WHAT DOES MODERN SCIENCE SAY ABOUT THE ORIGIN OF COOPERATION? SCIENCE CONFIRMS PHILOSOPHY

Marian Hillar
Center for Philosophy and Socinian Studies
Published in in *Dialogue and Universalism,* Vol. XXIII (3) 2013, pp. 23-34.

Philosophical Intuition

Investigation of the phenomenon of cooperation has a long history. Perhaps the most eloquent expression of this phenomenon was given by the Stoic, Marcus Aurelius (121-180 C.E.), Roman Emperor during the years 161-180 C.E. Aurelius followed the principles of the Stoic moral philosophy which emphasized the well-being of the community and the naturalistic basis of human behavior:

> Men exist for the sake of one another.
> We ought to do good to others as simply as a horse runs, or a bee makes honey, or a vine bears grapes season after season without thinking of the grapes it has borne.[1]

Aurelius wrote his *Meditations* during his campaign between 170-180 for his own guidance for he was a priest at the temple in Rome. His book was first published in print in 1558 in Zurich from a manuscript that is lost today. However, there exists another manuscript that survived to our times now located in the Vatican library. His book was read throughout the centuries for moral and spiritual edification by rulers, politicians, philosophers and writers.

Another Stoic philosopher, Cicero (106-43 B.C.E.), claimed that the pattern of human behavior changes from purely animal-like and instinctive to fully rational and involves five stages. They represent the development of human nature, but only a few people will reach the highest stages, because the process is not independent of a man's own effort. The "function" or goal of man in this process is attainment of the perfection of his nature. The term used by Cicero is *officium* (corresponding to the English office, duty or task, as the office of an official charged with certain duties) and the Greek term is *kathekon.* One could not talk about the "duty" of an animal or of an infant, but rather of their natural function. The term duty becomes appropriate in stages three-through-five in human development as the changes in behavior become the functions of a rational being.[2] Thus the Stoics recognized a natural biological basis for human behavior from which reason draws conclusions, develops rules and constructs a moral philosophy.[3] Even Immanuel Kant (1724-1804) wondered about the origin of the moral principle that humans display and which he called "goodwill":

> Duty! Thou sublime and mighty name that dost embrace nothing charming or insinuating but requirest submission and yet seekest not to move the will by threatening aught that would arouse natural aversion or terror, but only holdest forth a law which of itself finds entrance into the mind and yet gains reluctant reverence (though not always obedience) – a law before which all inclinations are mute even though secretly work against it: what origin is worthy of thee, and where is the root of thy noble descent which proudly rejects all kinship with the inclinations and from which to be descended is the indispensable condition of the only worth which men alone can give themselves?[4]

This classification of the behavioral levels derives from the Stoic intuitive philosophical doctrine[5] and corresponds to the stages of moral development of man through which community life and virtue are recognized as pre-eminently "things belonging to man" in their terminology and are related to the autonomous behavioral level (categorical imperative of Kant). In modern times such a Stoic view of the moral development of man in the Kantian modification was wholly confirmed by modern psychology and philosophy. Lawrence Kohlberg (1927-1987) suggested six stages of the moral development of children through three levels – the pre-conventional, conventional, and post-conventional, each subdivided into two stages. The first two levels correspond to the heteronomous behavioral level of Kant.[6]

Evolutionary Biology and Cooperation

Looking at the principles of evolutionary theory it seems at first that the existence of cooperation should be contradictory to the evolutionary process. This difficulty was noticed already by Darwin when he discussed the origin of social moral faculties in "the primeval man." Darwin admitted that such traits as courage and fidelity could increase in competition between tribes: "A tribe rich in the above qualities would spread and be victorious over other tribes."[7] But asking how within the same tribe could a large number of members become endowed with these social and moral qualities, Darwin answered himself:

> He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature. … Therefore it hardly seem probable, that the number of men gifted with such virtues, or that the standard of their excellence could be increased through natural selection, that is by the survival of the fittest; for we are not speaking here of one tribe being victorious over another.[8]

