Understanding the egalitarian revolution in human social evolution

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Humans are unique among animals in cooperating in large groups of unrelated individuals, with a high degree of resource sharing. These features challenge traditional evolutionary theories built on kin selection or reciprocity. A recent theoretical model by Gavrilets and colleagues takes a fresh look at the ‘egalitarian revolution’ that separates humans from our closest relatives, the great apes. The model suggests that information from within-group conflicts leads to the emergence of cooperative alliances and social networks.

Social evolution: kin selection and reciprocity
Orthodox evolutionary theory is based on gene- or individual-level selection, and assumes that such lower-level selection is more efficient than selection at higher levels such as groups or species [1–3]. Moreover, it is generally believed that lower-level (genic) selection would favor ‘selfish genes,’ that is, genes which maximize their fitness at the expense of other individuals. Such lower-level selection is therefore thought to restrain the evolution of altruistic behaviors and cooperation [3]. To explain the paradox that many organisms nevertheless cooperate extensively, it is therefore usually assumed that such (seemingly) altruistic behaviors have evolved by two mechanisms: kin selection and reciprocal altruism [4]. By extension to the economic sciences, buyers and sellers in markets are typically assumed to behave in a rational and self-regarding manner, that is, behave like the ‘economic man’ [5]. However, markets seldom follow the simple rules that traditional economic theory expects them to follow, and human social behavior often deviates from what would be expected from short-term economic and evolutionary self-interests [5].

Human social behavior: altruistic punishment and inequality aversion
To understand the social evolution of our own species, Homo sapiens, workers have recently begun to investigate alternative mechanisms to kin selection and reciprocal altruism to explain our extensive cooperative networks and activities. In a recent theoretical model, Sergey Gavrilets and colleagues have modeled the emergence of social networks and extensive cooperation between non-kin that is so characteristic of our own species [6]. Although the predictions of this model remain to be experimentally investigated, there is accumulating empirical evidence from recent work that is suggestive of extensive altruism in humans and possibly also some role for cultural or biological group selection.

For instance, recent experimental studies by Ernst Fehr and colleagues [4,5,7–10] challenge conventional thinking about the evolution of cooperation, and raise the question of whether gene selection alone could explain human behaviors or whether other mechanisms such as cultural or biological group selection could also have played a role [4]. Humans often engage in altruistic acts by providing costly benefits to other group members. Humans often engage in costly punishment behaviors toward ‘cheaters’ or ‘free riders’ who do not follow social norms and who try to exploit ‘common goods’ [7]. Moreover, such costly altruistic punishments of cheaters are associated with reward feelings at the neurobiological level (Figure 1). This is particularly puzzling given the costs of punishing and the lack of immediate fitness benefits to the punishers [8]. Another interesting piece of work from Fehr’s research team comes from a recent study of inequality aversion in children [10]. The authors found a widespread tendency for egalitarian sharing between group members and strong inequality aversion, a tendency that increased with age (Figure 2) [10].

These and other experimental studies on humans are difficult to reconcile with traditional, purely gene-centered models for the evolution of cooperation. Fehr and colleagues have consequently argued that human social behavior cannot solely be attributed to selective forces such as kin selection and reciprocal altruism, which function well in small groups or networks but are unlikely to explain the more extensive human cooperation involving nations, companies, organizations or governmental institutions [4]. Instead, other mechanisms, such as parochial altruism in combination with altruistic punishment of cheaters [7], are needed to explain such higher-level cooperation. These mechanisms might also operate in concert with cultural or biological group selection and through gene–culture coevolution [4]. Also challenging to traditional selfish gene theory is the recent demonstration of heritable variation in altruistic behavior within human populations [11]. Such variation implies the presence of genetic polymorphism in social behavior and hence evolutionary coexistence of cheaters and altruists [4]. The existence of extensive egalitarianism, sharing of benefits and a genetic basis of such fairness in humans is difficult to reconcile with the notion that all human individuals are only maximizing short-term own benefits (selfishness), without considering the situation of others [10,11].
Our ‘uniquely unique’ species and the ‘egalitarian revolution’
Humans do thus differ from our closest relatives (chimpanzees and other great apes) in that humans care much more about other group members, whether they are kin or non-kin, and such altruistic behavior appears to increase with age and socialization (Figure 2) [10]. Human social behavior also differs from our closest relatives in several other respects [12,13]. For instance, human societies are characterized by relatively weak leaders, extensive sharing of common property and large groups compared to the smaller and more hierarchically structured primate societies among our closest relatives [12,13]. This evolutionary transition from an ancestral hierarchical ape-like society to a society with more equal and fair division of labor and goods, as in the prehistoric human hunter-gatherer societies, has been coined the ‘egalitarian revolution’ [12,13]. The potential selection pressures underlying this egalitarian revolution have now been formally modeled by theoretical biologist Sergey Gavrilets and two colleagues in a paper recently published in *PLoS ONE* [6].

