Evolution of Norms in a Multi-Level Selection Model of Conflict and Cooperation

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Abstract: We investigate the evolution of social norms in a game theoretical model of multi-level selection and mutation. Cooperation is modelled at the lower level of selection by means of a social dilemma in the context of indirect reciprocity, whereas at the higher level of selection conflict is introduced via different mechanisms. The model allows the emergence of norms requiring high levels of cognition. Results show that natural selection and mutation lead to the emergence of a robust yet simple social norm, which we call stern-judging. Stern-judging is compatible with expectations that anthropologists have regarding the Pleistocene hunter gatherer communities. Perhaps surprisingly, it also fits very well recent studies of the behaviour of reputation-based *e-trading*. Under stern-judging, helping a good individual or refusing help to a bad individual leads to a good reputation, whereas refusing help to a good individual or helping a bad one leads to a bad reputation. The lack of ambiguity of stern-judging, where implacable punishment is compensated by prompt forgiving, supports the idea that simplicity is often associated with evolutionary success.

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1. Introduction

Natural selection is conventionally assumed to favour the strong and selfish who maximize their own resources at the expense of others. But many biological systems, and especially human societies, show persistent patterns of altruistic, cooperative interactions(1), forming large social groups in which cooperation among non-kin is widespread. Therefore, one may naturally wonder: How can natural selection promote unselfish behaviour?

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2. The Mathematics of Give and Take

The problem may be mathematically formulated in the context of evolutionary game theory(2). Following the work of Hamilton, Trivers, and Wilson(3-5), an act is altruistic if it confers a bene?t $\boldsymbol{b}$ to another individual in spite of accruing a cost $\boldsymbol{c}$ to the altruist (where it is assumed, as usual, that $\boldsymbol{b}>\boldsymbol{c}$). In this context, several mechanisms have been invoked to explain the evolution of altruism, but only recently an evolutionary model of indirect reciprocity has been developed by Nowak and Sigmund(6). According to Alexander(7), indirect reciprocity presumably provides the mechanism which distinguishes us, humans, from all other living species on Earth. Moreover, as recently argued in(8), "*indirect reciprocity may have provided the selective challenge driving the cerebral expansion in human evolution*". Unlike direct reciprocity, which reflects the common principle "*I scratch your back and you scratch mine*", indirect reciprocity conveys the motto "*I scratch your back and someone else will scratch mine*".We may assume an underlying mechanism of reputation through which an individual, by providing help to another, increases her reputation in such a way that it will become more likely for others to help her in turn, boosting cooperation. As became clear in the model developed by Nowak and Sigmund(6), the rule defining the conditions under which the reputation of an individual will change depending on her action towards a third party and that third party's reputation constitutes the norm of the society. Nowak and Sigmund showed that cooperation under indirect reciprocity is feasible when the ruling norm is "***image score***", whereby an individual always increases her reputation by helping another individual. Obviously, ***image score*** is but one example of a myriad of possible norms, some of which may ultimately promote cooperation, unlike others. The model developed by Nowak and Sigmund(6), despite dealing with a single norm, had an inherent level of strategic complexity which precluded its extension towards an exhaustive study of norms *per se.* On the other hand, the model provided clear-cut links between norms of cooperation and social norms studied long before in the context of economics(9), also associated with community enforcement(10). Before the development of the simpler models we shall address in the following, the consensus from both economics and evolutionary biology was that reputation based cooperation must be associated with norms requiring high levels of cognition(8).

3. From the Pleistocene to the Internet

Anthropologists have discussed for a long time the features and limitations related to the social structure of hunter-gatherers during the Pleistocene(11). Such egalitarian, small communities must have been under the influence of simple norms, more complex norms being associated with the emergence of societies at a larger scale(12, 13). Consequently, it has remained unclear to which extent indirect reciprocity may provide a mechanism to explain reputation based cooperation in more primitive societies.

More recently, and in the midst of the information age, studies have shown that relatively low levels of cognition (associated with simple norms) seem to be the rule in modern means of economic exchange such as *e*-trade, which also rely on reputation-based mechanisms of cooperation (14-16). Indeed, anonymous one-shot interactions between individuals loosely connected and geographically dispersed usually dominate *e*-trade, raising issues of trust-building and moral hazard (17). Reputation in *e*-trade is introduced via a feedback mechanism which announces rating of sellers. Despite the success and high levels of cooperation observed in *e*-trade, it has been found (14) that publicizing a detailed account of the seller's feedback history does not improve cooperation, as compared to publicizing only the seller's most recent rating. In other words, practice shows that simple reputation-based mechanisms are capable of promoting high levels of cooperation. In view of the previous discussion, it is hard to explain the success of *e*-trade on the basis of the results obtained so-far for reputation-based cooperation in the context of indirect reciprocity.

4. A World in Black and White

Considerable insight into the nature of social norms became possible after some major simplifications were introduced in the original model of Nowak and Sigmund (6). Ohtsuki and Iwasa (18) and Brandt and Sigmund (19) have developed, simultaneously and independently, a model of binary assessment in a world in black and white, in which reputations can only take one of two values – *GOOD* or *BAD*. This model has influenced many studies since then(8, 17-23). In the original work of Ohtsuki and Iwasa an exhaustive search has been made in infinite populations under the same social norm, spanning all possible social norms in such a world in black and white. In their model, the norm constitutes a rule defining the reputation of a focal individual A, given his action towards another individual B, A's reputation and B's reputation. These three factors contributing to define the new reputation of individual A define so-called third order norms.