Then Darwin postulated that though the high standard of morality may give a slight advantage to each individual in a tribe, yet an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity obedience, courage, and

sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most tribes, and this would be natural selection."[9] Evolutionary scientists classify such a selection as a "between-group selection." Moreover, cooperative and altruistic behavior, understood not in the everyday sense of conscious act, but as a behavior which benefits other organism at a cost to the donor, is widely common throughout the animal kingdom. It seems from the studies of many biologists that entire organisms like multicellular organisms with specialized cells could also be considered as organisms made of cooperating cells and entire colonies of social organisms depend on cooperation and often altruistic sacrifice of some individuals for the sake of the group.[10] Thus Martin A. Nowak building mathematical models for evolution considers **cooperation** the third fundamental process for evolution after **mutations** and **natural selection**.[11] The problem puzzled many biologists, economists and mathematicians. Darwin suggested that natural selection favored families whose members were cooperative and answered Kant's question about the origin of moral rule:[12]

> The following proposition seems to me in a high degree probable – namely, that any animal whatever endowed with well-marked social instincts, the parental and filial affection being here included, would inevitably acquire a moral sense or conscience as soon as its intellectual powers have become as weal, or nearly as well developed in man.

Such prediction by Darwin is confirmed today by scientific investigations postulating the existence of the "moral faculty."[13] This concept of the "moral faculty" goes back to antiquity when the ancients had a premonition of innate moral principles (moral sentiment, sense of justice, common moral thought) which were working subconsciously. It is the basis for the moral rules which like rules of logic or of natural sciences are objective truths, outcomes of rational choice. These rules were developed and formulated in various cultures with varying degree of success and today they are at the foundation of humanistic ethics. John Rawls (1921-2002) in his well known treatise *A Theory of Justice* (1971) suggested that these innate moral principles can be analogized to the "sense of grammaticality" (a "faculty of grammar") described by Noam Chomsky.[14]

Hamilton Model of Inclusive Fitness: "Kin Selection"

The process of group selection postulated by Darwin was first in early days of neo-Darwinism discredited as a weak evolutionary force.[15] Still the phenomenon of natural cooperative, altruistic behavior needed an explanation.

The advent of modern genetic science could attempt to explain and expand the intuitive speculations of philosophers and explain the observations of Darwin by providing insight into how biological mechanisms operate. Thus our focus is now on the genetic conditioning for cooperation. William Hamilton developed a model based on genetic studies of socials insects. It is based on the observation that the offspring of relatives count toward one's individual fitness by helping to spread shared genes. Such a situation exists in colonies of social insects composed of related individuals. The closer the degree of relatedness, the stronger the cooperation one may expect among

individuals. This theory seems to be an explanation of Darwin's dilemma and was already vaguely suggested by John Burdon Haldane (1892-1964) in the 1930s.[16] The Hamilton model can be illustrated by behavior as when a parent or a close relative jumps into the water to save one's own or closely related child. Such behavior contributes to the survival of one's own genes. The degree of relationship is an important parameter in predicting how selection will operate and the behavior which appears to be altruistic may, knowing the genetic relatedness of the organisms involved, be explained in terms of natural selection. The genes which are selected for this behavior contribute to their own perpetuation regardless of the individual in which the genes appear.[17]

Trivers Model of "Reciprocal Altruism"

The model of kinship cooperation, i.e., the kin selection model of Hamilton, however, cannot explain all cooperation. Humans, for example, belong to a species that developed a high degree of cooperation among genetically unrelated individuals. Such cooperation between genetically unrelated individuals is defined as altruistic behavior or as reciprocally altruistic. It can be selected even when the recipient is so distantly related to the organism performing the altruistic act that kin selection can be ruled out. Such cooperation will represent behavior between members of different species. It is a behavior that benefits another organism not closely related while being apparently detrimental to the organism performing the behavior. Here benefit and detriment are defined in terms of contribution to inclusive fitness. Natural selection favors these altruistic behaviors because, in the long run, they benefit the organism performing them.

