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3. Are We Selfish or Cooperative?
Evolutionary Roots of Social Behavior
Introductory Paper

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Dr. Arcadi Navarro

Unitat de Biologia Evolutiva

Departament de Ciències Experimentals i de la Salut

Pompeu Fabra University

Who trusted God was love indeed
And love Creation's final law --
Tho' Nature, red in tooth and claw
With ravine, shriek'd against his creed --

In Memoriam AHH

Lord Alfred Tennyson (1850)

Although the idea of Nature being mercilessly violent and bloody, "red in tooth and claw," is still seen as following naturally from Darwin's ideas, nowhere in the *Origin* did Darwin quote Tennyson's verses or mention such an extreme notion. Rather, he wrote about competition for food and mates and about the ability to withstand unfavorable climates (Darwin 1859). Nevertheless, Darwin's powerful description of the "struggle for life," a concept contained in the very title of his book, *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life,* caused a lasting impression in the minds of biologists, economists and sociologists alike.

The idea of a struggle for life, from which the better-adapted emerge victorious to engender the following generations, has been extremely fruitful. Derived concepts such as competition, predation and parasitism are right at the root of our understanding of nature and have empowered us to act upon it in previously unconceivable ways. But, most importantly, Darwin's ideas and its derivations have allowed us to recognize ourselves as another animal species and to reevaluate our position is the universe. Our capacities as a species, as wonderful and complex as they are, strongly depend on our genes, just like the traits that characterize any other organism (this is not necessarily the case for our differential capacities as individuals, and this is an important caveat). Human nature is the product of evolution and, thus, over millions of years, natural selection has been able to shape it. This realization is in the very basis of this dialogue.

After a century and a half of successfully explaining the world, it is now widely accepted that there is indeed a struggle for life and, thus, that nature is

fundamentally competitive. This does not imply, however, that the consensus among scientists is that nature is always "red in tooth and claw." Quite obviously, nature is not a continuous and ruthless fight between self-interested creatures. The natural world is bursting with counterexamples, full of very well-documented cases of cooperation and altruism. Wolves do get their teeth and claws red when hunting and killing deer, but they do so in cooperative packs; pigeons and petrels regurgitate food for their offspring; worker bees sacrifice their lives by stinging attackers of their beehive, and so on. The best and most elaborate examples of cooperation and altruism in nature are provided by humans: they live in enormously complex societies whose norms, laws and customs gravitate around mutual aid and how to ensure it. Humans die for king and country, have hyper-specialized and sometimes quite boring jobs, pay taxes and join NGOs. In fact, all around us we can see people contributing to the welfare of other people. Humans are so used to this high level of cooperation that, traditionally, we have not cared too much about what might be the explanation of such behavior or about its sociocultural implications.

The apparent paradox of an essentially competitive nature that presents so many instances of cooperation and the difficulties in explaining what is known about human societies in terms of sheer competition are caused by an over-simplistic view of evolution. In sharp contrast to the early misinterpretations of the struggle for life within a human context, which were presented as justifications for some of the most hideous policies in modern history, today we know that cooperation, just like conflict, is deeply ingrained in the evolutionary history of our species. In what follows, we will try to show how an evolutionary view of human nature and society can help us, not only to explain why we are the way we are, but also to push forward the limits of our political and social thought.

Teaming up. The hierarchical nature of life.

With some brilliant exceptions, until the late 1960s scientists tended to focus on the study of the conflictive interactions mentioned above: competition, parasitism or predation. Cooperation received far less attention because it was

believed to be of limited significance, only useful to explain some peculiar groups of organisms—such as ants or termites—but of little relevance for the rest of life forms on the planet. A deeper understanding of the organization of living organisms has changed this view. This improved knowledge comes from the realization that, since the appearance of life on Earth about 3.5 billion years ago, it is teamwork that has allowed the emergence of increasingly complex life forms.

The organization of the living world is hierarchical. Every form of life, from the simplest bacteria to complex eukaryotic, multicellular organisms, whose functions are coded by thousands of genes, and which may live in large social groups, is constituted by lower-level units that group together and cooperate to form higher-level units of organization (genes, chromosomes, bacteria, eukaryotic cells, multicellular organisms and societies). The major landmarks in the diversification of life have involved cooperation-driven transitions between these hierarchical levels (Maynard-Smith and Szathmáry 1995, Michod 1997, 1999). Every level in the hierarchy is formed by members that, in their individual state, might have fiercely competed but that, in their present form, display excruciatingly complex and selfless cooperative behaviors.