5. The Leading Eight

In this context, eight norms were found to be particularly efficient in promoting cooperation. These so-called ***leading eight*** are depicted in Fig. 1. It is noteworthy that the norm ***image-score*** proposed by Nowak and Sigmund(6) is not part of the ***leading eight***. On the other hand, this study addresses the stability of norms in infinite populations in which ALL individuals adopt the same strategy, information is public, no errors take place and stability is studied against invasion by individuals adopting a different norm and strategy. Despite the great insight provided by this study, many of simplifications adopted, with the aim of obtaining analytical solutions, raise questions concerning the connection of these results to real-world situations. Indeed, while it is reasonable to assume that a given population evolves under a common social norm, it is hard to imagine that all individuals adopt exactly the same strategy and that the society is free from errors both in what concerns decisions, but also in what concerns information spread. How do norms evolve in populations where such errors co-exist with diversity in individual strategies?

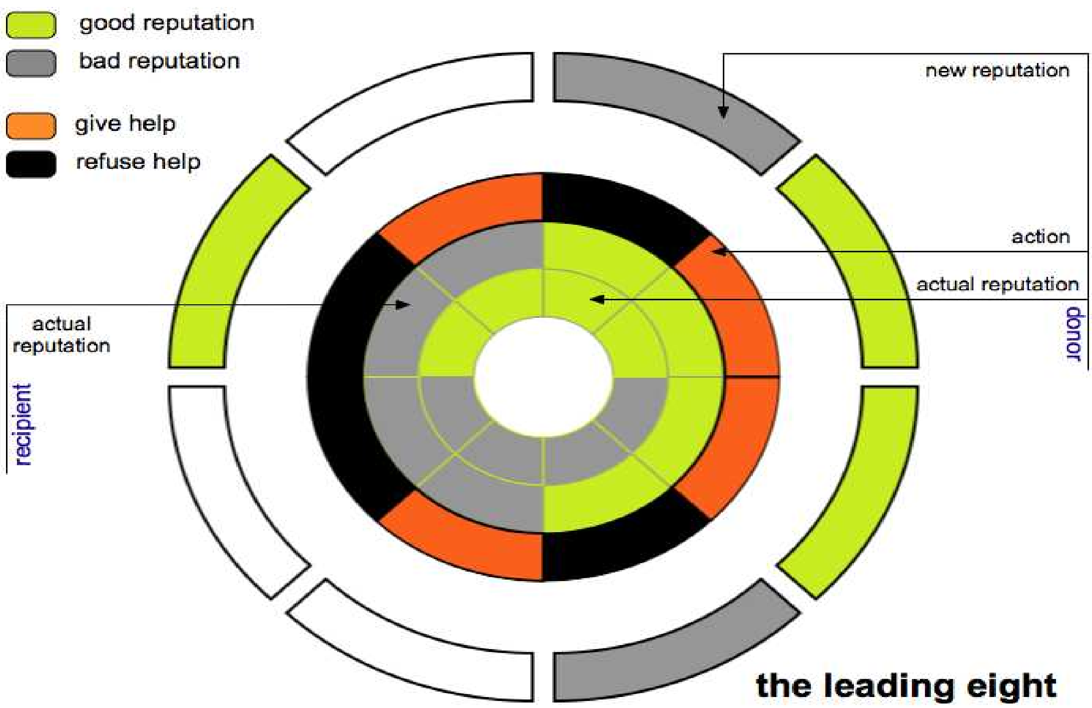

Fig. 1 Norm complexity and the Leading Eight Norms. The higher the order (and complexity) of a norm, the more "inner" layers it acquires. The outer layer stipulates the donor's new reputation based on the 3 different reputation/action combinations aligned radially layer by layer: Inwards, the first layer identifies the action of the donor. The second identifies the reputation of the recipient; the third the reputation of the donor. The 3 white "slices" can be associated with either *GOOD* (green) or *BAD* (grey) reputations. Consequently, we have 2^3 norms – the leading eight found by Ohtsuki and Iwasa. Note that, in this convention, second order norms exhibit a mirror symmetry with respect to the equatorial plane (disregarding the innermost layer). As a result, only two second order norms can incorporate the leading-eight.

6. A Model of Conflict and Cooperation

Let us consider a world in black and white consisting of a set of tribes, such that each tribe lives under the influence of a single norm, common to all individuals (see Fig. 2). Each individual engages once in the indirect reciprocity game with all other tribe inhabitants. Her action as a donor will depend on her individual strategy, which dictates whether she will *provide help* or *refuse to do it* depending on her and the recipient's reputation. In the indirect reciprocity game, any two players are supposed to interact at most once with each other, one in the role of a potential donor, while the other as a potential receiver of help. Each player can experience many rounds, but never with the same partner twice, direct retaliation being impossible. By helping another individual, a given player may increase (or not) her reputation, which may change the pre-disposition of others to help her in future interactions. However, her new reputation