Robert Trivers in the 1970s developed this idea of "reciprocal altruism" as a model for explaining cooperation between genetically unrelated strangers based on naturalistic observations.[18] One of them involves symbiosis. There are innumerable examples of fish of one species hosting of another to the host. It seems that this symbiosis evolved many times being favored by natural selection. In this symbiosis the hosts of the cleaning organisms, in turn perform several kinds of altruistic behavior such as not eating their cleaners and warning them about approaching predators. The host benefits from quickly and repeatedly returning to the same cleaner. Another example of this behavior is that of some birds which emit special calls warning other birds when spotting an approaching predator.

Human reciprocal altruism takes place in a number of situations and in all known cultures and is represented by such kinds of behavior as: helping in time of danger; sharing food; helping the sick, the wounded, or the very young and old; sharing tools and knowledge. This altruistic behavior meets the criterion of small cost to the giver and great benefit to the receiver. It seems that human altruistic behavior comes directly from reciprocity and not indirectly through nonaltruistic group benefits. Some social scientists and philosophers tended to explain human altruistic behavior in terms of benefits of living in a group without differentiating between nonaltruistic benefits and reciprocal benefits.[19]

Trivers' model explains the psychological mechanisms of emotions such as friendship, dislike, moralistic oppression, gratitude, sympathy, trust, suspicion, trustworthiness, aspects of guilt, forms of dishonesty, hypocrisy and moralistic aggression as adaptations to regulate the altruistic reactions. Anthropologists analyzed

these human behaviors in terms of group survival, but Trivers model is more basic. Nietzsche is an example of a philosopher who, from an early age, was interested in the provenance of morals and ethics.[20] The question of evil in the world to him was of primary importance and Nietzsche resolved it by separating it from theological inquiry with the question, "Under what conditions did man construct value judgments *good* and *evil*"? Nietzsche proposed that "All sciences are now under an obligation to prepare the ground for the future task of the philosopher, which is to solve the problem of value, to determine the true hierarchy of values."

In Trivers model each individual human is seen as possessing altruistic and cheating tendencies, the expression of which is sensitive to developmental variables that were selected to set the tendencies at a balance appropriate to the local social and ecological environments. Trivers postulated that emotions of friendship and intelligence are prerequisites for the appearance of altruism that transcends the limit of family relationships. The underlying emotional dispositions affecting altruistic behavior have a genetic thus instinctive and unconscious component, and display a certain set of universal characteristics:

1. dispositions are sensitive to nuances in behavior; often in such behavior it will pay to cheat and detection of subtle cheating may be difficult;
2. friendship and emotions of liking and disliking will be selected towards those who themselves are altruistic. Moreover, friendship and intelligence are prerequisites for the appearance of such altruism that transcends the limits of family relationship;
3. once emotional dispositions for altruistic behavior have developed the altruist is in a vulnerable position because cheaters will be selected to take advantage of the altruist's emotions. Such a situation produces a selection pressure for the development of a protective mechanism in the form of "indignation" and "moralistic aggression." These dispositions were selected in order to
    a. counteract the altruistic tendencies in the absence of reciprocity to continuing the altruistic acts;
    b. educate the unreciprocating individual by frightening him with immediate or future harm of not receiving moral aid;
    c. and, in extreme cases perhaps, select against the unreciprocating individual by injuring, killing or exiling him.

    Thus much of human aggression has moral overtones motivated by injustice, unfairness and lack of reciprocity.
4. dispositional emotions of gratitude, sympathy, and cost/benefit evaluations:
    Emotion of gratitude has been selected to regulate human response to altruistic acts and is sensitive to the cost/benefit evaluation of such acts.