Consider individual cells in a multicellular organism. Instead of trying to out-compete and out-reproduce each other in a mad race for resources, like bacteria in a culture would, the cells in our bodies grow in a harmonious and cooperative manner. Coordination is so complete that most of our cells renounce the ultimate goal of all living things: contributing to the next generations. Cells in our skin, intestines and brains delegate their reproductive functions to a few specialized sperms or ova. Still, conflict is possible. Some cells may act selfishly and go back to their old ways, reproducing without control and causing havoc in our bodies. We call that kind of conflict cancer. It illustrates how important cooperation is in our bodies to keeping us alive. Let us now consider eusocial organisms, such as ants, termites, bees or the naked mole rat. In all these cases, cooperation is so very extreme that workers have delegated reproduction to a few members of the colony: the queens. Again, selfish reproduction is possible in certain cases, but it is so harmful for the

community that these species have evolved amazing repressive strategies, sometimes resembling a police state (Ratnieks and Visscher 1989).

We could keep describing analogous situations in other levels of organization such as cooperation between genes to form genomes or cooperation between different genomes to form eukaryotic cells and so on, but the central idea should be clear by now. It is cooperation that has allowed all this complexity to exist. In the highly competitive struggle for life, cooperative strategies have proven successful over and over again.

There is an obvious parallel between the examples above and human society. Society can be thought of as an organism made up of many specialized units working in a coordinated way. Almost every aspect of social life can fit in this framework: school, religious institutions, hospitals, armies, laws. But is this a correct analogy? Can we be certain that the same biological mechanisms underlying cooperation in the natural world can be applied to human society? And, are there any lessons to be learned from the study of these questions? To tackle all these issues, we first need to understand how cooperation can come about in general, and in human societies in particular.

Different paths to cooperation.

Cooperation can be defined in terms of cost/benefit. Whenever an individual incurs a cost in order to provide a benefit for another individual or set of individuals, we say that the first individual is cooperating or acting altruistically (Axelrod 1984). The cost can be anything, ranging from food, money or time to the donation of an organ. Evolutionary studies provide five different models of how such behavior can be promoted by natural selection. We will discuss these models separately, but the principle underlying all them is simple: cooperation can be a successful adaptive strategy if individuals that cooperate tend to help other cooperators (Frank 1998). This is intuitively clear: if cooperators help selfish individuals equally or preferentially over other cooperators, it is selfishness that will prevail. Selfish individuals will incur in lower costs and yet reap the benefits of altruism: it will not pay to be a cooperator. Thus, natural

selection has favored the evolution of mechanisms that allow cooperators to focus their benefits on individuals who are likely to be cooperators themselves.

Selfish genes. The first way in which cooperation can be favored by selection was discovered in the 1960s by George C. Williams (1966) and William D. Hamilton (1964). It triggered what is known as the "Sociobiological Revolution," popularized by Edward O. Wilson in his books *Sociobiology: The New Synthesis* (1975) and *On Human Nature* (1978). Most famously, the main ideas of this revolution are summarized in the title of Richard Dawkins' bestseller *The Selfish Gene* (1976). The underlying idea is simple: if a cooperator's behavior is genetically coded, a cooperator can safely help its relatives, since they share genes and, thus, they will also tend to be altruists. This is better understood from the point of view of a gene promoting cooperation. The gene will increase its frequency in the population if the individual carrying it reproduces, but also if the individual carrying it helps other individuals who share the same gene to have their own offspring, even if, by doing so, the cooperator incurs in a large cost.

