of the social interaction is $q = 0.1$. For the sake of comparison, the probability of emergence of a plain adaptive trait with the same benefit and the same number of mutations needed is shown (crosses).



adaptive mutations. In the case of reciprocity, however, this gradual accumulation is impossible, because reciprocity is not an adaptation to an existing exogenous selective pressure, but an adaptation *to itself*, that is, the selective pressure favouring reciprocity is only present once reciprocity is already in place. As a result, in contrast to other composite functions, the ability to reciprocate cannot build up gradually. It needs to arise by chance (i.e. by the occurrence of just the right mutations) and then become favoured by selection, which is extremely unlikely.

Reciprocity in a broad sense

Interestingly, although this paper only presents a formal study of the case of direct reciprocity, there is good reason to think that the same argument applies to all forms of reciprocity. Most scholars define a reciprocal interaction in general as one in which the benefit of social behaviour is not 'immediate' but depends on the phenotypic response of other individuals (Connor, 1986; Leimar & Connor, 2003; Sachs *et al.*, 2004; Bergmüller *et al.*, 2007; West *et al.*, 2007b; Leimar & Hammerstein, 2010; Raihani & Bshary, 2011; Raihani *et al.*, 2012). Said differently, in reciprocity the action expressed by each individual is made adaptive by causes that are *endogenous* to other individual(s). This is true in direct, indirect and generalized reciprocity, but also in punishment (i.e. negative reciprocity), and even in partner choice. In all these interactions, therefore individuals are co-adapted to each other in the strong sense that each individual's phenotype constitutes the very incentive that makes the others' phenotype adaptive, which is the essential element that creates the evolutionary problem highlighted above. Hence, by their very definition, all forms of reciprocal interactions are likely to be subject to the same evolutionary difficulty. Note that this is not true of simpler mechanisms such as by-product mutualism, pseudoreciprocity and sanctions (as opposed to genuine punishment), an issue I will return to below.

Alternative explanations for the rarity of reciprocity

Other hypotheses have been proposed in the literature to explain the puzzling rarity of reciprocity. The most often cited explanation highlights the existence of constraints on cognition, claiming that reciprocity is too *complex* for nonhuman minds: 'cognitive limitations such as temporal discounting, numerical discrimination and memory make reciprocity difficult for animals' (Stevens & Hauser, 2004; and see also Stevens *et al.*, 2005; Hauser *et al.*, 2009).

This is not a satisfying evolutionary explanation, however, because it confuses proximate and ultimate causes. Reciprocity is indeed cognitively difficult for many animal species, but this is precisely because they

have not been shaped by natural selection to engage in it. Said differently, the fact that reciprocity is cognitively difficult for some species is a *restatement* of the observation that reciprocity is absent in these species, not an ultimate *explanation* of this observation. Because they have been shaped by selection to do so, many nonhuman species perform cognitive operations that are arguably even more 'complex' than reciprocity, such as seeing the world in 3D, managing foraging decisions in a variable environment, or hiding and retrieving hundreds of resources in different locations (Kamil & Jones, 1997). Hence, we need an explanation as to why these complex functions have evolved in many species, but reciprocity has not. The present paper proposes that the problem is not the absolute complexity of reciprocity as compared to other biological functions, but the irreducible complexity of the evolutionary *step* that it requires.

The second hypothesis, due to Whitlock *et al.* (2007), highlights ecological constraints on the evolution of reciprocity. On this hypothesis, the reciprocal exchange of a resource can hardly be evolutionarily stable, because it implies that the value of the resource changes through time for both individuals, and in opposite directions. While this argument does highlight an important constraint on the evolution of reciprocity, its generality may be doubted, for two reasons.

First, it is in fact very easy to find situations in which the reciprocal exchange of a resource has a net benefit. Typically, resources have diminishing returns; hence, in all species in which resources are heterogeneously distributed in time and space, it would be beneficial for individuals to share the product of their foraging efforts in a reciprocal fashion, yielding a reduction in the temporal variance of resource intake. In fact, the buffering effect of sharing, most typically in the case of meat, is one of the most important functions of reciprocal exchange in human societies (see e.g. Gurven, 2004).

