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The Evolutionary Origins of Human Generosity

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abstract: This article examines how altruism and self-interest are linked in human generosity, and what social scientists can learn from this linkage. The origins of generosity are explored by combining biological, psychological, anthropological and sociological evidence. Kinship altruism, reciprocal altruism, 'strong reciprocity', cultural norms and gene-culture co-evolution prove to be major explanations of the evolution of cooperation in human beings. Empirical research shows that human generosity is selective: kin and close relatives are favoured over others. Moreover, generosity generates its own rewards and is therefore again selective: the more you give, the more you receive. The selectivity of generosity reveals its evolutionary origins.

keywords: altruism ♦ evolution ♦ generosity ♦ kinship ♦ reciprocity

Kindness towards one's kin is viewed as a genetic investment, a way of spreading genes similar to one's own. Assisting kin thus comes close to helping oneself. (De Waal, 2001: 317)

Human generosity is commonly understood as doing good to other people or contributing to the society's common good. Altruism, solidarity, charity and gift giving are related terms that come to mind when thinking about generosity. The common underlying assumption seems to be that human generosity is a beneficial act that may be directed towards other human beings, the community or the society as such.

An important branch of social scientific literature on human generosity has focused on the practice of gift exchange (for an overview, see Komter, 2005). In view of the predominantly positive moral connotations embodied in common sense notions of the concept of generosity, Marcel Mauss's claim that 'generosity and self-interest are linked in giving' (Mauss, 1990 [1923]: 68) is an interesting one. Although Mauss's contribution as the

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founder of the theory of human gift giving and generosity is generally uncontested, his ideas about the role of self-interest in human generosity have not gone undisputed among contemporary scholars of human generosity. Especially in the literature on the gift inspired by French philosophy, the notion that generous behaviour can serve some interest tends to be resisted or downplayed. 'Real' gifts are assumed to be truly generous and are, or should be, 'unspoiled' by expectations or acts of reciprocity (e.g. Derrida, 1991). According to the American philosopher Alan Schrift (1997: 19), 'a narrowly self-interested notion of reciprocal return' has come to dominate the current discourse on generosity. Prominent gift scholars such as Alain Caillé (2000, 2005) and Jacques Godbout (1992) argue that calculation and reciprocity are not central to the gift; their work focuses on the altruistic and socially beneficial aspects of the gift.

A closer look into the origins of human generosity might reveal a more differentiated picture. Work from biologists and primatologists has demonstrated that generosity is not restricted to human beings but is also observed among both higher and lower animal species. Forms of cooperation have been observed between kin-related animals, but also between non-related individuals. Biologists have pointed at the significance of this phenomenon for the maintenance and further evolution of the species, and have developed concepts such as kinship altruism and reciprocal altruism to explain animal and human generosity and cooperation.

This article aims to explore what Mauss had in mind when he wrote the sentence quoted above, and what contemporary social scientists can learn from it. If it can be shown that generosity maintains some core interest of both the giver and the recipient, then it becomes possible to understand why generosity and self- or group interest are not mutually exclusive. If this is indeed the case, this seemingly contradictory insight and the implications it has for a proper understanding of human social behaviour should be incorporated within contemporary social theory.

My terminological focus on the concept of generosity ties in nicely with the way the concept of 'cooperation' has mostly been used in the biological literature, namely to indicate behaviour which is costly for the cooperator, while providing a benefit to the recipient (e.g. Nowak, 2006); in a similar vein, social scientists Mauss and Simmel have considered gift giving as being a sacrifice for a gain. Where the original literature refers to cooperation I do the same, whereas my own conclusions are drawn in terms of generosity.

In this article the origins of human generosity are explored by combining insights from (experimental) biology, primatology, psychology, anthropology and sociology. One important cautionary remark is in order here. Since the appearance of foundational works such as those of Hamilton (1964), Axelrod (1984) and Trivers (1971), the issue of animal and human cooperation and generosity has generated a vast and impressive body of

research, in particular in the fields of experimental biology and game theory. Since the 1980s, enormous scientific progress has been made in these disciplines, and a much more differentiated theoretical understanding has come into existence. It is beyond my competence as a social scientist, and therefore beyond the scope of this article, to attempt to provide a full overview or an in-depth assessment of this literature. My main aim is to familiarize social scientists with some of the core insights gained from these disciplines, and point out some striking continuities with findings in the field of social science.

Generosity in Games and Experiments

In trying to explain altruism, evolution theory has been facing a fundamental paradox: if natural selection, by being inherently selfish, promotes adaptations that primarily serve the individual, how can altruism and cooperation be explained? Why should an individual increase the fitness of another individual when it goes at the cost of its own? Although Darwin proposed various solutions for the problem of altruism, the theory of evolution with its focus on the struggle for life and competition for survival has dismissed cooperative phenomena for a long time (see Ridley, 1998). The revitalization of Darwin's attempts to understand altruism can for an important part be attributed to game-theoretical simulations of cooperation (e.g. Hamilton, 1964; Maynard Smith, 1964; Trivers, 1971).