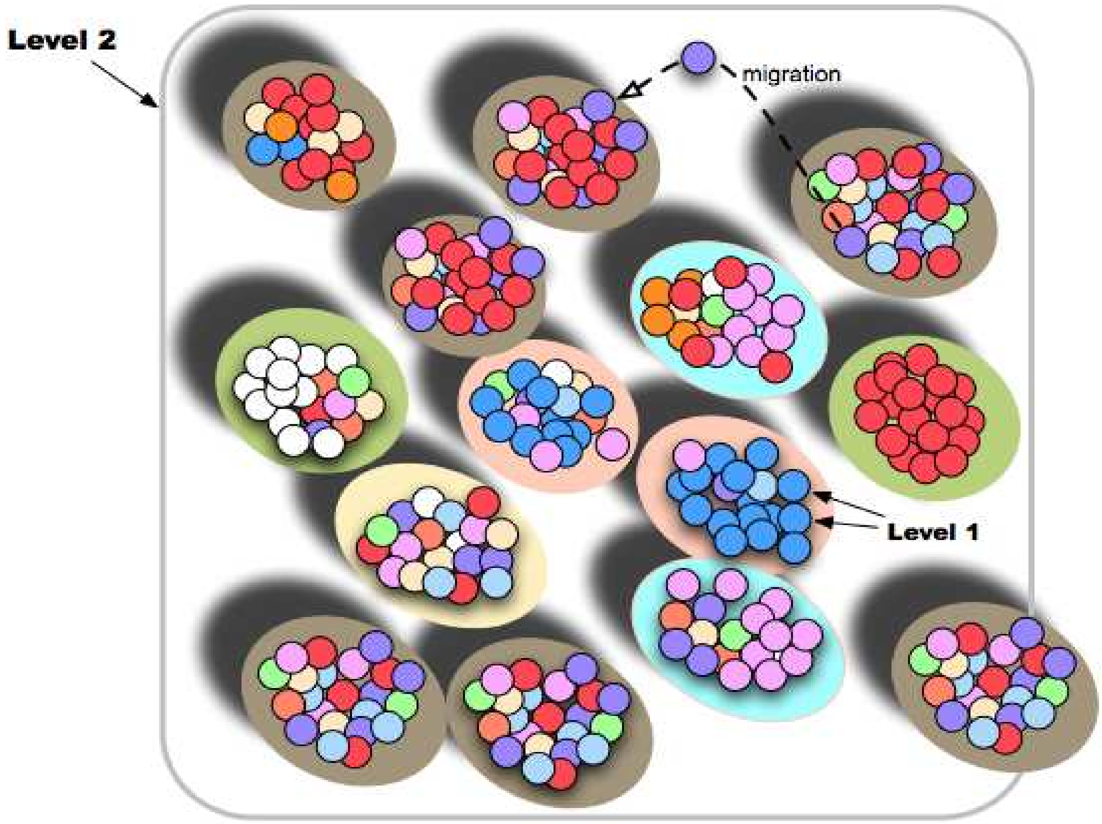

Fig. 2 Norm evolution under conflict and cooperation. Each palette represents a tribe in which inhabitants (coloured dots) employ different strategies (different colours) to play the indirect reciprocity game. Each tribe is influenced by a single social norm (common background colour), which may be different in different tribes. All individuals in each tribe undergo pairwise rounds of the game (lower level of selection, level 1 in figure), whereas all tribes also engage in pairwise conflicts (higher level of selection, level 2 in figure). As a result of the conflicts between tribes, norms evolve, whereas evolution inside each tribe selects the distribution of strategies which best adapt to the ruling social norm in each tribe.

depends on the social norm used by her peers to assess her action as a donor. Reputations are public: this means that the result of every interaction is made available to every one through the "indirect observation model" introduced in (18) (see also (21)). This allows any individual to know the current status of the co-player without observing all of her past interactions. On the other hand, this requires a way to spread the information (even with errors) to the entire population: Language seems to be an important cooperation promoter(24) although recent mechanisms of reputation spreading rely on electronic databases (e.g., in *e*-trade, where reputation of sellers is centralized). Since reputations are either *GOOD* or *BAD*, there are $\boldsymbol{2^4=16}$ possible strategies, encoded as shown in Table 1, further listed in more detail in Table 2, together with known names from previous studies. On the other hand, the number of possible norms depends on their associated order. The simplest are the so-called *first order norms*, in which all that matters is the action taken by the donor. In *second order norms* the reputation of one of the players (donor or recipient) also contributes to decide the new reputation of the donor. And so on, in increasing layers of complexity (and associated requirements of cognitive capacities from individuals) as shown in Fig. 1, which illustrates the features of third order norms such as those we employ here. Any individual in the tribe shares the same norm, which in turn raises the question of how each inhabitant acquired it. We shall not explore this issue here. It is likely that a common norm contributes to the

***donor*'s reputation**	***recipient*'s reputation**	***donor*'s action**
GOOD	*GOOD*	**Y** / **N**
GOOD	*BAD*	**Y** / **N**
BAD	*GOOD*	**Y** / **N**
BAD	*BAD*	**Y** / **N**

Table 1 Bit-encoding of individual strategies. Each individual has a strategy encoded as a four-bit string (Y=1 and N=0). For each combination pair of donor and recipient reputations, the strategy prescribes individual's action. There are a total of 2^4=16 strategies, identified in Table 2.

overall cohesiveness and identity of a tribe. For a norm of order $\boldsymbol{n}$ there are 2^{2^n} possible norms, each associated with a binary string of length 2^n. We consider third order norms (8 bit-strings, Fig. 1): In assessing a donor's new reputation, the observer has to make a contextual judgment involving the donor's action, as well as her and the recipient's reputations scored in the previous action. We introduce the following evolutionary dynamics in each tribe: During one generation all individuals interact once with each other via the indirect reciprocity game. When individuals "reproduce" they replace their strategy by that of another individual from the same tribe, chosen proportional to her accumulated payoff(19). The most successful individuals in each tribe have a higher reproductive success. This indirect reciprocity game provides the basis for the cooperation dilemma that each individual is facing in each tribe. Since different tribes are "under the influence" of different norms, the overall fitness of each tribe will vary from tribe to tribe, as well as the plethora of successful strategies which thrive in each tribe (Figure 2). This describes individual selection in each tribe (Level 1 in Fig. 2).