Second, this argument is valid only for the reciprocal exchange, back and forth, of a *single* kind of resource. According to Whitlock *et al.* (2007), heterogeneous forms of reciprocity, in which individuals exchange one resource/service for another, different resource or service, are much more frequent than homogeneous ones (Whitlock *et al.*, 2007, p. 1779). This claim is nonconsensual, however: most scholars argue that, quite to the contrary, all forms of reciprocal exchanges are equally rare in nonhumans (Connor, 1995a,b; Hammerstein, 2003; Bergmüller *et al.*, 2007; West *et al.*, 2007a; Clutton-Brock, 2009; Leimar & Hammerstein, 2010).

Finally, a group of scholars have very convincingly argued that most mutualistic interactions, both across and within species, can be explained by simpler, more parsimonious, mechanisms than reciprocity (Connor, 1986; Leimar & Connor, 2003; Bergmüller *et al.*, 2007; West *et al.*, 2007b; Leimar & Hammerstein, 2010; Raihani *et al.*, 2012). First, they argue that in many

interactions, cooperation is immediately beneficial for its provider, in which case we should speak of *by-product benefits*. Second, when by-product benefits are present, the receiver of these benefits can invest to trigger the production of even more benefits, in which case we should speak of *pseudoreciprocity* and not reciprocity. Third, in the negative case, individuals often have a direct interest in ‘punishing’, in which case we should speak of *sanction* rather than punishment.

However, whatever may be the empirical prevalence of these simpler mechanisms, it shall not be considered as an explanation of the rarity of reciprocal cooperation. Rather, the fact that most mutualistic interactions in extant species are based on other mechanisms is a further consequence of the bootstrapping problem raised by reciprocity. As this paper has shown, evolution cannot shape traits whose benefit is obtained via a conditional response on the part of others if this response must evolve at the same time as those very traits, because this raises a bootstrapping problem. However, evolution can yield cooperative traits whose benefit is obtained via a *pre-existing* response on the part of others, which occurs in simpler mechanisms.

To understand, consider the example of Lycaenid–ant associations described by Leimar & Connor (2003). The larvae of many species of butterflies from the family Lycaenidae associate with ants. Larvae secrete nectar from a dorsal gland, which is consumed by ants, who offer physical protection in exchange. Owing to the bootstrapping problem, this exchange could not have evolved as a reciprocal interaction, in which ants would produce nectar on purpose to provoke a protection response, and ants would protect larvae on purpose to trigger the continuous secretion of nectar. But that is not how this interaction evolved. Ants have a good reason to protect any food source, because it is adaptive for them to do so. Hence, lycaenid larvae could exploit this pre-existing response by secreting nectar, thus triggering ant protection. Whether this interaction should eventually be categorized as reciprocal or only pseudo-reciprocal can be debated, but it is not key. The important point is that it must have evolved, in one way or another, by recycling a pre-existing function which initially had more immediate benefits.

Relationship to other bootstrapping problems in evolution

Reciprocity is not the only kind of biological trait whose evolution raises a bootstrapping problem. In principle, any trait that entails an interaction between several genetic elements, either carried by the same or by different individuals, can raise the same problem. Within individuals, this includes all adaptive interactions between proteins in general and, in particular, all ‘send–receive’ systems in physiology (hormone-receptor, transcription factor-promoter, etc.). Across individ-

uals, the clearest example is communication. Hereafter, I use the term ‘multilateral adaptations’ to refer to these traits in general.

The bootstrapping problem raised by multilateral adaptations is nothing new. It has long been recognized in the case of communication, in which a signal and a response must appear together (Krebs & Dawkins, 1984). Surprisingly, however, this problem has never been acknowledged in the case of reciprocity. Evolutionary theorists have recognized, at least since Axelrod & Hamilton (1981), that the emergence of reciprocity requires the crossing of an invasion barrier, but not that the composite nature of reciprocity leads to a bootstrapping problem of the same sort as communication. This oversight may be explained by the fact that whereas communication and other send–receive systems clearly entail two different sides and thus two different abilities, it *seems* that reciprocity only entails one ability – the ability to perform ‘reciprocal cooperation’ – but, as this paper has argued, this is mistaken from a mechanistic point of view.

The comparison with other multilateral adaptations, however, does lead to a potential difficulty for the present hypothesis. Even though in principle all multilateral adaptations do raise the same bootstrapping problem, many such adaptations have evolved. In molecular and cellular biology, and in physiology, adaptive interactions between genes are ubiquitous. Similarly, in eusocial species, many sophisticated systems of communication have evolved among individuals whose evolutionary interests are very closely aligned (Hölldobler & Wilson, 2008 or see e.g. Seeley, 2010). This leads to the question: if other sorts of adaptations which also raise bootstrapping problems can evolve, then why is reciprocity so much rarer?

