Individual memory and the emergence of cooperation

João Moreira [a], Jeromos Vukov [a], Cláudia Sousa [b,c], Francisco C. Santos [a,d], André F. d'Almeida [a,b], Marta D. Santos [a], Jorge M. Pacheco [a,e,*]

[a] ATP group, Centro de Matemática e Aplicações Fundamentais, Instituto para a Investigação Interdisciplinar, Universidade de Lisboa, Lisboa, Portugal
[b] Centro em Rede de Investigação em Antropologia, Lisboa, Portugal
[c] Departamento de Antropologia, Faculdade de Ciências Sociais e Humanas, Universidade Nova de Lisboa, Lisboa, Portugal
[d] Departamento de Engenharia Informática & INESC-ID, Instituto Superior Técnico, Universidade Técnica de Lisboa, Portugal
[e] Departamento de Matemática e Aplicações, Universidade do Minho, Braga, Portugal

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The social brain hypothesis states that selection pressures associated with complex social relationships have driven the evolution of sophisticated cognitive processes in primates. We investigated how the size of cooperative primate communities depends on the memory of each of its members and on the pressure exerted by natural selection. To this end we devised an evolutionary game theoretical model in which social interactions are modelled in terms of a repeated Prisoner's Dilemma played by individuals who may exhibit a different memory capacity. Here, memory is greatly simplified and mapped onto a single parameter m describing the number of conspecifics whose previous action each individual can remember. We show that increasing m enables cooperation to emerge and be maintained in groups of increasing sizes. Furthermore, harsher social dilemmas lead to the need for a higher m in order to ensure high levels of cooperation. Finally, we show how the interplay between the dilemma individuals face and their memory capacity m allows us to define a critical group size below which cooperation may thrive, and how this value depends sensitively on the strength of natural selection.

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From a Darwinian perspective, the pervasiveness of cooperation in nature is a difficult phenomenon to explain. If evolution is characterized by competition and the survival of the fittest, why should selfish unrelated individuals cooperate with each other? Evolutionary game theory (Maynard Smith 1982; Hofbauer & Sigmund 1998; Gintis 2000; Nowak 2006a; Sigmund 2010) provides a suitable mathematical formalism to investigate the evolutionary dynamics of cooperation in a population, from bacteria to primates, both nonhuman and human (Nowak 2006b).

In the absence of genetic relatedness between individuals, in which case kin selection provides the traditional framework (Hamilton 1964), several mechanisms promoting the emergence of cooperation have been extensively studied in the last few decades, such as mutualism (Brown 1983; Stevens & Hauser 2004), direct reciprocity through repeated interactions (Trivers 1971; Axelrod & Hamilton 1981; Melis et al. 2008; Van Segbroeck et al. 2012), pre-play communication (in the form of costless or costly) signalling (Skyrms 2004, 2010; Santos et al. 2011), indirect reciprocity through reputation (Alexander 1974; Sugden 1986; Alexander 1987), punishment (Boyd & Richerson 1992; Brandt et al. 2003), voluntary participation (Hauert et al. 2002) and network reciprocity (Santos & Pacheco 2005; Ohtsuki et al. 2006; Szabó & Fáth 2007; Addessi & Rossi 2011), among others. None of the previous models focused on or considered cognition explicitly, although they recognized that maintaining tabs on individuals (such as reputation markers) is cognitively challenging (Nowak & Sigmund 2005).

The idea of a highly developed cognition as the result of selection pressures from the very complex social relations of primates was first devised in primatology as the 'Machiavellian intelligence' hypothesis (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988) and later summarized as the social brain hypothesis (Dunbar 1998). These hypotheses postulate that the cognitive evolution that took place in the primate order occurred mainly because of its propensity for intense sociality, which in turn may be connected with the necessity of achieving cohesive, cooperative groups. Here we used a simple mathematical model to investigate whether requiring communities to act cooperatively, combined with limited cognitive skills (see below), limits the size of those groups.

Primates engage in multiple social cooperative behaviours. For instance, grooming interactions occur very frequently and are a means of reducing stress, eliminating parasites and maintaining social bonds (Schino 2001; Crockford et al. 2008; Newton-Fisher &

* Correspondence: J. M. Pacheco, ATP Group, CMAF, Instituto para a Investigação Interdisciplinar, P-1649-003 Lisboa Codex, Portugal.
E-mail addresses: pacheco@cii.fc.ul.pt, jorgem.pacheco@gmail.com (J. M. Pacheco).

