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Altruism in humans: an evolutionary approach

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Altruism was originally defined as a co-operative act inflicting a cost to the donor and only giving a benefit to the recipient. However, no study has ever conclusively demonstrated the existence of altruistic behaviours that do not give any short- or long-term benefits to donors. Therefore, the term altruism is generally used for costly behaviours that may potentially also be beneficial for the donor. In accordance with this broader definition, two main concepts have been traditionally proposed to explain the evolution of altruism: inclusive fitness (Hamilton, 1964) and reciprocal altruism (Trivers, 1971). Altruism among kin evolves through kin selection (Hamilton, 1964), as donors may gain inclusive fitness benefits by helping their relatives. Regardless to the genetic relationship between two interactants, reciprocal altruism may become evolutionarily stable when individuals alternatively or simultaneously act as a donor or recipient of the altruistic behaviour, thus balancing the costs and benefits of the exchange over time. Since Hamilton and Trivers seminal papers, additional theories or factors favouring altruism have been proposed (reviewed in Kappeler & van Schaik, 2006; Nowak 2006), including indirect reciprocity, multi-level selection, and reputation. The concept of indirect reciprocity applies to interactions where the donor of the altruistic act may receive benefits from the former recipient different from those given, or where the benefit is returned by a third party. Reputation may be one of such benefits: individuals may act altruistically (e.g. through public donations to charities) to improve their reputation within the group and/or to signal potential mates or competitors that they may successfully afford the cost of altruism (Milinski *et al.*, 2002; Roberts, 1998). Multi-level selection suggests that groups composed of all altruistic members should be more cohesive and have a greater average fitness than groups composed of a mixture of altruists and defectors (i.e. individuals who rarely or never act altruistically despite benefiting from the altruism of others) and their proportion should thus increase within a population over time.

All the theories proposed so far share the same pre-requisites to reduce the risk of defection and for altruism to become evolutionarily stable: animals need to recognize and repeatedly interact with the same subjects over a given period of time, remember the type of interactions they had in the past, and modify their behaviour accordingly. There is increasing evidence that other animals than humans (mainly non-human primates, cetaceans and elephants) possess these capacities, at least to some extent.

It is somehow implicit in the previous requisites that the capacity to predict the behaviour of potential social partners may be a factor that favour altruism and reduce the risk of exploitation. This capacity may be built through repeated altruistic interactions with the same individuals where the positive outcome of the interaction helps increasing the investment in, and the overall quality of the relationship between two interactants. The choice of social partners and the establishment of social bonds become particularly important in relation to the scenario described by the *banker's paradox* (Tooby & Cosmides, 1996). The *banker's paradox* refers to the situation in which an individual desperately needing help is less likely to receive it because its uncertain condition makes that individual a potentially bad reciprocator. Under such a situation, altruism should not evolve. Tooby and Cosmides (1996) propose that the establishment of stable and friendly relationships between group members evolved as these favour the exchange of help when needed and thus reduce the risks of the situation described by the banker's paradox. This is probably one of the main reasons why friendly social relationships are observed in many social species (e.g. Silk, 2002).

Altruism is often studied using the *prisoner's dilemma* as an analytical tool (Axelrod, 1984). In this game, players have the option of either co-operation (i.e. giving a benefit to the other player) or defection (i.e. no benefit given). The benefit may be virtually of any kind depending on the experimental conditions and on the species under study: money, food, protection from predators or else. Based on the payoffs of the game (see Table 1 for a payoff matrix), altruism is rewarding when both players are willing to act altruistically. However, altruism is constantly at risk of exploitation as, according to the rules of the game, a defector gains a higher reward when playing with an altruist. Theoretical and empirical studies indicate that if the game is only played once, the best strategy is to defect. However, when the game

Tab. 1 - Payoff matrix of the prisoner's dilemma game where the benefits for each player are in the following order: α > β > γ > δ (C = co-operation; D = defection).

		Player B	
		C	D
Player A	C	β	δ / α
	D	α / δ	γ

is iterated altruism may be beneficial and may become an evolutionarily stable strategy. To test this hypothesis, Robert Axelrod (1984) run a computer-based tournament, using a prisoner's dilemma played by different strategies submitted by various scientists in a range of different fields (from mathematics and economy to biology and sociology). Strategies covered the whole spectrum from "all-defect" to "all-co-operation" (i.e. two strategies that, respectively, always defect or co-operate no matter what the other player does). The strategy that won the tournament was called "tit-for tat". Tit-for-tat always co-operates in round one and then simply copies what the other player has done in the previous round. Therefore, tit-for tat is a co-operative strategy (as it keeps co-operating if the other players does so) that punishes the other player in the first round following a defection. The fact that tit-for-tat won the computer tournament proves that co-operation is favoured when players interact repeatedly over time (as it happens in the iterated prisoner's dilemma) and when the temptation to defect is kept low by the risk of punishment.

The utility of the IPD as a tool to analyse co-operative interactions has been questioned due to its simplicity and based on the fact that it forces players to simply choose between cooperation and defection (Frean, 1996). The simplicity of the game might be its weakness but also constitutes its strength, as this allows obtaining a quantitative measure of co-operation and to experimentally manipulate various variables to test their importance. Moreover, because the game is very simple and it resembles real life situations the prisoner's dilemma has been applied to a large range of species, from interactions between a host and the cleaner fish to social relationships in baboons and humans (e.g. Barrett *et al.*, 2000; Bshary, 2002; Roberts & Sherratt, 1998). In response to the critique about the strict dichotomous choice (i.e. co-operation versus defection) that the prisoner's dilemma involves, various studies have now incorporated the possibility for players to vary their level of co-operation. This new approach potentially allows the existence of an almost infinite number of strategies. However, two main strategies have been more consistently tested in both humans and other animals (Roberts & Sherratt, 1998; Barrett *et al.*, 2000). In the "give as good as you get" strategy, a player matches the other player's previous move continuously throughout the game or over repeated interaction. In the "raise the stakes" strategy a player starts with a low level of co-operation while gradually increasing it if the other player matches this co-operation. The "give as good as you get" strategy is expected to be observed mostly between individuals who have a stable relationship. The "raise the stakes" strategy is particularly beneficial for players who do not know each other and first need to "taste the water" in order to determine the other player's willingness to be co-operative. Data on humans support this picture. In an experiment using the prisoner's dilemma, humans were more altruistic towards friends than towards unfamiliar subjects (Majolo *et al.*, 2006). Friends maintained an overall high and stable level of co-operation across rounds that is, they used a "give as good as you get" strategy. Conversely, unfamiliar players used a "raise the stakes" strategy, indicating that this strategy is particularly beneficial to reduce the risk of receiving defection and to build co-operative relationships.

Despite the constantly increasing number of studies on altruism conducted by scientists in various fields, our understanding of the topic is still relatively poor. The challenges for the next few years will be to analyse the importance of concepts, such as the one of competitive altruism, involving polyadic interactions and to incorporate the findings from various discipline into a coherent and comprehensive framework. This is important not only from a scientific and theoretical point of view but also because understanding which factors affect the occurrence of altruism has significant implications on how we view human societies.

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