Kinship Altruism and Reciprocal Altruism

Since the 1960s and early 1970s evolution theory has acquired two kinds of extensions: the theory of genetic kinship altruism and the theory of reciprocal altruism. The first theory stipulates that by helping one's relatives one contributes to spreading one's own genes – which is supposed to increase survival chances – whereas the second theory allows for the explanation of altruistic behaviour among genetically non-related individuals of the same species or even among members of different species. William Hamilton was the first to mathematically model the genetic evolution of social behaviour. He argued that sacrifices involved in parental care can maximize the 'inclusive fitness' of the organisms involved because more adult offspring are left as a result; this way, the genes causing its possessor to give parental care will leave more replica genes in the next generation than genes having the opposite tendency (Hamilton, 1964). Whereas Hamilton's theory of inclusive fitness explains cooperation between close relatives, the question why unrelated organisms cooperate was still left unanswered. Using a formal cost–benefit approach, biologist Robert Trivers (1971) developed the theory of reciprocal altruism. This theory extends beyond genetically related organisms and argues that

returning favours to unrelated individuals can also serve survival goals. The core idea of the theory of reciprocal altruism is that providing benefits to other individuals leads to direct or indirect (through third parties) reciprocation, which serves the survival chances of all parties involved.

Since the 1970s, a firm tradition of empirical research inspired by game theory has been established, and hypotheses derived from the theory of reciprocal altruism have been tested in various ways. A crucial unanswered question was how, in cases of interaction between non-genetically related individuals, an evolutionary trend to cooperative behaviour could ever have started in the first place; a next question concerns the maintenance of cooperation: why would it serve you to continue cooperation if it is not certain that your generous input will be rewarded?

Direct and Indirect Reciprocity

Reciprocal altruism involves both direct and indirect reciprocity. In direct reciprocity there are repeated encounters between the same two individuals: 'my behaviour depends on what you have done to me. Indirect reciprocity means that there are repeated encounters within a group; my behaviour depends on what you have done to others' (Dreber et al., 2008: 348).

Departing from the assumption that interactions between pairs of individuals occur on a probabilistic basis, political scientist Axelrod and biologist Hamilton (1981) use an iterated Prisoner's Dilemma and a computer tournament to demonstrate how cooperation can emerge from a previously asocial state, and how it is maintained once established. *Tit-for-tat*, or responding to the other player's action in an identical way, proves to be an evolutionary robust strategy: it gradually replaces all other strategies in a simulation of a great variety of decision rules. Moreover, if the interactions between non-related individuals have a sufficiently large probability of continuing, *tit-for-tat* is evolutionary stable, that is, it is maintained over time. 'Thus cooperation based on reciprocity can get started in a predominantly noncooperative world, can thrive in a variegated environment, and can defend itself once fully established' (Axelrod and Hamilton, 1981: 1395).

The Prisoner's Dilemma has often been based on a two-player matrix. If the standard game is played only once, the evolutionary best strategy for both players is to defect but if the play is repeated, it usually leads to cooperative solutions (Wedekind, 1998). In Prisoner's Dilemma games with multiple players, solutions are often less cooperative. Whereas direct reciprocity is assumed to promote the evolution of generosity in dyads or in small groups, the fact that human beings also cooperate in large groups of unrelated individuals poses a problem (Nowak and Sigmund, 1998, 2005). In real-life interactions between human beings direct reciprocity as captured in the principle 'You scratch my back, and I'll scratch yours' is

widespread. But how can we make sense of the phenomenon of indirect reciprocity that is also frequently observed: 'You scratch my back and I'll scratch someone else's' (or 'I scratch your back and someone else will scratch mine')? Nowak and Sigmund (1998) have done game simulations to understand the evolution of indirect reciprocity by postulating that it involves reputation building and moral norms which – in their turn – foster generosity. Nowak and Sigmund's assumption is that individuals gain social status in the group by helping others. Indirect reciprocity can evolve if the other group members base their future actions on this information. Having observed whether a player gave help or not significantly influences one's own giving or withholding help. Being observed giving something to another person increases your social status, whereas withholding your gift decreases it. Social status, according to Nowak and Sigmund, makes cooperation on a larger scale possible and binds larger groups of individuals together.

Experimental psychological research on the role of 'competitive altruism' shows similar results: in a reputation environment when contributions are public, people are more altruistic. Selective benefits are apparently associated with altruistic behaviour for reputation reasons (Hardy and van Vugt, 2006). Competitive (public) altruism can account for cooperation in large groups because it serves as a 'signal' that people are potentially interesting exchange partners (van Vugt et al., 2007). Hardy and van Vugt (2006) argue that competitive altruism may be widespread in human societies; as examples they mention public displays of generosity – called *potlatch* – as they have been documented by anthropologists (e.g. Malinowski, 1922; Mauss, 1990 [1923]). Similarly, social psychological literature shows that an increase in the visibility and a decrease in the anonymity of individuals enhances their cooperation in social dilemmas. However, while competition, reputation and visibility may be important forces accounting for human generosity and cooperation, not all individuals are cooperative to the same extent; experiments demonstrate the existence of different reciprocal types, of which some are more inclined to cooperate while others tend more towards competition or free-riding (Kurzban and Houser, 2005; van Vugt and van Lange, 2006).