Tribes engage in pairwise conflicts with a small probability, associated with selection between tribes. After each conflict, the norm of the defeated tribe will change towards the norm of the victor tribe, as detailed in the METHODS section (Level 2 in Fig. 2). We consider different forms of conflict between tribes, which reflect different types of inter-tribe selection mechanisms: *group selection*(7, 13, 25-29) based on the average global payoff of each tribe (involving different selection processes and intensities – imitation dynamics, a Moran-like process as well as selection resulting from inter-tribe conflicts modeled in terms of games: The display game of war of attrition, and an extended Hawk-Dove Game(20, 22). We perform extensive computer simulations of evolutionary dynamics of sets of 64 tribes, each with 64 inhabitants. Once a stationary regime is reached, we collect information for subsequent statistical analysis (cf. methods). We

strategy name	*GG*	*GB*	*BG*	*BB*
ALLD	N	N	N	N
1	N	N	N	Y
AND	N	N	Y	N
SELF	N	N	Y	Y
4	N	Y	N	N
5	N	Y	N	Y
6	N	Y	Y	N
7	N	Y	Y	Y
8	Y	N	N	N
9	Y	N	N	Y
CO	Y	N	Y	N
OR	Y	N	Y	Y
12	Y	Y	N	N
13	Y	Y	N	Y
14	Y	Y	Y	N
ALLC	Y	Y	Y	Y

Table 2 Different individual strategies in indirect reciprocity game. We identify the different strategies and how they determine the action of a donor (**N**=no, do not provide help, **Y**=yes, provide help), given the reputation pair donor/recipient. Whereas some of these strategies have assumed well-known designations in the literature, others remain named by their numeric order.

compute the frequency of occurrence of bits ***1*** and ***0*** in each of the 8 bit locations. A bit is said to fixate if its frequency of occurrence exceeds or equals *98%*. Otherwise, no fixation occurs, which we denote by "***X***", instead of "***1***" or "***0***". We analyze 500 simulations for the same value of ***b***, subsequently computing the frequency of occurrence φ_1, φ_0 and φ_X of the bits "***1***", "***0***" and "***X***", respectively. If $\varphi_1 > \varphi_0 + \varphi_X$ the final bit is ***1***; if $\varphi_0 > \varphi_1 + \varphi_X$ the final bit is ***0***; otherwise we assume it is indeterminate, and denote it by "•". It is noteworthy that our bit-by-bit selection/transmission procedure, though artificial, provides a simple means of mimicking biological evolution, where genes are interconnected by complex networks and yet evolve independently.

7. Results

The results, for different values of ***b*** are given in Table 3, showing that a unique, ubiquitous social norm emerges from these extensive numerical simulations. This norm is of ***second-order***, which means that all that matters is the action of the donor and the reputation of the receiver. It is depicted in Fig. 3. In other words, even when

b	Imitation dynamics	Moran	Pairwise Comparison	War of attrition	Hawk-Dove
2	1001 1001	1•01 1001	1001 1001	•••• ••••	1001 1001
≥ 3	1001 1001	1001 1001	1001 1001	1001 1001	1001 1001

Table 3 Emerging social norm. For each value of the benefit b (c=1), each column displays the eight-bit norm emerging from the analysis of 500 simulations employing the conflict method between tribes indicated as column headers. Irrespective of the type of conflict, the resulting norm which emerges is always compatible with stern-judging.

individuals are equipped with higher cognitive capacities, they rely on a simple norm as a key for evolutionary success. In a nutshell, "*helping a good individual or refusing help to a bad individual leads to a good reputation, whereas refusing help to a good individual or helping a bad one leads to a bad reputation*". Moreover, we find that the final norm is independent of the specifics of the second level selection mechanism, i.e., different types of conflict will alter the rate of convergence, but not the equilibrium state. In this sense, we conjecture that more realistic procedures will lead to the same dominant norm.