    Emotion of sympathy has been selected to motivate altruistic behavior as a function of the plight of the recipient of such behavior and increases with the increase of the potential of the benefit even to strangers or disliked individuals.
5. guilt and reparative altruism: Catching a cheater and making him pay dearly will produce a selection for a reparative gesture. This creates an emotion

of guilt which is selected to motivate the cheater to compensate for his misdeed and to behave reciprocally in the future and in this way to prevent the rupture of the reciprocal relationship.

6. mimicking the behavior: Once the emotions favoring altruistic or cooperative behavior develop, they select behavior for mimicking these traits in order to influence the behavior of others to one's own advantage.
7. detection of subtle cheaters: trustworthiness, trust, and suspicion. These dispositions are selected for in order to detect and discriminate against subtle cheaters. In classical philosophical and sociological considerations this issue was presented in terms of a problem how to define altruism, whether in terms of motives – a "real altruism" or "calculated altruism" or in terms of behavior, regardless of the motivation.
8. setting up altruistic relationships: natural selection will favor for establishing reciprocal relationships.
9. multiparty interactions: selection will favor more complex interactions than two-party interactions. This involves:
   a. learning from others indirectly by observation and language;
   b. helping to deal with cheaters;
   c. generalizing altruism;
   d. developing rules of exchange – language facilities formulating and codifying multiparty interactions. Anthropology and cultural history provide abundant evidence for these interactions.
10. developmental plasticity: Human evolution set up a selection pressure for psychological and cognitive powers which contributed to an increase in human brain size during the Pleistocene period (from 2.5 million to 12,000 years ago).

Trivers' model of reciprocal altruism constitutes a biological foundation for the **naturalistic social theory**. Already Nietzsche had an inkling into it when he attempted to describe the origin of "guilt" or "bad conscience" in the human psyche of emotions and the evolution of punishment and its purpose as an expression of moral rule. Nietzsche explains that the feeling of guilt is a product of the oldest relationship between humans, that of "buyer and seller, creditor and debtor." With this origin is linked the concept of punishment as compensation for the contractual relation between debtor and creditor. Damage produced by not keeping a contract results in rage and for every damage some equivalent for compensation may be found, even in inflicting pain. In older civilizations drastic pledges were made by the debtor in order to guarantee fulfillment of the promise. These compensations were in the form of inflicting bodily harm through which the creditor, in place of material compensation such as land or money, was receiving pleasure. Later this punitive authority was passed on to the legal authority and the creditor then enjoyed seeing the debtor despised and mistreated. Thus through such a process of contracts and legal obligations these moral concepts were developed: guilt, conscience, duty.[21]

Axelrod and Hamilton[22] inspired by the Trivers studies developed computer simulations of his model and created game programs such as Prisoner's Dilemma in which two players have the option to cooperate. It was found that such computer game

models evolve and can be maintained between two people if they follow the rule of reciprocity and learning in subsequent encounters. Prisoner's Dilemma games increased in complexity in further studies by allowing a gradation of responses mimicking more closely the complexity that evolved in the behavior of species like ourselves and our close relatives.[23] Also, the studies of reciprocal altruism were extended to many animal species.[24]

Reputation and Reciprocal Altruism Model

But these new models could not explain how large cooperative groups could evolve. In such groups the possibility of reencountering a person who is helping or who has been helped is quite small. Also one has to consider the situation when some people are cheating and become freeloaders, others may follow the cheaters and the stability of the group could be jeopardized.

To overcome these problems Martin Nowak and Karl Sigmund[25] developed a mathematical model in which people decide what to do based not only on whether others have helped them but also whether others have helped others. Thus a person with a reputation of a helper can get help even from someone who has not benefited directly from such a person in the past. Such a model was confirmed by Robert Boyd and Peter J. Richerson in 2004 who showed that those who did not help or had a reputation of being freeloaders were shunned.[26]