The conditions under which public displays of generosity lead to reputation formation have been varied in a number of empirical studies (e.g. Fehr and Fischbacher, 2003; Wedekind and Braithwaite, 2002; Wedekind and Milinski, 2000) but the results remain essentially the same: the receivers' history of giving has a significant impact on the donors' decision (not) to give. According to these researchers indirect reciprocity is one of the major evolutionary concepts to explain generous behaviour in small groups. Although generous players may not be aware of the self-interested and strategic element in their behaviour, generosity in indirect reciprocity can

only evolve if it eventually leads to a net benefit in the long run, and having a good reputation significantly helps to achieve that benefit. Thus, if giving something to other people pays off in the long run because in future interactions these people will take your social status into account, giving can be regarded more as an investment into one's own future than as a real altruistic act (Wedekind, 1998).

Dugatkin and his colleagues (e.g. Dugatkin and Mesterton-Gibbons, 1996) have argued that the importance of reciprocity for both animal and human cooperation should not be overstated, and suggest additional explanations, for instance mutualism. Whereas reciprocal altruism extends cooperation into the future by being based on score-keeping, mutualism operates in the present, but only indirectly, through feedback from the environment: non-cooperation rebounds against the actor. Among primates the evidence for reciprocity is indeed scarce, according to some biologists. One explanation might be the complexity of the mental machinery involved in non-trivial examples of reciprocity, such as the capacity to classify other individuals' actions as cooperative, intentionally uncooperative or unintentionally uncooperative (Hammerstein, 2003). As Stevens and Stephens (2002) have demonstrated in their game-theoretical model, mutualistic explanations instead of the more complex mechanisms of kinship altruism or reciprocal altruism, can account for behaviour such as food sharing.

'Strong Reciprocity' and Cultural Forces

Whereas kinship altruism and direct and indirect reciprocity may explain cooperation in families and among friends, cooperation in larger groups of strangers whom one may only meet once, requires different types of explanation. As Nowak (2006) has shown, several other mechanisms may be involved here, for instance network reciprocity, in which cooperators form network clusters where they help each other, and group selection, which involves between-group competition; groups of cooperators will grow faster than pure defector groups, and will therefore be selected.

Fehr and his colleagues (e.g. Fehr and Fischbacher, 2003; Fehr and Gächter, 2002) have argued that human cooperation may involve 'strong reciprocity'. This is a combination of altruistic rewarding (i.e. rewarding others for cooperative behaviour) and altruistic punishment (imposing sanctions on others for non-cooperative behaviour). Whereas reciprocal altruists reward and punish only if this is in their (long-term) self-interest, strong reciprocators do so even if they gain no benefit whatsoever from their acts. Fehr and Fischbacher (2003) demonstrate that strongly reciprocal individuals reward and punish in anonymous one-shot interactions but increase their rewards and punishments in repeated interactions or when their

reputation is at stake. Apparently, they are motivated by a combination of altruistic and selfish concerns. 'Their altruistic motives induce them to cooperate and punish in one-shot interactions and their selfish motives induce them to increase rewards and punishment in repeated interactions or when reputation-building is possible' (Fehr and Fischbacher, 2003: 788; see also Fehr and Gächter, 2002). In addition to reciprocal altruism and reputation-based cooperation, 'strong reciprocity' can explain cooperation in larger groups through the selection of cultural norms favouring cooperation, and involving altruistic punishment and reward. As Boyd et al. (2003) have demonstrated, strong reciprocity is not a separate mechanism for the evolution of cooperation; ultimately the evolution of strong reciprocity builds on group selection. Both altruistic punishment and altruistic cooperation are maintained in populations engaged in one-time, anonymous interactions, thereby allowing for the cultural evolution of cooperative behaviour in larger groups.

On the basis of their review of experimental and game-theoretical research, Fehr and Fischbacher (2003: 790) conclude that there is 'fairly convincing evidence that cultural forces exert a significant impact on human altruism'. One such cultural force might be what has been termed 'conformist transmission' (Boyd and Richerson, 1985), a social learning strategy that consists of adopting behaviours that are common (and therefore apparently adaptive) among a population; such a strategy may in the end lead to cultural group selection, that is the selection of group-beneficial norms such as strong reciprocity. Such behaviour sometimes continues to be displayed even though it has lost its evolutionary benefits. For instance, fear of spiders and snakes is more readily learned than fear of contemporary dangers like automobiles or guns. From an evolutionary point of view this has been interpreted as a behavioural 'mismatch' (Hagen and Hammerstein, 2006).

The paradigm of game-theoretical models of human behaviour has recently been criticized by Hagen and Hammerstein (2006) because of the highly abstract structure of most experimental economics games and the lack of explicit framing or contextualization. Players are given the rules, the payoffs, but are deliberately not provided with explicit information about the broader context of the game. Are the players friends or competitors, members of one's in-group or an out-group? Although it is obviously one of the strengths of experimental research to remain abstract by *not* providing contextual information, this also severely complicates the interpretation of the results of such games.