Imagine a gene that makes me help my brothers and sisters. Because, on average, I share 50% of my genes with any of my brothers (we have the same mother and father), if I die to save the lives of, say, four of them, I will still be helping two copies of my genes (50% of 4) to be passed on to the next generation. From the genes' point of view, this is a great deal. By causing the cooperator to help its relatives, the gene is selfishly helping to copy itself. It follows, of course, that the closer the relatives, the more advantageous it is to cooperate with them (West *et al*. 2002). This kind of selection is known as **kin selection** and is based on a simple principle, known as Hamilton's rule (Hamilton 1964). According to this rule, cooperation is evolutionarily advantageous if costs to the cooperator are lower than the total benefits bestowed upon the individuals it benefits, corrected by the degree of kinship of these individuals with the cooperator. Hamilton's rule proved to have enormous explanatory power. It accounted perfectly well for

multicellular organisms (all the cells are genetically identical, so it makes sense for them to delegate reproduction) and eusocial organisms (it can be shown that it is more efficient for a worker bee to help its queen reproduce than to reproduce herself). Needless to say, kin selection has a privileged role in human affairs. It certainly helps explaining nepotism, for instance. But in both humans and other animals, it is clear that cooperation extends to non-relatives. The selfish gene does not explain it all.

Reciprocity. Another way to guarantee that a cooperator helps other cooperators is to make sure that the individual that profits from a cooperative act will, sooner or later, repay (Axelrod 1997). It is easy to get an intuitive idea of this mechanism, since it is based on common sense and we all became familiar with it in nursing school: "**if you scratch my back, I'll scratch yours.**" By applying reciprocity, individuals can interact preferentially with other cooperators. Thus, it plays a role in our day-to day life, whenever we go shopping, for example. However, detailed mathematical models show that reciprocity is far less powerful in promoting cooperation than kin selection and, moreover, there is little evidence of reciprocity in nonhumans (Hammerstein 2003). Also, it is clear that humans and other organisms cooperate far beyond reciprocity. In our large and complex societies, we do scratch the back of individuals who we are unlikely to meet again.

Indirect reciprocity. Mathematical and simulation studies show that some of the problems posed by reciprocity are solved if individuals can keep tract of each other's helping records (Axelrod 1997). If a cooperator helps somebody who has previously shown to be a helper (i.e., somebody who has a **good reputation**), then cooperators will tend to interact with other altruists and it will become possible for cooperation to evolve. We can readily see examples of how this operates in our society but, again, it is obvious that we cooperate with people we have never heard of. What compels us to do so?

Social norms and punishment. Human societies are regulated by law or, at the very least, by some kind of norms and traditions that are only loosely dependent on rational choices of the individuals that implement and obey them. Norms can be defined as a number of shared prescriptions about how to behave in interactions with both known and unknown individuals. They present interesting features that fall under the common name of **strong reciprocity** (Fehr *et al*. 2002, Fehr and Fischbacher 2003): experiments show that law-abiding individuals will be rewarded by third parties, even at a cost for the rewarders. This behavior has been termed **altruistic rewarding** (Fehr and Fischbacher 2003). On the other hand, when individuals do not adhere to norms, third parties may undertake punitive actions. Experimental work shows that these punitive actions are a form of altruism: individuals that punish lawbreakers do it at a cost for themselves. Both the lawbreaker and the punisher pay a cost and there are no direct profits from that action. The benefits are indirect, and can be found in the fact that punishment induces the correct behavior in potential lawbreakers. This kind of behavior is known as **altruistic punishment** and its importance in securing high-level cooperation has recently been proven crucial (Fehr and Gatcher 2002, Fehr and Fischbacher 2003). Altruistic rewarding and punishment constitute powerful incentives for cooperation even when reciprocality is not possible and information about reputation is not available, because cooperators will reward those who cooperate and punish those who defect.

There are many examples of such norms and their enforcement in human societies: from dress codes and table manners to rules for community living, marketplace regulations and religious beliefs. Mathematical models, simulations and experiments based on these ideas, however, show how these mechanisms can help fix maladaptive attitudes in a society (Boyd and Richerson 1992). That is, once a reward and punishment system is set up, almost any norm can be established in a society, independently of whether it is beneficial to

anyone or even if it is clearly detrimental (as in the case of clitoridectomy, for example). Thus, this kind of mechanism fails to explain why are there so many cooperative social norms instead of senseless sets of arbitrary determined rules.

Group selection. The latter problem is solved, and the picture completed, by considering a further level in the hierarchy of nature: groups of individuals within a species. The idea behind models of **group selection** is that groups can compete among themselves just as individuals or species do. Social groups with more cooperative norms that improve their access to resources increase their reproductive rates or make their warfare techniques more efficient may dominate and/or conquer other groups, either by the force of arms and demography or by prestige-biased transmission, which induces individuals to preferentially imitate successful groups. It has been shown that the norms of a successful group can preferentially spread from group to group relatively rapidly (Boyd and Richerson 2002). Because cooperation fosters success, these processes can lead to the preferential proliferation of cooperative norms. Numerous examples of such processes have been observed in the ethnographic, archaeological and historical record (Boyd and Silk 2000, Boyd and Richerson 2002).