Lee 2011; Tiddi et al. 2011). Although it is assumed that most of the cooperative events occur between kin, given the dynamics of the composition of the social groups, that is not always the case as several studies show (Schino 2001; Crockford et al. 2008; Newton-Fisher & Lee 2011). Chimpanzees, *Pan troglodytes*, for example, are male philopatric and are hence expected to be living and cooperating with male relatives. Lukas et al. (2005) analysed several chimpanzee groups and found a very low relatedness, suggesting that social interactions may not be driven primarily by kin relationships.

Experiments of food exchange made with capuchin monkeys, *Cebus apella*, showed that grooming had a greater influence on subsequent food-sharing behaviour in nonhabitual pairings than in habitual grooming pairs (de Waal 2000). Capuchins also seem to exchange grooming for other commodities such as tolerance and food sharing (Tiddi et al. 2011); in rhesus macaques, *Macaca mulatta*, previous alliances led to increased grooming (de Waal & Yoshihara 1983) whereas in longtailed macaques, *Macaca fascicularis*, experimental manipulation of grooming between individuals was seen to influence support in agonistic interactions (Hemelrijk 1994). It has been argued that maintaining a stable partnership relaxes the need for keeping tight tabs on behaviours, thus increasing the amount of social tolerance (de Waal 2000; Brosnan & de Waal 2002; de Waal & Brosnan 2006; de Waal & Suchak 2010). Cooperation and the maintenance of tabs on individuals, and in general the social relations of primates, are thought to require that individuals recognize others in their own group (Tomasello & Call 1997).

Several studies have shown that primates, like other animals, have the ability to recognize individuals based on vocal cues (Snowdon & Cleveland 1980; Rendall et al. 1996; Fitch & Fritz 2006) and from their faces (Pascalis & Bachevalier 1998; Parr et al. 2000; Neiworth et al. 2007; Dufour et al. 2009). Nevertheless, some authors (Proops et al. 2009) have argued that individual recognition can only be shown if the individuals are able to match individual cues in different modalities (cross-modal approach), that is, to match, for example, a picture of a groupmate with its vocalization, because it requires the subject to have a mental representation of the individual (Zayan 1994). In spite of the difficulties of training nonhuman primates to perform in auditory–visual intermodal matching (Hashiya & Kojima 2001b; Martinez & Matsuzawa 2009) some breakthroughs have been achieved, with some species of nonhuman primates showing the capacity for auditory–visual cross-modal representation (Hashiya & Kojima 2001a; Adachi et al. 2006; Adachi & Fujita 2007; Martinez & Matsuzawa 2009).

Here we assume that each individual in a community of size N has the capacity to remember the previous action of m ($m \leq N - 1$) of her conspecifics. Hence, individuals are able to identify (1) who the other $N - 1$ members of the community are, and, for m of these members, (2) what action (cooperation or defection) they have taken towards the focal individual in their previous social interaction. The fact that social interactions are frequent alleviates the requirement for long-term memory. We devised a theoretical framework to address in simple terms the coevolution of reciprocal cooperation and this stylized form of memory, thus investigating how reciprocal cooperation may emerge in response to evolutionary constraints (Stamps 1991; Brosnan & de Waal 2002; Brosnan et al. 2010). More specifically, we focused on the individual's capacity to remember the previous action of a limited number m of her conspecifics in a population of size $N > m$ (thereby assuming, also, the capacity for individuals to recognize and distinguish their conspecifics). Limited memory capacity has been described in previous theoretical and empirical studies (Milinski & Wedekind 1998; Cox et al. 1999; Qin et al. 2008; Alonso-Sanz 2009; Stevens et al. 2011; Volstorf et al. 2011).

In our model, individuals make up a finite population engaging in iterated Prisoner's Dilemma (PD) games, the harshest social dilemma of cooperation, given that both the fear of being cheated and the temptation to cheat act to drive the population towards the tragedy of the commons (Hardin 1968). We investigated how different levels of the individual capacity m of an individual to remember the previous action of others, thereby enabling individuals to respond accordingly in future interactions, help maintain cooperation.