In Gavrilets et al.’s stochastic model, networks of allies (‘coalitions’) emerge as a result of within-group competition between individuals for resources, social status or mates. Social networks and the high cognitive abilities of humans play a key role in this process. Group members utilize information from within-group conflicts (dyadic interactions), and can then form coalitions based on the information they have obtained from these antagonistic interactions. This leads to a self-reinforcing positive feedback loop, or a ‘runaway’ process, in which coalitions grow larger and larger, and they might ultimately encompass all or most members of the original group. As the network grows, individuals outside the coalition are at a disadvantage, and at some point it pays to join the coalition and becomes almost impossible to remain outside. Alliances often emerge in ‘phase-like’ rapid transitions if group size, awareness, aggressiveness and persuasiveness of individuals are large and the decay rate of individual affinities is small [6].

There are several interesting and novel insights gained from utilizing this model that could not have been obtained by traditional modeling approaches such as game theory and classical population genetics. First, coalition formation is an emergent property of strong within-group competition, and becomes possible because individuals are able to read and utilize information from agonistic dyadic interactions. Second, the model suggests that the transition from a hierarchical ape-like society to a more egalitarian society of hunter-gatherers (egalitarian revolution) could have been extremely fast, that is, in a phase-like transition; hence it is appropriate to call it a ‘revolution.’ Third, this egalitarian revolution is likely to be a direct result of the increase in human cognitive ability, because this ability makes it possible to process the information from...
observed interactions in dyadic conflicts. Fourth, once stable and group-wide egalitarian alliances have formed, cultural norms favoring group interests over individual interests can spread in the population. This last point provides a theoretical framework to explain the emergence of social norms and phenomena such as parochialism and egalitarianism documented in experimental studies by Fehr and his colleagues [4,7–10]. A key role for the extraordinary role of human cognitive abilities in our social evolution has also been suggested in another recent model by Gavrilets: ‘the Machiavellian brain’ hypothesis suggests that male–male competition for mates caused the evolution of increased human intelligence [14].

Other interesting aspects of the models emerge with cultural inheritance. If social networks are culturally inherited, which is often the case in humans and other primates, coalition formation is facilitated and a single alliance including all group members can emerge even faster [6]. Moreover, if there are sex differences in cultural inheritance of social networks (e.g. daughters inherit the networks of their mothers, but sons do not inherit that of their fathers), the sex which has a higher level of cultural inheritance will be particularly prone to form extensive social networks. With complete cultural inheritance, coevolutionary cycling of average affinities can also result, with coalitions forming, growing and dissolving at regular intervals (Figure 3). Although within-group conflicts do promote the ‘egalitarian revolution,’ there will not necessarily be peace and harmony afterward. The networks grow and dissolve as a result of new and ongoing conflicts (Figure 3). These and other predictions of the model need to be empirically tested in humans, but they certainly seem plausible and consistent with recent empirical studies on the social dynamics of Homo sapiens [4,5,7–10].

Conclusions
Recent empirical and theoretical work on the evolution of human cooperation has revealed the importance of altruistic punishment [7,8], parochialism [9] and egalitarianism [10], and how within-group competition leads to alliance formation [6]. These factors, in combination with our advanced cognitive abilities, make Homo sapiens ‘uniquely unique’ among animal species [12,13]. Taken together, this work strongly suggests that neither kin selection nor reciprocal altruism is sufficient to explain the evolution of human cooperation. This work points to the potential roles of cultural or biological group selection and social networks and suggests that alliance formation can arise as an emergent property of within-group conflicts. These novel insights in turn raise questions about the utility of the metaphor ‘the economic man’ in the economic sciences [5], as humans behave neither rationally nor selfishly, at least not in the short term. With the current financial crisis fresh in our minds, and with increasing criticisms against neoliberal economic theories, greedy capitalism and unregulated markets, a deeper understanding of human social evolution and behavior is more urgent than ever. Coalition formation, such as the famous ‘coalition of the willing’ that preceded the Iraq War in 2003, seems to be an inherent biological characteristic of Homo sapiens at several levels of our social organization. The interesting new model by Gavrilets and colleagues provides some clues to the evolutionary origin of coalition formation in our species.

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References

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Figure 3. Dynamic coevolutionary cycle with complete cultural inheritance of social networks, based on a recent model by Gavrilets and colleagues [6]. The y axis shows the average (blue) and standard deviation (red) affinities within groups over time. Social networks and alliances might be formed, rapidly grow in size, but are then dissolved and the process starts over again [11].