Punishment and Reciprocal Altruism Model

The reputation model for reciprocal altruism still could not explain fully the cooperative nature of human interactions. Ernst Fehr and others observed in their labor market studies that people tend to be more cooperative than the economic theory would predict. Fairly paid employees worked harder than predicted solely from their self-interest. To explain such behavior he suggested, by using game-playing experiments, that punishment was a factor in cooperative behavior. In a game model, participants could decide whether to keep money they were given or to contribute some or all of it to a group project and, at the same time they had the option to punish non-contributing participants. In this game participants were chose to punish the non-contributors and the majority of those who punished were those whose contributions were above-average. In a situation when punishment was not an option, average contributions dropped. Also, it was demonstrated that a mere threat of punishment was enough to prevent cheating.[27]

It is thought that altruistic learning may be instinctive because, in small groups of evolving humans, reputation always counted. Moreover, punishment had less importance since in human encounters rewards work better than punishment.[28]

Group Selection Model

The other model was developed on the premise that competition among groups can foster cooperation within them. Natural forces may work in different directions, e.g., natural selection may make individuals less cooperative, but competition between groups may push them to cooperate within the group enhancing thus the survivability of the group. This was observed by Darwin and is still observed for modern warring groups and

from military history. Archaeological studies, on evidence about 50,000 years ago, and historical reports demonstrated that death from warfare averaged about 14 %, significantly higher than in 20th century Europe with two world wars.[29] This result was confirmed by using game theory simulation. Thus it seems that cooperation between groups increased significantly with time in human evolution.

Cooperation among Viruses and Microbes

It is interesting that cooperation was also observed among such low level organisms as bacteriophages, viruses that live in bacterial cells. Two researchers Joel Sachs and James Bull[30] injected into a bacterial strain two different types of viruses at the same time. After many generations, the two viruses packaged their genomes within a single coating protein thus ensuring the transmission of both of their genomes to the next bacterial host. Other researchers expanded such studies on cooperation between bacterial strains showing that, when they sense the accumulation of other bacteria nearby, so-called *quorum sensing*, they increase secretion of certain biochemicals which are of benefit to all bacteria present.[31] The best known among social microbes is the slime mold *Dictyostelium.* It was shown that these single-cell amoeba organisms often merge to form stalks with fruiting bodies on top, thus allowing some cells to produce spores which may disperse to more food-rich places. But among these amoeba cells are also cheaters, cells that mutated, and which infiltrate the fruiting body, thus avoiding becoming the nonreproductive stalk. A large number of genes were discovered that confer the ability to cheat. At the same time studies showed that amoebas can keep cheating in check because mutations that make cheating possible prevent cheaters from getting into the aggregation at all. One of the genes, called the green-beard gene, enables an amoeba to recognize others with the same gene and help perpetuate copies of the gene in others regardless of relatedness.[32]

The existence of such type of genes for cooperation was postulated a long time ago by Hamilton. Many other organisms from termites to meerkats provide examples of cooperation. "The origin of sociality is unlikely to be encompassed by a single explanation. Sociality like multicellularity, has happened numerous times, in diverse taxa, and reached many different levels of integration."[33]

Acknowledgement

Author wishes to express his thanks to Mrs. Claire Stelter for reading the manuscript and he comments.

Bibliography

[1] Marcus Aurelius, *Meditations,* translated with an introduction by Maxwell Staniforth (Harmondsworth, UK: Penguin Books, 1964).

[2] Cicero, *On the Good Life*, translated with an introduction by Michael Grant ((Harmondsworth, UK: Penguin Books, 1986). Marian Hillar, "Natural development, Rationality, and Responsibility in Stoic Ethics," in *Essays in the Philosophy of Humanism*, Robert D. Finch, M. Hillar, F. Prahl, eds., Vol. 6, pp. 44-78. American Humanist Association, Houston, 1998.

[3] Marian Hillar, "Natural Development, Rationlity, and Responsibility in Stoic Ethics," published

in the *Essays in the Philosophy of Humanism*, Robert D. Finch, M. Hillar, F. Prahl, eds., Vol. 6, pp. 44-78. American Humanist Association, Houston, 1998.