METHODS

Prisoner's Dilemma

We investigated the evolutionary dynamics of a finite and small, well-mixed population of size N in which individuals play an iterated two-person PD game with each of the members of the population (Axelrod & Hamilton 1981). In each interaction, individuals can opt between two possible choices: to cooperate or to defect. Mutual cooperation leads to the reward R, while mutual defection results in a punishment P for both individuals. The remaining two outcomes occur when one player cooperates and the other defects, resulting in the payoff values of S (sucker's payoff) for the cooperator and T (temptation to defect) for the defector. The PD game is characterized by $T > R > P > S$; consequently, in a one-shot interaction, rational (that is, payoff maximizer) individuals will always choose defection, as it yields a higher payoff independently of the partner's decision, resulting in the payoff P for both of them instead of the higher reward R for mutual cooperation: Hence the dilemma. Without losing generality, we normalize the reward R to 1 and the punishment P to 0. At the same time, we rewrite the payoffs as a function of costs and benefits: a cooperator invests the cost c to grant the (higher) benefit b to the partner, i.e. $R = b - c = 1, P = 0, T = b$ and $S = -c$; given that b and c become interdependent through R, this leaves only one free parameter, so the payoffs take the following form: $R = 1, P = 0, T = b$ and $S = 1 - b$.

Moreover, we equipped individuals with the ability to recognize other individuals and to remember their past actions. This capacity is characterized by a single parameter m, defined as the number of partners whose previous action an individual can recall. In our model, individuals can adopt either the unconditional Defector strategy (D) or the (memory constrained) Conditional Cooperator (C_C) strategy, the latter associated with a particular value of m. Ds always defect, so the value of m is obviously of no use to them. C_C strategists, on the other hand, cooperate with neighbours as long as they do not remember their previous move. Otherwise, a C_C repeats the neighbour's previous action. That is, a C_C strategist behaves as a tit-for-tat (TFT) strategist (Rapoport & Chammah 1965) against 'known' partners and as an unconditional cooperator against 'unknown' partners. Hence, the C_C strategy interpolates between unconditional cooperators and conventional TFT, allowing a simple and overall analysis of the outcome of cooperation for an arbitrary m and population size N. Whenever $m = 0$, nothing will distinguish a C_C from an unconditional cooperator, whereas when $m = N - 1$, C_C becomes equivalent to TFT. Needless to say, errors in perceiving the partner's action or an accidental failure in responding in accord with C_C can have detrimental effects in strict TFT-like interactions. The introduction of 'generous TFT'-like strategies can help to avoid alternating defective moves via occasional forgiveness. However, we kept our model simple and did not consider explicitly errors during the interactions. As a result, we are able to discuss the model analytically, leading to simple expressions (see below). It is worth noting that concerning the memory of individuals, a similar approach was suggested by Aktipis (2006) in a one-shot PD model set-up with unconditional strategies, where individuals could

remember either the opposing defectors or cooperators while having the option to avoid interacting with 'undesirable' members of the population.

We take fitness as the accumulated payoff obtained from all interactions in which an individual participates. The average fitness per interaction for each of the strategies as a function of k, the number of cooperators in the population, is given by

$$f_{C_C}(k) = \frac{k-1}{N-1}R + \frac{N-k}{N-1}\left[\frac{m}{N-1}(wP+(1-w)S) + \frac{N-1-m}{N-1}S\right]$$
$$f_D(k) = \frac{N-1-k}{N-1}P + \frac{k}{N-1}\left[\frac{m}{N-1}(wP+(1-w)T) + \frac{N-1-m}{N-1}T\right] \quad (1)$$

where w is the probability of occurrence of a next game round in the iterated PD. The fitness for C_C accounts for interactions with other C_C strategists (first term) and with Ds, both those present in memory (first term in parenthesis) and absent from it (last term). The terms in the defector fitness can be explained in a similar way. The formulas are normalized by the average number of rounds $(1 - w)^{-1}$ to give the average fitness per round. If repeated interactions happen with a large enough frequency ($w \rightarrow 1$), then we can simplify the above expressions to:

$$f_{C_C}(k) = \frac{k-1}{N-1}R + \frac{N-k}{N-1}\left(\frac{m}{N-1}P + \frac{N-1-m}{N-1}S\right),$$
$$f_D(k) = \frac{N-1-k}{N-1}P + \frac{k}{N-1}\left(\frac{m}{N-1}P + \frac{N-1-m}{N-1}T\right) \quad (2)$$