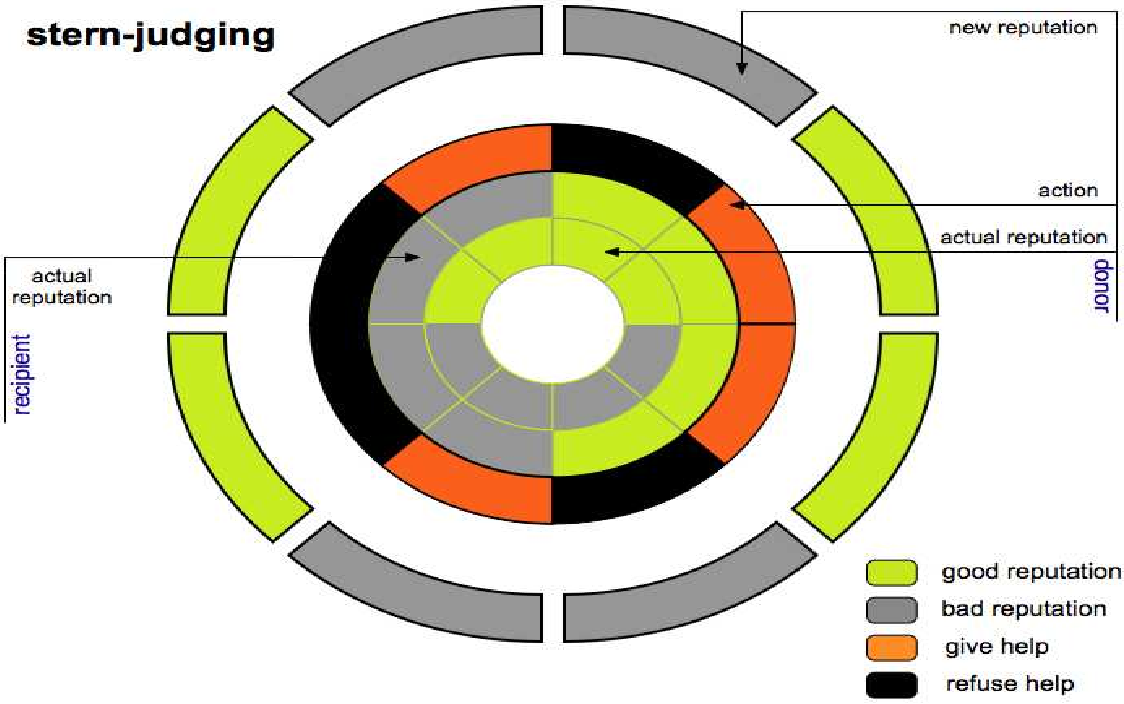

Fig. 3 Stern-judging. Out of the 2^8 possible norms, the highly symmetric, second order norm shown as the outer layer emerges as the most successful norm. Indeed, *stern-judging* renders the inner layer (donor reputation) irrelevant in determining the new reputation of donor. This can be trivially confirmed by the symmetry of the figure with respect to the equatorial plane (not taking the inner layer into account, of course).

8. Prompt Forgiving and Implacable Punishment

The success and simplicity of this norm relies on never being morally dubious: To each type of encounter, there is one *GOOD* move and a *BAD* one. Moreover, it is always possible for anyone to be promoted to the best standard possible in a single move. Conversely, one bad move will be readily punished(30, 31) with the reduction of the player's score. This prompt forgiving and implacable punishment leads us to call this norm ***stern-judging***(22).

Long before the work of Nowak and Sigmund(6) several social norms have been proposed as a means to promote (economic) cooperation. Notable examples are the *standing* norm, proposed by Sugden ..(9) and the norm proposed by Kandori ..(10) as a means to allow community enforcement of cooperation. When translated into the present formulation, *standing* constitutes a third-order norm, whereas a fixed-order reduction of the social norm proposed by Kandori (of variable order, dependent on the benefit to cost ratio of cooperation) would correspond to ***stern-judging***. Indeed, in the context of community enforcement, one can restate ***stern-judging*** as: "*Help good people and refuse help otherwise, and we shall be nice to you; otherwise, you will be punished".*

It is therefore, most interesting that the exhaustive search carried out by Ohtsuki and Iwasa(18, 21) in the space of up to third-order norms found that these two previously proposed norms were part of the so-called leading-eight norms of cooperation. On the other hand, *image-score*, the norm emerging from the work of Nowak and Sigmund(6) which has the attractive feature of being a simple, second-order norm (similarly to ***stern-judging***) does not belong to the leading-eight. Indeed, the features of *image-scoring* have been carefully studied in comparison to *standing*(32-34), showing that *standing* performs better than *image-scoring*, mostly in the presence of errors(19).

9. The Emergence of Good and Evil

Although we used the words GOOD and BAD to describe possible tags, these are somewhat unfortunate choices, as can easily lead to the impression that ***good*** and ***bad*** are previously defined concepts. It is important to notice, therefore, that nothing would change if we have used 1 and 0, instead. The central idea of these works is to show that morality (i.e., the means to distinguish between good and bad behaviours) can evolve as a consequence of economic success. In our case, such economic success results from cooperation within groups and conflict among groups. Once a leading norm emerges, then 1 and 0 can be correctly interpreted as ***good*** and ***bad***, respectively. Moreover, as shown in a series of previous works, our economic behaviour is not necessarily pay-off maximizer: in some simple games, like the "ultimatum" or "dictator" games, the typical human behaviour is off Nash-equilibrium(35, 36). In some cases we violate economic principles necessary for proving market equilibrium, generating economic inefficiency(37, 38). One possible explanation relies on the existence of a certain inner morality which limits our ambition of being maximizers at all times. For a comprehensive explanation of the role of ethics in economics, see(37, 39).