The evolution of multilateral adaptations always entails some recycling. One side needs to evolve first and then be used in a (more or less) novel way, when the other side evolves subsequently. The problem is that, in the specific case of reciprocity, this scenario entails very specific preconditions which are not likely to be met in general. To understand why, it is useful to compare reciprocity with communication.

Communication, and other send–receive systems, can evolve along two routes: ritualization or manipulation (Krebs & Dawkins, 1984; Scott-phillips *et al.*, 2012). In spite of important differences, the key point is that, in both routes, communication can evolve to the extent that the sender and the receiver have an *objective common interest* such that the effect of one on the other can be mutually beneficial. Otherwise communication cannot be evolutionarily stable. This explains why communication is particularly frequent among the individuals of eusocial species, and why send–receive systems are ubiquitous within organisms.

This also explains why the evolution of reciprocity is an order of magnitude more complex. By definition, in contrast with other mechanisms promoting cooperation

(by-product benefits, pseudoreciprocity and kin altruism), reciprocity does not require individuals to have an *objective* common interest. This is important because it allows reciprocity to generate mutual benefits in a much wider array of circumstances, because individuals on both sides actively respond to one another rather than relying on an exogenous common interest. However, this also makes the gradual evolution of reciprocity much less likely than other types of multilateral adaptations. Because the fitness benefits to the two individuals are not automatically aligned, the interaction must really benefit them *independently*. As compared to communication, the requirements are thus doubled. Communication is a mutually beneficial manipulation of *one* individual by another. Reciprocity is a mutually beneficial manipulation of *two* individuals by one another. Consequently, scenarios for its gradual emergence are far more constrained.

Scenarios for the gradual evolution of reciprocity

Such scenarios do exist, but they entail very specific preconditions. A detailed characterization of these preconditions in relationship to known instances of reciprocity in nature will require the construction of specific models, which will be the object of a further study. As an illustration, let me simply describe a possible scenario in the famous example of reciprocal allogrooming (e.g. as observed in impalas by Hart & Hart, 1992). Assume that, for an independent reason, some allogrooming is immediately beneficial to the groomer (say, owing to kinship). The geometric symmetry of grooming entails that when one individual grooms a partner's head, it is also easier for the partner to groom the first individual simultaneously, which generates a simple, contingent form of 'responsiveness'. Eventually, this contingent form of responsiveness can then select for an adaptive one, because it creates a selective pressure to give priority to grooming those who are also in a 'grooming mood'. Hence, the pre-existence of some cooperation, together with a spatial constraint, can eventually lead to the emergence of reciprocation.

As this example (and the prior example of Lycaenid-ants associations) illustrates, scenarios for the emergence of reciprocity imply some responsiveness to the cooperation of others that pre-exists for independent reasons and that is then accessorially recycled to contribute to reciprocity. This sheds light on the relative rarity of reciprocity, as there is no reason why this responsiveness should be found in general, other than under specific conditions (e.g. spatial symmetry). Moreover, this explains why most instances of reciprocity are debatable and can also be seen as mere instances of pseudoreciprocity (as was illustrated in the Lycaenid-ants example), because they all evolved by recycling a pre-existing responsiveness which initially brought more immediate benefits. Hence, disentangling

instances of genuine reciprocity from mere pseudoreciprocity is likely to be often difficult.

Human cooperation

Arguably, the major puzzle of reciprocity is the fact that humans offer plenty of evidence of it, whereas evidence in other species is very rare. The present paper does not offer an immediate solution to this puzzle, but I believe that it offers a prospect for a future solution. The insight that the major constraint limiting the evolution of reciprocity is of a mechanistic nature suggests that the origin of human uniqueness may be found in cognitive mechanisms. Reciprocity, like communication, can emerge through the recycling of functions that evolved for other purposes. Intuitively, therefore, it can be understood that the more 'generalizable' the cognitive mechanisms of a given species are, the easier it will be for such recycling to occur. This principle likely explains both why humans are exceptional communicators and exceptional reciprocators, but demonstrating this will require further formalization.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Data S1 Mathematical methods.

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