It is time to shift our perspective from players in games and subjects in experiments to subjects living in real-life circumstances, having real-life motives and purposes. Under what conditions do they display generosity, and to what extent does their behaviour resemble that of game-players?

Generosity in Animals

Reciprocal Altruism among Chimpanzees

Empirical research conducted by primatologist Frans de Waal has demonstrated that reciprocity and notions of morality, empathy and generosity are also present in our closest relatives: chimpanzees. Chimpanzees are able to show empathy towards one another, as is for instance shown by their stroking and patting a victim of attack or sharing food with a hungry companion. They also have the capacity to keep track of what they receive and give: they use a kind of 'moral book-keeping'. In particular grooming, food sharing and offering help are subject to rules of reciprocity: if you do not groom an individual who has groomed you, then the relationship ceases to exist. The same applies to helping: if you do not repay a favour received from a certain individual, you will not receive favours yourself anymore. Also negative reciprocity has been observed among chimps: an eye for an eye, a tooth for a tooth. Chimpanzees have a taste for revenge and a sense of justice and fairness which is demonstrated in their tendency to act negatively towards a stingy individual, either by direct or indirect retaliation (De Waal, 1996, 2005, 2006).

Reciprocal altruism among chimpanzees is a complex mechanism based on the remembrance of favours given and received. It does not merely involve the levels of genes and behaviour but also includes emotions and psychological considerations. De Waal (1996) summarizes the three main characteristics of reciprocal altruism: first, the exchanged acts, while beneficial to the recipient, are costly to the performer; second, there is a time lag between giving and receiving (exchange with immediate rewards does not count as reciprocal altruism); and third, giving does not necessarily follow upon receiving: giving and receiving are contingent. Complex cognitive mechanisms are involved; for instance, reciprocal altruism depends on trust and requires the punishment of free-riders. It only works if individuals regularly meet, have good memories and more or less stable relationships.

De Waal and his co-workers recorded nearly 5000 interactions over food among the chimpanzees in the Yerkes zoo in Atlanta (De Waal, 1996). Food transfers were analysed in all possible directions among adults. Confirming the reciprocity hypothesis, De Waal found that the number of transfers in each direction was related to the number in the opposite direction. If individual A shared a lot with individual B, the reverse was generally also the case; and if individual A shared little with C, this was reciprocated by little sharing by C with A. An additional confirmation of the reciprocity hypothesis was the finding that grooming affected subsequent food sharing. If A had groomed B, A had better chances for getting food from B afterwards. Apparently, reciprocity in one area flows over to other areas, thereby strengthening the principle.

So far we have been talking about reciprocal altruism among chimpanzees, but to what extent do motives that give rise to strong reciprocity such as have been found among humans also produce cooperation in primate groups? Silk and her colleagues (Silk, 2005; Silk et al., 2005) conclude on the basis of experimental tests with chimpanzees that their cooperative behaviour is mainly limited to kin and reciprocating partners, and is virtually never extended to unfamiliar individuals. Silk et al. (2005) argue that the absence of other-regarding preferences in chimpanzees may indicate that such preferences are tied to the sophisticated capacities of cultural learning, perspective taking and moral judgement that are characteristic for human beings.

Reciprocal Altruism among Lower Species

Reciprocal altruism is not restricted to 'higher' animals such as chimps but also occurs, for instance, among vampire bats, birds and dolphins. Vampire bats feed at night on the blood of larger animals (Wilkinson, 1984). Since not every bat is successful in finding a meal, and since without blood bats starve to death within three days, they solve this problem by resorting to cooperation. Those who have found blood regurgitate blood into the mouths of bats that have not. Recipients of these favours return them on subsequent nights to those bats that have helped them in the past; and conversely, bats refuse help to those who denied them in the past. Like chimpanzees, bats are able to recognize free-riders and to expel them from the system. Apparently, bats are able to remember the history of their relationships with other bats. When the short-term benefits of providing help outweigh the costs to the donor, in the long run a stable system of reciprocal altruism will evolve.

Unrelated jackdaws have been found to display high rates of food sharing, a behaviour that has been explained as functional for engaging in and sustaining social relationships (De Kort et al., 2003). Yet another fascinating example of cooperation (or mutualism, as it is mostly called) are the 'cleaner fish' which live in coral reefs, where they enter the mouths of larger 'client fish' to remove parasites. Also, dolphins have been shown to be reciprocal altruists (Connor and Norris, 1982). They offer help to other animals in distress, including human beings, by pressing them to the sea surface. The supportive animal usually does not feed during this helping act, which can be seen as an additional sacrifice. Apparently reciprocal altruism does not only include kin, near relatives and non-related same-species individuals but even animals belonging to different species.

One can wonder what exactly is *reciprocal* to this behaviour, since no immediate or even delayed acts of reciprocity are apparent. In the course of their evolution dolphins have developed a generalized sensitivity for

other individuals in distress, irrespective of whether they belong to the same or a different species. Regardless of the dolphins' 'awareness' of this, their helping behaviour will be rewarded at some point in time, either by a same-species individual or by a member of a different species.