The question of how a morality, which is not optimal from the economic point of view, can evolve (which is the case of stern-judging, which ranks second in the work of Ohtsuki and Iwasa, where norm selections are not involved) remains unanswered in general. But as many have pointed before (see (7) and references therein) group selection plays an important role and norms that are successful during "peace" time are not necessarily stable when a conflict takes place. This means that under stress (a between-group con-

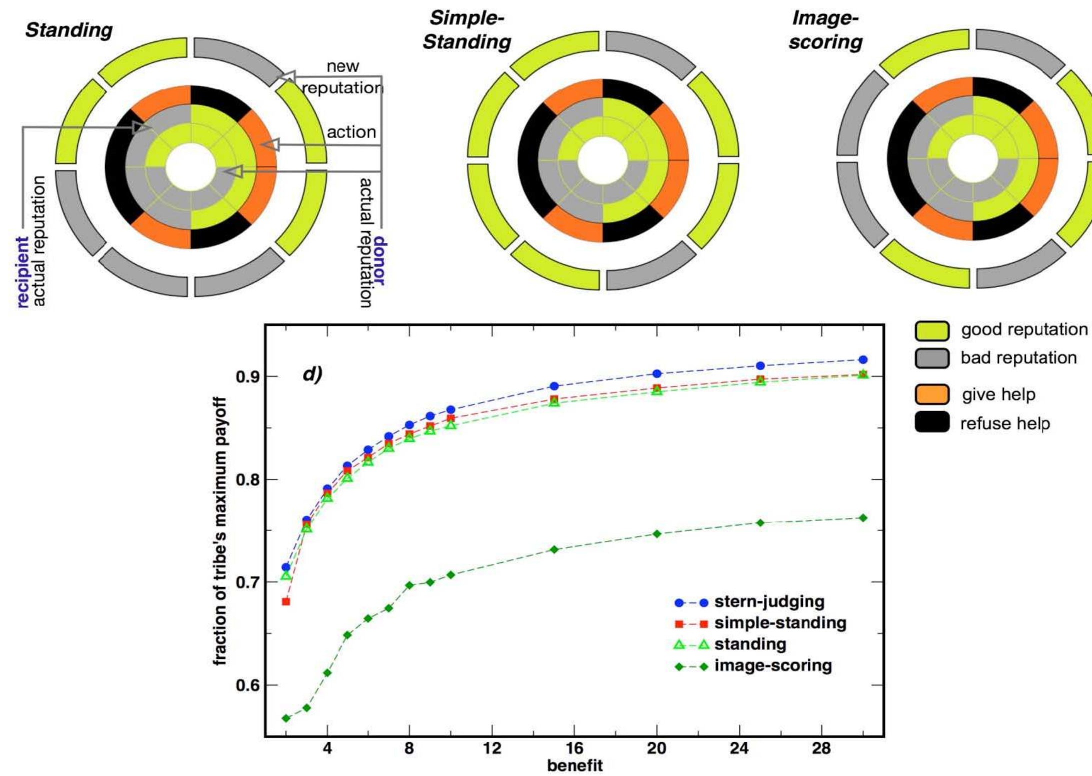

Fig. 4 Cooperation under a selected social norm. We depict the three popular norms (besides stern-judging pictured in Fig.3), the performance of which we analysed. *Stern-judging*, *simple-standing* and *image-scoring* are symmetric with respect to the equatorial plane, and as such are second order norms. As for *standing*, it clearly breaks this symmetry, constituting a third order norm. In the lower panel, we plot the ratio between the average payoff attained by each tribe under the influence of a single, fixed norm, and the maximum value possible, given the population size (64), the benefit from cooperation (b) and the cost of cooperation ($c = 1$).

flict, natural catastrophes or epidemic outbreaks, for example) characteristics other than economic efficiency (e.g., the existence of a social security network) may be fundamental.

10. Discussion

Among the leading-eight norms discovered by Ohtsuki and Iwasa(18, 21), only ***stern-judging***(8) and the so-called *simple-standing*(23) constitute second-order norms. Our present results clearly indicate that ***stern-judging*** is favored compared to all other norms. Nonetheless, in line with the model considered here, the performance of each of these norms may be evaluated by investigating how each norm performs individually, *taking into account all 16 strategies simultaneously.* Such a comparison is shown if Fig. 4. The results show that the overall performance of ***stern-judging*** is better than that of the other norms over a wide range of values of the benefit b. Furthermore, both standing and simple standing perform very similarly, again pointing out that reputation-based cooperation can successfully be established without resorting to higher-order (more sophisticated) norms. Finally, image-scoring performs considerably worse that all the other norms, a feature already addressed before(32-34). Within the space of second order norms, similar conclusions have been found recently by Ohtsuki and Iwasa(23). Clearly, ***stern-judging***'s simplicity and robustness to errors may contribute to its evolutionary success, since other well-performing strategies may succumb to invasion of individuals from other tribes who bring along strategies which may affect the overall performance of a given tribe. In this sense, robustness plays a key role when evolutionary success is at stake. We believe that ***stern-judging*** is the most robust norm promoting cooperation.

The present results correlate well with the recent findings in*e*-trade, where simple reputation-based mechanisms ensure high levels of cooperation. Indeed, ***stern-judging*** involves a straightforward and unambiguous reputation assessment, decisions of the donor being contingent only on the previous reputation of the receiver. We argue that the absence of constraining environments acting upon the potential customers in *e*-trade, for whom the decision of buying or not buying is free from further ado, facilitates the adoption of a ***stern-judging*** assessment rule. Indeed, recent experiments(40) have shown that humans are very sensitive to the presence of subtle psychologically constraining cues, their generosity depending strongly on the presence or absence of such cues. Furthermore, under simple unambiguous norms humans may escape the additional costs of conscious deliberation(41).