That is, the strategies present in the population transform on average the original PD game into a different game, represented by the modified payoff matrix

$$
\begin{array}{cc}
& \begin{array}{cc} C_C & \quad\quad\quad D \end{array} \\
\begin{array}{c} C_C \\ D \end{array} &
\left(
\begin{array}{cc}
R & \frac{m}{N-1}P + \frac{N-1-m}{N-1}S \\
\frac{m}{N-1}P + \frac{N-1-m}{N-1}T & P
\end{array}
\right)
\end{array} \quad (3)
$$

Individuals revise their behaviour by copying those who are perceived as more successful. Successful behaviours will thus be copied and will tend to spread in the population. At each round an individual i adopts the strategy of a randomly chosen individual j with a probability W which may be written in terms of the so-called Fermi distribution $W(\Delta f) = [1 + e^{-\beta\Delta f}]^{-1}$, where $\Delta f = f_j - f_i$ stands for the fitness difference and β represents noise associated with the individuals' ability to perceive the fitness differences and thereby errors in decisions about strategy adoption. This update mechanism is known as the pairwise comparison update rule (Traulsen et al. 2006; Szabo et al. 2009). Hence, β introduces the possibility that an individual copies the strategy of another whose fitness is actually lower. For high values of β, strategies with higher fitness are almost always adopted and we obtain (in the limit of very large β) pure copying dynamics. This corresponds to the limit of strong selection. For $\beta \rightarrow 0$ selection becomes so weak that evolution proceeds by random drift. Note that, in fact, this update rule is similar to Schlag's (1998) proportional imitation rule and not a copy-if-better rule. In our terms, an individual copies another that performed better with a probability that increases with the fitness difference between them. One of the reasons for avoiding copy-if-better is that it has been described as rare in nature (Laland 2004). Moreover, to the simplicity of the evolutionary dynamics used here one may add the fact that it is general enough to be employed for both cultural and genetic evolution (see e.g. Sigmund

2010). While in the former case one can argue that individuals will be influenced by the actions and achievements of others, in the latter it is noteworthy that our dynamics can be recast in the form of a (frequency-dependent) death–birth process ubiquitous in models of genetic evolution (see e.g. Nowak et al. 2004; Traulsen et al. 2006; Nowak 2006a).

Gradient of Selection

Using the pairwise comparison update rule given above, one can compute the probabilities $\Omega^+(k)$ and $\Omega^-(k)$ for the number k of C_C's in the population to grow or diminish by one in a given round:

$$\Omega^+(k) = \frac{N-k}{N}\frac{k}{N-1}W[f_{C_C}(k) - f_D(k)]$$
$$\Omega^-(k) = \frac{k}{N}\frac{N-k}{N-1}W[f_D(k) - f_{C_C}(k)] \quad (4)$$

where the first two factors give the probability that a C_C and a D meet each other while the $W(\Delta f)$ function shows the probability of the respective strategy adoption process.

The difference $G(k) = \Omega^+(k) - \Omega^-(k)$ describes the gradient of selection (Pacheco et al. 2009a, b; Souza et al. 2009; Pacheco & Santos 2011; Santos & Pacheco 2011) that indicates the most likely outcome of evolution when the population is composed of k C_C individuals: When $G(k) > 0$ ($G(k) < 0$), the direction of selection acts to increase (decrease) the number of C_C individuals.

Fixation Probabilities

In finite populations, and in the absence of mutations, the evolutionary dynamics will only stop whenever the population reaches a monomorphic state. Hence, it is often of interest to evaluate the fixation probability φ_k, that is, the probability that the system fixates in a monomorphic cooperative state starting from a given number k of C_C's. This quantity is given by (Traulsen et al. 2006)

$$\varphi_k = \sum_{i=0}^{k-1}\prod_{j=1}^{i}\rho_j \bigg/ \sum_{i=0}^{N-1}\prod_{j=1}^{i}\rho_j \quad (5)$$

where $\rho_k = \frac{\Omega^-(k)}{\Omega^+(k)}$. Under neutral selection (that is, in the limit $\beta \rightarrow 0$) the fixation probability trivially reads $\varphi_k^N = k/N$, providing a convenient reference point. For a given k, whenever $\varphi_k > \varphi_k^N$, natural selection will favour cooperative behaviour, the opposite being true when $\varphi_k < \varphi_k^N$.