In their explanation of this phenomenon biologists point to the fact that the evolutionary climate for reciprocal altruism in both humans and dolphins was formed in a similar way: strong predatory pressures in the case of dolphins and invasion of the savannah in the case of pre-humans resulted in highly mutually dependent societies in both cases (Alexander, 1974). It is assumed that 'this marked increase in mutual dependence contributed significantly to the evolution of the higher order intelligence . . . by producing strong selection pressures for individuals to practice reciprocal altruism with greater sophistication' (Connor and Norris, 1982: 370). As long as individuals live in an environment where mutual dependence is low and thus are relatively self-reliant, the costs of not participating in altruistic exchanges are low; but as mutual dependence increases, the costs and the benefits of their interactions with others increase, which means in evolutionary terms that interactions have a greater effect on their fitness.

This produces strong selection pressures for more sophisticated mechanisms for gaining advantage in reciprocal interactions, which are manifested as more complicated emotional systems, better memory and foresight, greater learning capacity and the ability to make second order abstractions, etc. (i.e. many of the components we associate with intelligence) (Connor and Norris, 1982: 370).

Here we see the idea frequently expressed in the more recent work of Frans de Waal, that moral notions of altruism and generosity have their evolutionary origin in a set of learned societal understandings of how to behave with respect to fellow individuals. Human emotions, morality and generosity have their evolutionary origins in ancient behaviour patterns of animals, not only of higher but also of lower animal species.

Human Generosity

Anthropological and Sociological Views

We have seen that the principle of reciprocal altruism is a common occurrence among many animal species, and human beings form no exception to this principle. A seminal illustration is found in Bronislaw Malinowski's book *Argonauts of the Western Pacific* (1922), in which he extensively documented the 'principle of give-and-take'. This principle is reflected in the *Kula*, the ceremonial exchange of gifts by the inhabitants of the Trobriand Islands near New Guinea. The *Kula* is a form of exchange on the part of the communities inhabiting a wide ring of islands, which form a closed

circuit. Along this route, articles of two kinds constantly travel in opposite directions. Necklaces move in a clockwise direction, while bracelets move in a counter-clockwise direction. After some time, these articles meet articles of the other class on their way, and are exchanged for them. This practice shows that it is not the articles that count, but the principle of give-and-take, as Malinowski terms it. One of the main characteristics of gifts is that they should be given and reciprocated. Somebody who owns something is expected to share it, to pass it on. A gift that does not 'move' loses its gift properties. If a man keeps a gift too long, he will develop a bad reputation and be literally excommunicated.

Various types of motives underlying gift exchange can be distinguished: disinterested gifts where no (immediate) returns are expected, more or less equivalent reciprocity attended by clear expectations of returns and 'barter', which is mainly motivated by expected gains. According to Malinowski, gifts to kin and partners are more often given disinterestedly, whereas more or less direct expectations of returns and elements of barter are more characteristic of gifts given to persons farther away in the kinship hierarchy. Apparently, the motivation underlying generosity is connected with a dimension of genetic (and social) relatedness.

The *Kula* example illustrates how the continuous circulation of gifts keeps the principle of give-and-take alive, thereby helping the community to survive. Another example of a gift cycle can be found in Marcel Mauss's description of the habits and traditions of the native tribes in New Zealand, the Maori (Mauss, 1990 [1923]). The Maori have a word, *hau*, which means spirit, in particular the spirit of the gift. Returning from the forest where they have killed birds, the hunters of these tribes give a part of their game to the priests, who cook the birds at a sacred fire. After they have eaten some of them the priests have an offering ceremony in which they return the *hau*, in the form of a part of the birds, to the forest where it is supposed to produce a new abundance of birds to be killed by the hunters again. Like in the *Kula*, there is a cycle of gift giving: the forest gives its richness to the hunters, the hunters give it to the priests and the priests return it to the forest. The ceremony performed by the priests is called 'nourishing *hau*', feeding the spirit, a literal form of feed-back. The spirit of the gift is only kept alive by returning it to where it comes from. By placing the gift back in the forest, the priests treat the birds as a gift of nature.

The principle of reciprocity returns in the work of Lévi-Strauss (1996 [1949]), who argued that this principle is not limited to so-called primitive societies, but also applies to western society. He mentions examples in the sphere of offering food and the exchange of presents at Christmas. Far from being neutral objects without any special symbolic value, gifts are 'vehicles and instruments for realities of another order: influence, power, sympathy, status, emotion; and the skilful game of exchange consists of a

complex totality of maneuvers, conscious or unconscious, in order to gain security and to fortify one's self against risks incurred through alliances and rivalry' (Lévi-Strauss, 1996 [1949]: 76).

Marshall Sahlins (1972) made a distinction between 'generalized', 'balanced' and 'negative' reciprocity. In generalized reciprocity – the disinterested extreme – the expectation of returns is indefinite, and returns are not stipulated by time, quantity, or quality. Like Malinowski, Sahlins mentions the circle of near kin and loved ones as an example. Balanced reciprocity refers to more or less equivalent exchange without much delay and is more likely in relationships that are emotionally more distant. Negative reciprocity can be seen as the 'attempt to get something for nothing' (Sahlins, 1972: 195). Sahlins (1972: 196) summarizes his model as follows: 'kindred goes with kindness', quoting classical anthropologist Edward B. Tylor, who was the first to point at the linguistic connection between the words 'kin' and 'kindness' in Indo-European language (Tylor, 1958 [1871]).