11. Methods

We considered sets of 64 tribes, each tribe with 64 inhabitants. Each individual engages in a single round of the following indirect reciprocity game(8) with every other tribe inhabitant, assuming with equal probability the role of donor or recipient. The donor decides if *YES* or *NO* she provides help to the recipient, following her individual strategy encoded as a 4-bit string (18-20). If *YES*, then her payoff decreases by ***1***, while the recipient's payoff increases by $\boldsymbol{b}>\boldsymbol{1}$. If *NO*, the payoffs remain unchanged (following common practice(6, 17, 19, 20, 32) we increase the payoff of every interacting player by ***1*** in every round to avoid negative payoffs). This action will be witnessed by a third-party individual who, based on the tribe's social norm, will ascribe (subject to some small error probability $\mu_a = 0.001$) a new reputation to the *donor*, which we assume to spread efficiently without errors to the rest of the individuals in that tribe(18-20). Moreover, individuals may fail to do what their strategy compels then to do, with a small execution error probability $\mu_e = 0.001$. After all interactions take place, one generation has passed, simultaneously for all tribes. Individual strategies in each tribe replicate to the next generation in the following way: For every individual ***A*** in the population we select an individual ***B*** proportional to fitness (including ***A***)(19). The strategy of ***B*** replaces that of ***A***, apart from bit mutations occurring with a small probability $\mu_s = 0.01$.

Subsequently, with probability $\boldsymbol{p_{CONFLICT}}$**=0.01**, all pairs of tribes may engage in a conflict, in which each tribe acts as an individual unit. Different types of conflicts between tribes have been considered:

1) Imitation Selection: We compare the average payoffs $\prod_A$ and $\prod_B$ of the two conflicting tribes ***A*** and ***B***, the winner being the tribe with highest score.

2) Moran Process: In this case the selection method between tribes mimics that used between individuals in each tribe; one tribe ***B*** is chosen at random, and its norm is replaced by that of another tribe ***A*** chosen proportional to fitness.

3) War of attrition: We choose at random two tribes ***A*** and ***B*** with average payoffs $\prod_A$ and $\prod_B$. We assume that each tribe can display for a time which is larger the larger its average payoff. To this end we draw two random numbers $\boldsymbol{R}_A$ and $\boldsymbol{R}_B$ each following an exponential probability distribution given by $exp(-t/\prod_A)/\prod_A$ and $exp(-t/\prod_B)/\prod_B$, respectively. The larger of the two numbers identifies the winning tribe.

4) Pairwise comparison: We choose at random two tribes ***A*** and ***B***, with average payoffs $\prod_A$ and $\prod_B$, respectively; then norm of tribe ***B*** will replace that of ***A*** with a probability given by

$$p = \left[1 + e^{-\beta(\Pi_B - \Pi_A)}\right]^{-1}$$

whereas the inverse process will occur with probability $(1 - p)$. In physics this function corresponds to the well-known Fermi distribution function, in which the inverse temperature β determines the sharpness of transition from$p = 0$, whenever$\prod_B < \prod_A$, to $p = 1$, whenever $\prod_A < \prod_B$. Indeed, in the limit $\beta \to +\infty$ we obtain imitation dynamics (strong selection), whereas whenever $\beta \to 0$ ***B*** replaces ***A*** with the same probability that ***A*** replaces ***B*** (½ - neutral drift).

5) Extended Hawk-Dove Game: This method of tribal conflict has been developed in Ref.(20) and is based on an extended Hawk-Dove game introduced in Ref. (42) Full details are provided in Ref. (20) Similarly to the other types of conflict, we choose at random two tribes ***A*** and ***B***, with average payoffs $\prod_A$ and $\prod_B$, to engage in a conflict. For each tribe there are two possible strategies, HAWK and DOVE, as described in Ref.(20).

As a result of inter-tribe conflict the norm of the loosing tribe (***B***) is shifted in the direction of the victor norm (***A***). Convergence of such a non-linear evolutionary process dictates a smooth norm crossover. Hence, each bit of norm ***A*** will replace the corresponding bit of norm ***B*** with probability

$$p = \frac{\eta \Pi_A}{\eta \Pi_A + (1 - \eta)\Pi_B}$$

which ensures good convergence whenever $\eta \le 0.2$, independently of the type of conflict (a bit-mutation probability $\mu_N = 0.0001$ has been used). Furthermore, a small fraction of the population of tribe ***A*** replaces a corresponding random fraction of tribe ***B***: Each individual of tribe ***A*** replaces a corresponding individual of tribe ***B*** with a probability $\mu_{migration} = 0.005$. Indeed, if no migration takes place, a tribe's population may get trapped in less cooperative strategies, compromising the global convergence of the evolutionary process(27).

Each simulation runs for 9000 generations, starting from randomly assigned strategies and norms, in order to let the system reach a stationary situation, typically characterized by all tribes having maximized their average payoff, for a given benefit $\boldsymbol{b} > \boldsymbol{c=1}$. The subsequent 1000 generations are then used to collect information on the strategies used in each tribe and the norms ruling the tribes in the stationary regime. We ran 500 evolutions for each value of ***b***, subsequently performing a statistical analysis of the bits which encode each norm, as detailed before. In our simulations, we adopted the following values: η=0.1, μ_N=0.0001, μ_S=0.01, μ_a=μ_e=0.001. The benefit ***b*** varied from ***b*** =2 to ***b***=36. Each individual, in each tribe, has a strategy (chosen randomly at start) encoded as a four-bit string, which determines the individual's action (**N**=no, do not provide help; **Y**=yes, provide help) as a donor, knowing hers and the recipient's reputation, as detailed in Table 1. This results in a total of 16 strategies, ranging from unconditional defection (***ALLD***) to unconditional cooperation (***ALLC***), as detailed in Table 2.
The results presented are quite robust to variations of the different mutation rates introduced above, as well as to variation of population size and number of tribes. Furthermore, reducing the threshold from *98%* to *95%* does not introduce any changes in the results shown.