Evolutionary Dynamics in Large Populations

In the continuous limit ($N \rightarrow \infty$), evolution is conveniently described by the replicator equation (Hofbauer & Sigmund 1998) $\dot{x} = x(1-x)(f_{C_C} - f_D)$ ($x = k/N$). In this limit, the condition for C_C to be an evolutionarily stable strategy $\left(R > \frac{m}{N-1}P + \frac{N-1-m}{N-1}T\right)$ (Maynard Smith 1982; Hofbauer & Sigmund 1998) takes the following simple form: $\frac{m}{N-1} > \frac{T-R}{T-P}$. For the PD game defined as $T = b$, $R = b-c$, $P = 0$ and $S = -c$ we obtain

$$\frac{m}{N-1} > \frac{c}{b} \quad (6)$$

This shows how a population of individuals who have the necessary cognitive skills to keep a record of previous encounters may sustain cooperation for the entire range of the PD.

RESULTS AND DISCUSSION

The results depicted in Fig. 1 show that, with increasing memory capacity (increasing m), the minimum number of C_C required to promote the emergence of cooperation in the population (given by the intercept of $G(k)$ with the horizontal axis) is reduced. Furthermore, the shape of the gradients of selection clearly indicate that, population-wide, the game at stake changes with m, exhibiting several thresholds: For $m < m_1 = (N-1)/2$ the game remains a PD, with a single stable fixed point associated with full defection; for $m_1 < m < m_2 = (N-1)$ we obtain an effective coordination game (also known as a stag-hunt game, Skyrms 2004), where two stable fixed points (full cooperation and full defection) are separated by an internal, unstable fixed point; finally, for $m = m_2 = (N-1)$ we obtain a cooperator dominant scenario (Hofbauer & Sigmund 1998), also known as a harmony game, where cooperation is mostly advantageous and the only stable fixed point becomes full cooperation. Notably, this occurs even for the most stringent dilemma conditions studied ($b = 2.0$) which translates into a high temptation to defect and also high cost to pay if an individual cooperates and is cheated upon by the partner. In the case of the coordination region, the final composition of the population depends on the initial frequency of C_C.

These results contrast with the predictions of earlier studies ($m = 0$), where cooperators are always at a disadvantage with respect to defectors and the fixation of cooperators in populations as small as $N = 20$ would only be possible under very weak selection, associated with small values of the parameter β, such as β = 0.01 (Traulsen et al. 2006).

Clearly, being able to keep track of the actions of more and more individuals leads C_C to spread through the population. Given that, population-wide, the effective game played by individuals changes with m, we now investigate the influence of increasing competition (by means of the dilemma) and the complexity of social groups (by changing their size and m) in the observed levels of cooperation. To this end, we calculate the fixation probability ϕ_1 of a single C_C, in groups (populations) of different sizes and, for each size, the critical value m_{cr} above which the fixation probability exceeds the neutral value $\phi_1 = 1/N$. The results are shown in Fig. 2, where we plotted m_{cr} for several values of b: 1.1, 1.25, 1.50, 1.75 and 2.0 (keeping $c = b-1$ and β = 1.0) as a function of group size. Indeed, N can vary

Figure 2. Critical m values as a function of the group (population) size N for different values of b and β = 1.0. By diminishing the strength of the dilemma, the pressure for a higher cognition is reduced and the fixation of a single C_C is facilitated.

between 2 and 30 in accord with average maximum population sizes described in several species of primates (Kudo & Dunbar 2001; Dunbar & Shultz 2007a, b; Pérez-Barbería et al. 2007; Shultz & Dunbar 2010).