Sociologists such as Georg Simmel (1950 [1908]) and Alvin Gouldner (1973) have come to similar conclusions regarding the role of reciprocity in creating and maintaining social ties and community. Simmel considered the gift as 'one of the strongest sociological functions' without which society could not come about. In addition to the norm of reciprocity, Gouldner distinguished the 'norm of beneficence', or the norm of giving 'something for nothing': the expression of real altruism; as examples he mentions gifts to people in need of care or help, for instance children or frail elderly.

The type of motives underlying gift giving depends on the nature of the relationship between giver and recipient, on the level of genetic and/or emotional relatedness between them and on the (conscious or unconscious) aims of the giver (see Komter, 2005, 2007). The functions and meanings of gift exchange are complex and multidimensional – which is why Mauss called it a 'total social phenomenon'. It is exactly this multifunctionality and complexity of the gift that enables it to fulfil a stabilizing function in the always unpredictable and in principle insecure interaction with other human beings.

Generosity and Kin Selection

In order to disentangle the role of biological and social factors in human generosity, gift giving within the circle of the family has to be distinguished from gift giving in wider circles than the family. Let us start with the family. Not only in animal species but also among human beings there are manifold signs of kin selection by means of help and care to close relatives (De Waal, 1996; Sahlins, 1972). We help our family and close relatives first, while friends, neighbours and strangers only come afterwards. In a Dutch empirical research project, we studied giving as well as receiving (Komter

and Schuyt, 1993). Our main, and very simple, research question was: who gives what to whom, and why? We distinguished between material gifts, such as presents and money gifts, and non-material gifts, such as giving care or help, offering dinner to people or letting them stay in one's house. A series of questions, derived from this main question, were posed as to each type of gift ('Did you give/receive any gift during . . .?'; 'To/from whom did you give/receive this gift?'; 'What was the occasion?'; 'How did you feel about giving/receiving this gift?', etc.). One of our findings was that people with children were less supportive towards their friends and wider family than those without children; furthermore, parents and other family members receive more than twice as much help than do friends (Komter and Vollebergh, 2002). Apparently, offering care or help has a selective character, favouring primary and extended family over friends. Bowles and Posel (2005) report similar results: they found that genetic relatedness is an important factor in explaining the level of remittances from migrant workers to their families.

Acts of generosity are not restricted to close family but can also involve friends, neighbours, colleagues and even complete strangers. Charity to anonymous beneficiaries is an important area of human generosity (e.g. Bremner, 1994; Radley and Kennedy, 1995). However, there is a clear hierarchical ordering in gift giving that reveals its evolutionary origins: the closer the genetic (and socioemotional) relatedness, the more readily generosity will be displayed.

In sum, human generosity is in the first instance oriented towards one's own kin-related group and only afterwards towards non-relatives. Behaviour that benefited the fitness of the closest relatives was selected, and therefore kin selection has been a primordial factor in the evolution of generosity. In the words of Frans de Waal (1996: 214): 'If altruism evolved because of a need to cooperate against hostile forces, solidarity with what is close against what is distant is an integral part.'

Generosity towards Non-Relatives

We have seen how reciprocity rules the behaviour of grooming chimps. Can the same principle be observed among modern western citizens? In the previously mentioned research into gift giving in the Netherlands we could establish patterns of reciprocity since we examined giving as well as receiving. Not only in Malinowski's and Mauss's non-western cultures but also in our own society the principle of reciprocity proved to be the underlying rule of gift giving (Komter, 1996a, 1996b, 2005). Those who gave most were the greatest recipients, and those who gave the least were also the poorest recipients. Apparently, doing well has its own reward. Who are the poorest givers and recipients? Unemployed people appear to give less to others than all other categories of respondents, and this holds

for all kinds of gifts. The unemployed also appear to receive less than the other respondents on all kinds of gifts, except staying at another person's house. Many authors have pointed at the restricted social networks of people living on minimum wages or on unemployment benefits. Together with their poor financial resources, this might explain the low level of gift exchange among the unemployed. For those living on a retirement pension the same pattern is revealed as with the unemployed. Except for money gifts, retired people give somewhat less to others, compared to the other categories of respondents. Retired people, however, also receive less than the other categories of all kinds of gifts, except presents; in general, they are the lowest recipients of all categories of respondents.

Like with giving to family vs friends, we discovered that certain people benefit over others. People seem to choose – probably mostly not in a conscious way – those social partners in their gift relationships who are 'attractive' to them, because they can expect them to give in return at some time. The principle of reciprocity tends to disadvantage those who are already in the weakest social position; in evolutionary terms, the fitness of those who engage in reciprocal behaviour is favoured over the fitness of those who don't. However, as we have seen, human beings distinguish themselves from non-human primates by having other-regarding preferences and by showing strong reciprocity: forms of altruism that transcend the limitations of genetic or close socioemotional relatedness. In order to fully understand human cooperation and generosity we need to broaden our perspective to forms of gene-culture co-evolution. We return to biological studies for illustrations.