[4] Immanuel Kant, *Critique of Practical Reason,* edited and translated with notes and introduction by Lewis White Beck, third edition, (New York: Macmillan Publishing Company, 1993), p. 90.

[5] *Stoicorum Veterum Fragmenta* Collegit Ioannes Ab Arnim (Stutgardiae: In Aedibus B.G. Teubneri MCMLXIV). Vol 1-4. (abbreviated as SVF). SVF 1.197.

[6] Lawrence Kohlberg, *Essays on Moral Development,* (San Francisco: Harper & Row, 1981, 1984), Vols. 1, 2. Marian Hillar, "Foundation of Kant's Moral Philosophy and its Reinterpretation. A Quintessential Humanistic Doctrine," in *Essays in the Philosophy of Humanism*, Vol. 17 (1), 2009, pp. 71-90.

[7] Charles Darwin, *The Origin of Species* and *The Descent of Man and Selection in Relation to Sex*, (Toronto: Modern Library, reprint of the second edition of 1860, no date). p. 498.

[8] Ibid. p. 499.

[9] Ibid. p. 500.

[10] James H. Hunt, *The Evolution of Social Wasps* (Oxford: Oxford University Press, 2007). Bert Hölldobler and E. O. Wilson, *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies* (NEW York: W. W. Norton & Company, 2008).

[11] Martin A. Nowak, *Evolutionary Dynamics: Exploring the Equations of Life* (Cambridge, MA: Belknap Press of Harvard University Press, 2006).

[12] Charles Darwin, *The Descent of Man and Selection in Relation to Sex, op. cit.* p. 471-472.

[13] Marc D. Hauser, *Moral Minds. How Nature Designed Our Universal Sense of Right and Wrong,* (New York: HarperCollins Publishers, 2006).

[14] Noam Chomsky, *Aspects of the Theory of Syntax* (Cambridge, MA: Harvard University Press, 1965), pp. 3-9.

[15] G. C. Williams, *Adaptation and Natural Selection* (Princeton: Princeton University Press, 1966). Maynard Smith J., "Group Selection and Kin Selection," *Nature*, 201, 1145-1147, 1964. R. Dawkins, *The Selfish Gene* (Oxford: Oxford University Press, 1976).

[16] Robert L. Trivers and Hope Hare, "Haplodiploidy and the Evolution of the Social Insects," in *Robert Trivers, Natural Selection and Social Theory. Selected papers of Robert Trivers* (Oxford: Oxford University Press, 2002), pp. 164-206. John Burdon Haldane, *The Causes of Evolution* (Princeton: Princeton University Press, 1990, first published in 1932). John Burdon Haldane, *What I Require from Life: Writings on Science and Life from J. B. S. Haldane*, edited by Krishna Dronamvain (Oxford: Oxford University Press, 2009).

[17] Hamilton W. "The Genetical Evolution of Social Behavior," *J. Theor. Biol*., 7:1-52, 1964.

[18] Robert L. Trivers, "The Evolution of Reciprocal Altruism," in Robert Trivers, *Natural Selection and Social Theory. Selected papers of Robert Trivers, op. cit.*, pp. 18-51.

[19] Baier, K., *The Moral Point of View,* (Ithaca, N.Y.: Cornell University Press, 1958). Rousseau, J. J., *The Social Contract,* (Chicago: Henry Regnery Co., 1954).

[20] Marian Hillar, "Friedrich Nietzsche: Social Origin of Morals, Christian Ethics, and Implications for Atheism in His *The Genealogy of Morals*," in *Essays in the Philosophy of Humanism,* Vol. 16 (1) Spring-Summer 2008. American Humanist Association, Washington, DC, pp. 59-84.

[21] Friedrich Nietzsche, *The Birth of Tragedy and The Genealogy of Morals*, translated by Francis Golfing, (New York: Anchor Books, 1956).

[22] Axelrod R., Hamilton W. "The Evolution of Cooperation," in *Science*, Vol. 211, pp. 1390-1396, 1981.