The above list includes mechanisms of increasing complexity which are not mutually exclusive. It is worth stressing that the most complex mechanisms (group selection, rewarding and punishment), which require very advanced mathematical or simulation tools to describe and study them, are intuitively clearer to us than the simpler, gene-based, kin-selection ideas. This just goes to show how very accustomed we are to acting according to such complex mechanisms.

Identity and cheating.

Besides the fact that they all promote interactions between cooperators, there is an obvious common feature in the mechanisms presented above: they all rely on distinguishing cooperators from selfish individuals. When thinking about multicellular organisms this is no big problem. Being attached to the same body guarantees that, if one individual (a cell) is a cooperator, the individuals it will interact with will be cooperators as well. If we consider social groups, however, the situation becomes more intricate. How can a cooperator be sure to be helping other cooperators? Clear identity markers are needed.

A straightforward possibility is a "green beard gene" (Dawkins 1976). If individuals with green beards (or, for that matter, any clearly distinguishable feature) cooperate, but do so exclusively with other green-bearded individuals, cooperation will quickly spread and the world will become a peaceful paradise of green-bearded cooperators. But this fairy-tale world is fragile. It can easily be invaded by mutant cheaters who, in spite of boasting luxuriant green beards that induce others to help them, would never cooperate with their fellow beings. Cooperators would soon vanish, as their world is quickly taken over by such selfish individuals. Making sure that an apparent cooperator is indeed a cooperator is, thus, the key issue.

Inextricably tied to higher levels of cooperation, new opportunities for cheating and conflict arise. Thus, the increasingly complex cooperation-promoting mechanisms outlined above depend on increasingly complex identity markers. These have been studied in detail and the overall picture is that, parallel to the addition of hierarchical levels in nature, continuous arms races are being waged between cheaters, who try to cunningly disguise themselves as cooperators, and cooperators who try crafty strategies to uncover them (Axelrod 1997). Because of the everlasting conflict between cheaters and cooperators, these identity markers are a fundamental part of cooperation mechanisms.

Consider, for example, kin selection. Kinship creates numerous possibilities to distinguish relatives, with whom one cooperates, from other individuals. Close kin, besides sharing the tendency to cooperate, may share a similar appearance or smell that natural selection may use as cues to build an instinct

like "help those who look like you." In other cases, when family groups tend to remain in the same territories, simple proximity can be used as a cue (West *et al*. 2002): "help those who are around your parents". Kin selection is important for humans and, because we have elaborate cognitive capabilities, our kin-recognition systems are sophisticated. The available evidence suggests that humans use a variety of cues to assess kinship, including physical similarity to oneself and other family members, scent, proximity during youth and, of course, social learning of relationships (Wolf 1995). Interestingly, researchers have shown that men are more kindly disposed towards babies that resemble themselves (Platek *et al*. 2002, 2003).

In the case of higher primates, especially humans, multilevel recognition systems operate because cooperation is also multileveled. Of course, more intricate cooperation mechanisms depend on correspondingly complex identity-recognition systems. At the highest level, the importance of group-recognition mechanisms is a consequence of the enormous importance of group structures in primate evolution. Indeed, our species has only recently (over the last few thousand years) started organizing itself in large societies formed by several million individuals. Until then, hominids lived in loosely organized small groups (Boyd and Silk 2000). It is crucial to realize that evolution has shaped us to exist under the latter conditions and that adaptive explanations of our behavior must therefore take them into account (Incidentally, some of the traits that were adaptive in one environment may not be adaptive or may even be detrimental under our present conditions). By getting together in small bands, hominids not only protected themselves from predators but also created boundaries between groups and generated the conditions for selection among hominid groups. According to research conducted in recent decades, intergroup conflict among hominid groups has been a crucial force in the evolution of humans (Alexander 1989). It not only allowed the extension of the cooperation-inducing norms that, as explained above, made certain groups more successful than others, but also posed a difficult challenge to our ancestors: to quickly distinguish in-group members from out-group individuals, so that each could be treated accordingly. Conflict between groups may have selected individuals with higher cognitive abilities and generated not only strong in-group cooperative bonds and

recognition methods, but also other typically human features, for example intragroup status hierarchies, to facilitate the coordination of group work toward a common goal.