Gene-Culture Co-Evolution

There are clear indications that a huge cultural variety exists in the ways cooperation and generosity are expressed, not only throughout history but also across cultures, as Henrich et al. (2001) have shown. Their behavioural experiments in 15 small-scale societies revealed large variations in cooperation, depending on the economic and social conditions existing in these societies.

In a recent article, Bowles (2006) discusses archaeological evidence suggesting that intergroup competition in the form of exceptionally lethal warfare took place in the late Pleistocene, and that this competition may account for the evolution of altruism among early human groups; empirical estimates based on this evidence confirmed his hypothesis. Distinctive human practices such as food sharing beyond the immediate family and monogamy were crucial to the evolution of altruism, according to Bowles. These culturally transmitted practices presuppose advanced cognitive and linguistic capacities, that may explain the distinctive forms of altruism, other than reciprocal and kin altruism, characteristic of human beings.

Apparently, hostility to outsiders and within-group altruism were two sides of the same coin, a phenomenon that is still visible in contemporary forms of in-group solidarity and out-group hostility (Komter, 2005).

Gintis et al. (2003) assume that strong reciprocity can emerge from reciprocal altruism through group selection: when a group is threatened with extinction or dispersal, cooperation is most needed for survival. If group selection is part of the explanation of the evolution of cooperation by individuals, then it is likely that group-level characteristics – such as relatively small group size, limited migration, or frequent intergroup conflicts – that enhance group selection pressures co-evolved with cooperative behaviours. The authors argue that group-level characteristics and individual behaviours may have synergistic effects, resulting in the construction of institutional environments that limit within-group competition and reduce variation within groups. Under the pressure of between-group competition, costly but in-group-beneficial behaviours can thus co-evolve with supporting environments. Based on these assumptions Gintis et al. did a series of experimental simulations which indeed revealed the human predisposition to cooperate with unknown others and to punish those who violate the norms of cooperation, at personal cost, even when no expectation of repayment of this cost exists. Once again it appears that the evolutionary success of the human species is predicated upon motivations that go beyond inclusive fitness and reciprocal altruism.

‘Ultimate’ and ‘Proximate’ Explanations of Generosity

We have seen that human generosity and cooperation involve a wide range of explanatory mechanisms depending on the level of genetic and socioemotional relatedness and on group size: kinship altruism, direct and indirect reciprocity, ‘strong’ reciprocity (involving altruistic rewarding and altruistic punishment), group selection, cultural norms and forms of gene-culture co-evolution. However, a full insight into the phenomenon of generosity is impossible without having a proper understanding of the distinction between proximate and ultimate explanations. Whereas ultimate causes are responsible for the evolution of the individual’s responses (*why* does a bird sing?), proximate causes govern the responses of the individual to immediate factors explaining the behaviour (*how* does a bird sing?) (see Mayr, 1961; Tinbergen, 1963). Proximate causes can involve the physiology, biochemistry and psychological and social mechanisms underlying behaviour, whereas ultimate explanations highlight the adaptive functions for the survival of the organism (see Goldsmith and Zimmerman, 2000). As Mayr (1961: 1503) pointed out: ‘causes exist at each of these levels; therefore, theories that refer to different levels are not in

conflict'. For instance, a proximate explanation for gift giving is that you give something to another person because you wish to convey your sympathy or gratitude towards this person; the ultimate explanation is that generosity offers selective advantages to those who are able and willing to reciprocate, thereby creating social ties and community; both explanations are valid and complement each other.

The distinction between ultimate and proximate explanations is comparable to what other authors have analysed as a distinction between subjective motives and objective effects (see Bourdieu, 1996 [1977]; see also Adloff and Mau, 2005); however, the former distinction has a larger scope in the sense that it explicitly refers to the adaptive functionality of behaviour for survival and, thus, involves a biological component in addition to the social explanation of behaviour.

Since Darwin – the founding father of ultimate explanations – the complementary nature of ultimate and proximate explanations has been generally recognized by biologists but within social science these different types of explanation are often either ignored, or confused. Within sociological and anthropological theory on gifts and generosity, for instance, the two levels tend to be confused: gift giving is either seen as generous *per se*, which is a proximate explanation, or as ultimately self-interested, stressing its adaptivity for society (Komter, 2005).