By reducing b (and at the same time c), we are correspondingly reducing the competitive pressure on the population. Translating this into primate grooming terms means that grooming without being reciprocated is less severe for lower b, as in this case there are, for instance, favourable conditions that reduce competition, such as abundance of food, low predation risk, among others (te Boekhorst & Hemelrijk 2000). If one returns to the above-mentioned example of grooming, this means that grooming other individuals without remembering if they groomed before is less costly for lower values of b, which would help maintain group cohesion. Grooming can be costly for the individual performing it as it can reduce both resting and foraging time, which could cause problems such as altered cortisol levels (Van Schaik et al. 1991), as was shown in mouse-eared bats, *Myotis myotis* (Giorgi et al. 2001). Also, if an individual is groomed and is not groomed back, he/she can accumulate parasites that could also be costly in the long-term. In our case, b could be translated into lower parasitic rates for example, which would mean that the cost of grooming and not being groomed back would be lower to each individual.

The results in Fig. 2 clearly show that m_{cr} grows linearly with group size, increasing also with increasing dilemma strength. This relation means that the critical memory capacity is always at the same fraction of the population. However, from the individual point of view, it means that the group members have to remember the actions of more and more groupmates with increasing group sizes. The results also provide important clues as to why primates preferentially aggregate in social cliques within larger group sizes. Savannah baboons, *Papio* spp., constitute, perhaps, the most striking example, as these aggregate in group sizes ranging from 10 to 200 individuals, but have been known to associate in smaller clique sizes when foraging, depending on seasonal food abundance and distribution (Anderson 1981; Whiten et al. 1991; Henzi & Barrett 2003; Swedell 2011).

With cliques, selection pressures of social complexity on the evolution of a highly developed and very energetically expensive cognition could be reduced. However, there may have been a point in primate evolution where predation risk was probably high enough to promote an increase in group size, thus affecting group cohesion by means of increasing intergroup competition (Janson & Goldsmith 1995). With more nonrelated individuals being introduced into the group as a consequence of such risks (and
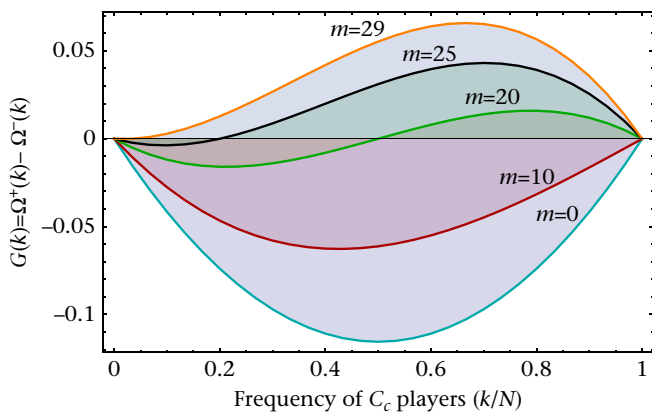
Figure 1. The gradient of selection $(\Omega^+(k) - \Omega^-(k))$ is plotted as a function of the frequency of C_c reciprocators for different values of m in a population of $N = 30$ (parameters are $b = 2.0$, $c = b-1$ and β = 1.0). The minimum number of C_C's required for overcoming defectors decreases with increasing memory capacity. When $G(k) = 0$, the sign of $G(k)$ in the vicinity of these points indicates whether it is a stable ($G(k) > 0$ to the left, $G(k) < 0$ to the right) or unstable ($G(k) < 0$ to the left, $G(k) > 0$ to the right) fixed point. The same qualitative results remain valid as the population size increases up to $N = 300$.
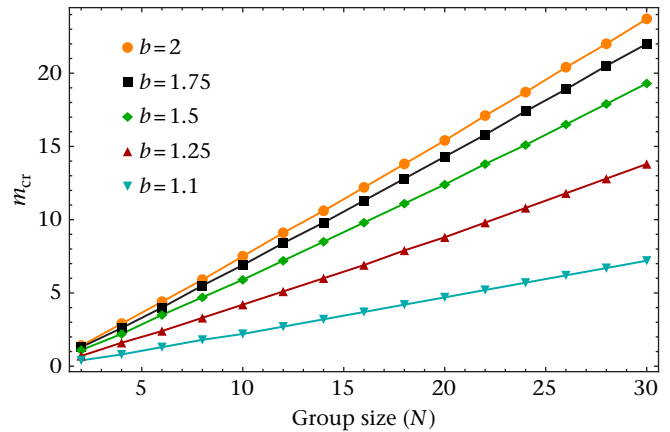
consequential genetic diversity), one would potentially witness an added pressure for the evolution of better memory if cooperation were to be maintained (Van Schaik 1989; te Boekhorst & Hemelrijk 2000). To verify whether this last premise holds under varying degrees of selection pressures, we plotted m_{cr}/N as a function of b for various values of β. Figure 3 shows that the further we depart from neutral drift and the harder the game becomes (larger b), the more difficult it is to maintain cooperation without higher cognitive capacity. For example, for a dilemma characterized by $b = 1.1$, an m_{cr}/N of 0.32 (that is, remembering the past actions of about one-third of the population) is needed at β = 1.0, while at β = 10 an m_{cr}/N of 0.51 is now required to reach the same outcome. This entails a significant pressure for larger memory capacity to evolve.