Because group identity recognition is so complex, social learning of the appropriate identity markers is far more important than in the case of kin-recognition systems, for example. These markers are complex and, like a Russian doll, include markers of lower level. Appearance-related markers, such as pigmentation, stature or facial resemblance, and proximity markers, such as close territory sharing since childhood, which are key as kin-recognition systems, can be used, since an individual's blood relatives tend to belong to the same group. Other markers are essentially social, such as clothing or tattoos. Interestingly, the social conventions and norms that these cooperation mechanisms have been crucial to establishing are themselves identity markers. Religion, rituals and language are among the most important. Language, in particular, has been studied in detail as a group marker, and surprising results have been obtained. In a series of famous (and polemical) experiments performed in the UK, black youth stigmatized a recording of speakers of Black Vernacular English as low class, but simultaneously picked the speakers as a likely source of support in a fight, compared to voice speaking Standard English (Labov 1972).

It is vital to realize that evidence suggests that there is no genetic determination of these markers, at least not as usually interpreted. What is clearly coded in our genes is the tendency and capacity to become skilled in the detection of certain markers, but not the specific form they take in any given culture (Boyd and Silk 2000). Our brain is ready to become tuned to certain classes of signals, but we learn the signals themselves after we are born. This is also the case in chimpanzees. Experiments performed with chimpanzees that have been raised in human families show that they can distinguish and classify images of other chimpanzees and of humans in different groups. There is one mistake they usually make, however: they classify their own image with those of their human families, because they have learned to recognize them as their own group.

What have we learned? A short list of questions and proposals.

I hope that this brief overview has shown how our knowledge about human altruism has advanced over the last two decades. Some of the newest results may defy long-cherished yet naive prejudices. Most certainly, they raise interesting questions and suggest avenues of research that we must certainly explore. A short list of examples follows.

1. Experimental evidence indicates that reputation formation, rewards and, crucially, punishment, have been and are powerful determinants of human behavior (Fehr and Fischbacher 2002). Altruist punishment, in particular, allows for the success of cooperation because it dissuades people from breaking laws and, in general, reduces deception and conflict. For instance, we altruistically keep criminals in jail not only because we want to reeducate them, but as an example to potential noncooperators. Should this second and, from an evolutionary point of view, more important social role of punishment receive more attention? Should "punishment as an example" be limited to primary school, or perhaps completely ruled out of our societies? What would be the social consequences of a reevaluation of the roles of reward and punishment in our educational system?

2. Different human groups are characterized by different social norms. Some of these are cooperative, some not. Some norms may have been produced by rational or adaptive choices from the groups that practice them, but a good number of them were not. Some norms are clearly maladaptive: they are the by-product of innate and very efficient norm-formation systems. Some of these clearly undesirable norms, on the other hand, have been transformed into robust group identity markers. To what extent are they dependent situation (environment)? How should we act upon these norms? What could be the consequences of these actions for the identity of the affected groups?

3. Campaigns to suppress identities that exclude, and thus create an increasing feeling of "comprehensive human identity," are usually based on the promotion

of overly abstract concepts, such as "solidarity." Because such abstractions don't reflect any specific identity markers, they don't make use of innate predispositions to distinguish members of our own group, but rather they actually fight these predispositions. Early formation of multicultural and multiethnic social groups, together with the early promotion of common human physical and cultural traits and universal values (such as those proposed by the Forum) as group markers, should be an efficient way to promote the feeling of belonging to a single "human group."

I am aware that these ideas are too schematic. The systematic study of sociological problems from an evolutionary perspective and the use of both theoretical and empirical techniques has produced amazing results but is a relatively young field. Lots of interesting research is currently being conducted which might add surprisingly important pieces of information or help reinterpret available evidence. Yet, it is on these scientific grounds that we can try to push our understanding of identity and society and, perhaps, contribute to the central goal of this Forum, which coincides, in my view, with a major goal of humanity in our times: making our cultural differences our main asset, rather than our main problem.

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