Over the last two decades an interesting paradigmatic development within contemporary social science is manifesting itself: evolutionary approaches, both within psychology and in sociology, are rapidly gaining ground. Journals and handbooks adopting an evolutionary stance have been published (e.g. Buss, 2005; Dunbar and Barrett, 2007; Lenski, 2005; Sanderson, 2001), and the American Sociological Association has a Section on Evolution, Biology and Society. However, in social scientific accounts of generosity and cooperation the focus still tends to be on proximate explanations. For instance, psychologists have explained generosity and cooperation by proximate factors such as empathy and trust (see van Vugt and van Lange, 2006). Evidence from other disciplines (sociology, anthropology) has emphasized the role of proximate mechanisms of a social nature, such as norms of fairness and morality, for regulating exchanges between members of groups and bringing solidarity and cooperation about. It has been recognized that advanced proximate (cognitive and motivational) mechanisms are needed to recognize who is a group member and who isn't, and there is ample empirical evidence from various disciplines showing that members of in-groups are favoured over out-group members, who are often faced with xenophobia (e.g. De Waal, 1996, 2005; Tajfel and Turner, 1986). However, only by taking both proximate and ultimate explanations into account can one understand how and why in-group favouritism and out-group hostility come into existence.

As Malinowski argued, the inhabitants of the Trobriand Islands are involved in mutual gift exchange, not only because they feel mutually obliged to do so or because they simply like it, but also because the pattern of giving and receiving supports a larger system of mutual relationships. Chimpanzees do not only groom each other because it feels good but also because it is functional for the maintenance of community. Jackdaws share food, not only because they want to be nice to each other but also because they need to safeguard their social relationships. The same reasoning applies to the reciprocal altruism of dolphins and vampire bats. Time and again a certain 'immediate' behaviour is performed that, though often difficult to interpret for human beings, in the end appears to serve the 'fitness' of the individual or group displaying the behaviour. In most cases, reciprocity is not a consciously and rationally pursued strategy. You don't give a gift because you want to get something back at all, but, whether you want it or not, you will end up with a return gift, as the empirical research in the Netherlands has shown.

While saving lives, not only of kin-related but also of non-related individuals, can be explained by (extensions of) kinship altruism, also sacrificing one's own life for some ideological belief or conviction can be interpreted along evolutionary lines: it will bring benefits to the group because close group ties and solidarity are reinforced by it (Komter, 2005; Koopmans, 2006; Ridley, 1998).

Conclusions

The distinction made by biologists between kinship altruism and reciprocal altruism finds an interesting parallel in anthropological and sociological research and theory. Insights gained by Malinowski, Sahlins and Gouldner converge in their emphasis on the role of the 'kinship hierarchy' in gift exchange: 'kindred goes with kindness'. A first conclusion, then, is that both biological and anthropological approaches to human generosity have demonstrated that generosity is more frequently and more generously displayed towards recipients who are genetically and socioemotionally related to the giver: kin selection is a quintessential explanation of human generosity.

Second, both biological and social scientific research has shed light on the important role of reciprocity as a system fostering the evolution of generosity. Whether the reciprocity is direct (in dyads or in small groups) or indirect (in larger groups), it invariably promotes altruism and cooperation, and in doing so serves the survival chances of all parties involved. Whereas reciprocity occurs both in higher animals and in human beings, and even among lower animal species such as bats and dolphins, there is no species in which it is as common, and highly developed as among

humans (van Vugt and van Lange, 2006). An interesting similarity between the results of computer simulations, on the one hand, and psychological and anthropological research, on the other hand, is the role of reputation. Whereas research inspired by game theory has shown that giving pays off in the long run because in the future the social status of the giver will be taken into account, both Malinowski's field studies and more recent psychological studies reveal that public generosity can act as a 'signal' of evolutionary fitness. If the inhabitants of the Trobriand Islands did not pass along their gifts, they would develop a bad reputation and their 'fitness' as recipients of gifts would be reduced.

Not only is kinship altruism selective, reciprocity in human interactions has a selective character as well. Human reciprocity needs to be studied both in its positive and its negative manifestations; the latter are still too often overlooked. Reciprocity not only serves to create social ties and cooperation, but also makes 'victims' by acting as a 'principle of exclusion': reciprocity can be seen as a double-edged sword (Komter, 1996b, 2001). Those who are generous givers receive amply in return, while those who are not in the position to give generously to other people receive very little. Generosity generates its own rewards and is therefore selective: those with good social opportunities benefit most from mutual gift exchange, whereas those who are already lacking in formal resources such as work and income are also the least favoured recipients of informal gift giving.

Third, there is no perfect continuity between cooperation and generosity among higher primates and human beings: the mechanisms of kinship and reciprocal altruism are not sufficient to explain generosity and cooperation among humans. Both from biological and social scientific evidence it has become apparent that human beings differ from other social species in the sense that they have evolved a unique capacity for generosity towards genetic strangers. Human beings cooperate with non-relatives and engage in heroic moral behaviour (for instance, saving lives at personal risk). Mechanisms such as 'strong reciprocity', group selection, cultural norms and forms of gene-culture co-evolution can account for these more complex behaviours.

Finally, in order to solve the apparent contradiction between self- or group interest, and altruistic concerns in generosity and cooperation, the awareness of the ultimate-proximate distinction among social scientists needs to be increased. It is exactly the intricate combination of longer-term interest (or evolutionary 'fitness') and short-term altruism that makes generosity such a splendid force in animal and human evolution. In the words of the psychologist Ronald Cohen: 'Because giving is such an adaptive feature for the maintenance of social life, it is so ubiquitous among human societies' (Cohen, 1978: 96).

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