[23] Nowak M., Sigmund K., "The Dynamics of Indirect Reciprocity by Image Scoring," in *Nature,* Vol. 393, pp. 573-577, 1998. Nowak M, Sigmund K., "The Dynamics of Indirect Reciprocity," in *J. Theor. Biol., 194, 561-574, 1998.*

[24] Connor R, Heithaus M, Barre, L. "Superalliance of Bottlenose Dolphins," in *Nature*, 397, pp. 571-572, 1999. Godin J., Davis S., "Who Dares, Benefits: Predator Approach Behavior in Guppy (*Poecilia reticulata*) Deters Predator Pursuit," in *Proc. Roy. Soc. Lond. B*. 209: pp. 193-200, 1995.

[25] *Selecta Mathematica*: Volume 1 (German and English Edition) by Karl Menger, Bert Schweizer, Abe Sklar, and Karl Sigmund, eds. (Berlin: Springer, 2002). *Selecta Mathematica:* Volume 2 (German and English Edition) by Karl Menger, Bert Schweizer, Abe Sklar, and Karl Sigmund, eds. (Berlin: Springer, 2003).

[26] Robert Boyd and Peter J. Richerson, *The Origin and Evolution of Cultures* (New York: Oxford University Press, 2005). Peter J. Richerson and Robert Boyd, *Not by Genes Alone: How Culture Transformed Human Evolution* (Chicago: University of Chicago Press, 2006). Robert Boyd, *How Humans Evolved* (New York: W.W. Norton & Co., 2009).

[27] Herbert Gintis, Samuel Bowles, Robert T. Boyd, and Ernst Fehr, eds., *Economic Life. Economic Learning and Social Evolution* (Cambridge, MA: MIT Press, 2006). by Joseph Henrich, Robert Boyd, Samuel Bowles, and Colin Camerer, eds., *Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies* (New York: Oxford University Press, 2004). W. Glimcher, Colin Camerer, Russell Alan Poldrack, and Ernst Fehr, *Neuroeconomics: Decision Making and the Brain* (New York: Academic Press, 2008).

[28] Hisashi Ohtsuki, Yoh Iwasa, Martin Nowak, "Indirect Reciprocity Provides only a Narrow Margin of Efficiency for Costly Punishment," in *Nature*, Vol. 457, No. 7225, pp. 79-82.

[29] Samuel Bowles, "Did Warfare Among Ancestral Hunter-Gatherers Affect the Evolution of Human Social Behaviors?," in *Science*, 5 June 2009, Vol. 324, no. 5932, pp. 1293-1298.

[30] Joel Sachs and James Bull, *Proc. Natl. Acad. Sci.,* 102, 390, 2005.

[31] Stuart A. West, Andy Gardner, "Altruism, Spite and Greenbeards," in *Science*, 12 March 2010, Vol. 327, no. 5971, pp. 1341-1344.

[32] Anupama Khare, Lorenzo A. Santorelli, Joan E. Strassmann, David C. Queller, Adam Kuspa, Gad Shaulsky, "Cheater-Resistance is not Futile," in *Nature 461,* 980-982 (30 September 2009). Asher Mullard, "Cheating Bacteria Could Treat Infections," *Nature News* (21 January 2009). David C. Queller, "Behavioral Ecology: The Social Side of Wild Yeast," in *Nature* 456, 589-590 (3 December 2008). Lorenzo A. Santorelli, Christopher R. L. Thompson, Elizabeth Villegas, Jessica Svetz, Christopher Dinh, Anup Parikh, Richard Sucgang, Adam Kuspa, Joan E. Strassmann, David C. Queller, et al., "Facultative Cheater Mutants Reveal the Genetic Complexity of Cooperation in Social Amoebae," in *Nature*, 451, 1107-1110 (13 February 2008).

[33] Quoted by Elizabeth Pennisi, "On the Origin of Cooperation," in *Science*, 4 September 2009, Vol. 325, pp. 1196-1199.