Finally, in Fig. 4, we ran 500 simulations for each tribe with 64 inhabitants, and used the last 1000 generations from a total of 10000.

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References

[1] Smith, J. M. & Szathmry, E. (1995) *The Major Transitions in Evolution* (Freeman, Oxford).

[2] Smith, J. M. (1982) *Evolution and the theory of games* (Cambridge University Press, Cambridge USA).

[3] Hamilton, W. D. (1996) *Narrow Roads of Gene Land Vol.1* (Freeman, New York).

[4] Trivers, R. (1985) *Social Evolution* (Benjamin Cummings, Menlo Park).

[5] Wilson, E. O. (1975) *Sociobiology* (Harvard Univ. Press, Cambridge, Massachusetts).

[6] Nowak, M. A. & Sigmund, K. (1998) *Nature* **393,** 573-7.

[7] Alexander, R. D. (1987) *The Biology of Moral Systems* (AldinedeGruyter, NewYork).

[8] Nowak, M. A. & Sigmund, K. (2005) *Nature* **437,** 1291-8.

[9] Sugden, R. (1986) *The economics of rights, co-operation and welfare* (Basil Blackell, Oxford, UK).

[10] Kandori, M. (1992) *The Review of Economic Studies* **59,** 63-80.

[11] Boem, C. (1999) *Hierarchy in the forest* (Harvard University Press, Cambridge, MA, USA).

[12] Dunbar, R. (1996) *Grooming, gossip, and the evolution of language* (Harvard University Press, Cambridge, MA, USA).

[13] Mackie, J. L. (1995) in *Issues in Evolutionary Ethics*, ed. Thompson, P. (State University of New York Press, NY), pp. 165-177.

[14] Dellarocas, C. (2003) *MIT Sloan School of Management working paper* 4297-03.

[15] Bolton, G. E., Katok, E. & Ockenfels, A. (2004) *Manage.Sci.* **50,** 1587-1602.

[16] Keser, C. (2002) *IBM-Watson Research Center, CIRANO working paper* 2002s-75k.

[17] Brandt, H. & Sigmund, K. (2005) *Proc Natl Acad Sci U S A* **102,** 2666-70.

[18] Ohtsuki, H. & Iwasa, Y. (2004) *J Theor Biol* **231,** 107-20.

[19] Brandt, H. & Sigmund, K. (2004) *J Theor Biol* **231,** 475-86.

[20] Chalub, F. A. C. C., Santos, F. C. & Pacheco, J. M. (2006) *J Theor Biol* **241,** 233-240.

[21] Ohtsuki, H. & Iwasa, Y. (2006) *J Theor Biol* **239,** 435-44.

[22] Pacheco, J. M., Santos, F. C. & Chalub, F. A. C. C. (2006) *PLoS-Computational Biology* **2,** e178.

[23] Ohtsuki, H. & Iwasa, Y. (2007) *Journal of Theoretical Biology* **244,** 518-531.

[24] Brinck, I. & Gardenfors, P. (2003) *Mind & Language* **18,** 484-501.

[25] Bowles, S. & Gintis, H. (2004) *Theor Popul Biol* **65,** 17-28.

[26] Bowles, S., Choi, J. K. & Hopfensitz, A. (2003) *J Theor Biol* **223,** 135-47.

[27] Boyd, R. & Richerson, P. J. (1985) *Culture and the Evolutionary Process* (University of Chicago Press, Chicago).

[28] Boyd, R. & Richerson, P. J. (1990) *J Theor Biol* **145,** 331-42.

[29] Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. (2003) *Proc Natl Acad Sci U S A* **100,** 3531-5.

[30] de Quervain, D. J., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A. & Fehr, E. (2004) *Science* **305,** 1254-8.

[31] Gintis, H. (2003) *J Theor Biol* **220,** 407-18.

[32] Leimar, O. & Hammerstein, P. (2001) *Proc Biol Sci* **268,** 745-53.

[33] Panchanathan, K. & Boyd, R. (2003) *J Theor Biol* **224,** 115-26.

[34] Panchanathan, K. & Boyd, R. (2004) *Nature* **432,** 499-502.

[35] Hofmann, E., McCabe, K., Shachat, K. & Smith, V. (1994) *Games and Econ. Behav.* **7,** 346-380.

[36] Sigmund, K., Fehr, E. & Nowak, M. A. (2002) *Sci. Am.* **286,** 82-87.

[37] Sen, A. (1987) *On ethics and economics* (Blackwell Publishers).

[38] Sen, A. (1993) *Econometrica* **61,** 495-521.

[39] Collard, D. (1978) *Altruism and economy: a study in non selfish economics* (Martin Robertson).

[40] Haley, K. J. & Fessler, D. M. T. (2005) *Evolution and Human Behaviour* **26,** 245-256.

[41] Dijksterhuis, A., Bos, M. W., Nordgren, L. F. & van Baaren, R. B. (2006) *Science* **311,** 1005-7.

[42] Crowley, P. H. (2000) *J Theor Biol* **204,** 543-63.