We further note that the results of Fig. 2 are contained in the β = 1 line of Fig. 3 (for $N = 30$). Naturally, the model leads to results in agreement with those obtained by Traulsen et al. (2006) for one-shot games, in which very high values of the intensity of selection render cooperation more difficult.

By copying the action of the partner in a previous encounter in a group in which multiple 2 × 2 iterated PD games are played in a constrained memory capacity set-up, we are thus able to account for the evolution of cooperative behaviour in a social group, for varying group sizes and selection pressures. In the real world, there has been a debate on the possibility and function of episodic-like memory in primates (Schwartz & Evans 2001; Cheke & Clayton 2010). Our model provides a less demanding type of memory that could explain the maintenance of cooperation in large group sizes. Unlike episodic-like memory, we do not require individuals to remember information about an event (what, where and when) based on single-trial learning (Schwartz & Evans 2001), over long periods of time.

In keeping with this discussion, we hope that future field and experimental data will help reveal whether this type of memory may be identified in primates. This might be achieved by explicitly manipulating experimental procedures to assess whether specific individuals remember how they were treated in a previous session. Needless to say, reciprocal behaviour across primates is also difficult to assess. It should be noted, for instance, that the little solid evidence that exists for the costs involved in a cooperative act, probably owing to the difficulty in assessing them (Hammerstein 2003), has previously led some behaviours such as harassment, begging, tolerated food theft, stress reduction or nepotistic cooperation to be characterized as reciprocal and cooperative, when in fact, they may not be (Stevens & Stephens 2002; Stevens 2004;
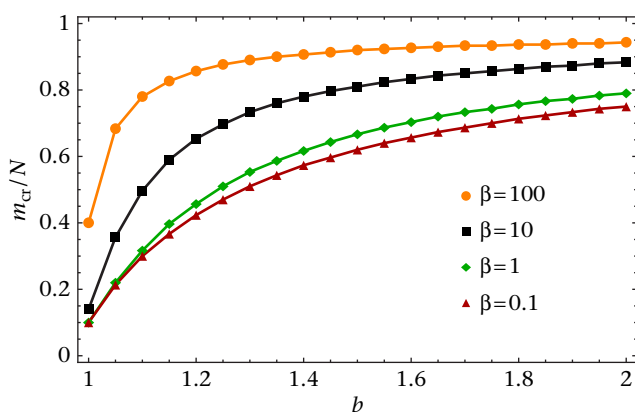
Stevens & Gilby 2004; Gilby 2006; Jensen et al. 2006; Crockford et al. 2008; Silk 2009; Jaeggi et al. 2010), and there is evidence that suggests that harassment and begging behaviours account for much of the supposed reciprocal behaviour in primates (Stevens & Stephens 2002; Stevens 2004; Stevens & Hauser 2004; Jaeggi et al. 2010).

CONCLUSIONS

We have presented a simple evolutionary game theory model that shows how the ability to remember past actions, relate them to specific individuals, and acting according to this registry promotes cooperation. We showed that increasing the group sizes adds pressure for individuals to remember actions from more and more members of their group in order for cooperation to survive. This simple form of memory can maintain cooperation in larger and possibly more complex societies, in line with Schino & Aureli (2009) and other primate literature on reciprocity, establishing a well-defined association between the size of cohesive groups in which cooperation may thrive, and the memory capacity needed to manage and use information on past interactions.

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