Neurosciences and the Human Person: New Perspectives on Human Activities
Pontifical Academy of Sciences, *Scripta Varia* 121, Vatican City 2013
www.casinapioiv.va/content/dam/accademia/pdf/sv121/sv121-nowak.pdf

Natural cooperation

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Evolution is a process which organizes the living world. Loosely speaking we talk about the evolution of genes, genomes, cells, organisms, species, but the only entity that really evolves are populations. Populations of reproducing individuals instantiate the evolutionary process. Individuals carry information which they pass on during reproduction. This process of reproduction is not perfectly accurate but subject to variation. Thereby new mutants are generated. If different mutants have different reproductive rates, natural selection comes into play. Natural selection chooses among the variants that are generated by mutation. In the classical formulation, mutation and selection are the two fundamental components of the evolutionary process.

In recent years I have proposed that cooperation can be seen a third fundamental component of evolution. Cooperation means that two individuals, who are competitors in the process of natural selection, help one another. Without cooperation there is no construction. Cooperation is present at the origin of life, when nucleotide sequences help each other to reproduce within protocells. Cooperation is involved when individual cells stay together to form the first multi-cellular organism. Cancer is a breakdown of cooperation among the cells of a multi-cellular organism. Cooperation is needed for the emergence of the superorganism of insect societies, which represents a distinct form of biological organization. Cooperation is crucial for the evolution of human society and human language.

In the absence of a specific mechanism, natural selection opposes cooperation. In any well-mixed population defectors have a higher payoff than unconditional cooperators. Therefore natural selection needs help to favor cooperation over defection. Thousands of scientific papers have been written on this topic. All suggestions so far can be categorized into five mechanisms, which I will now discuss. A mechanism for the evolution of cooperation is an interaction structure, specifying how the individuals of a population interact to accumulate payoff and compete for reproduction.

1) Direct reciprocity arises if there are repeated encounters between the same two individuals, who use conditional strategies that depend on previ-

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ous outcomes. Direct reciprocity is based on the concept of repeated games and embodies the simply idea: I help you and you help me. Successful strategies of direct reciprocity include generous tit-for-tat and win-stay, lose-shift. Generous tit-for-tat starts with cooperation, it always cooperates if the other person has cooperated, and it sometimes cooperates even if the other person has defected. Win-stay, lose-shift repeats its current move whenever it does well, but changes to the opposite move whenever it does badly.

2) Indirect reciprocity operates if there are repeated encounters in a population of individuals. Some encounters are observed by others. Information about those encounters spreads through communication. Individuals can adopt conditional strategies that base their decision on the reputation of the recipient. My behavior towards you depends on what you have done to me and to others. The key aspect of indirect reciprocity is reputation. Cooperation is costly but leads to the reputation of a helpful individual who might receive help from others. A strategy for indirect reciprocity consists of a social norm and an action rule. The social norm specifies how to evaluate interactions between individuals. The action rule specifies whether or not to cooperate given the information about the other individual. Indirect reciprocity can lead to cooperation, if the probability to know someone's reputation is sufficiently high.

3) Spatial selection can lead to the evolution of cooperation without strategic complexity. Behaviors need not be conditional on previous outcomes. Cooperators form clusters which prevail even if they are surrounded by defectors. The fundamental idea is that neighbors help each other. More generally, population structure affects the outcome of the evolutionary process, and some population structures can lead to the evolution of cooperation. The population structure can be static or dynamic. It can represent geographic distribution or social networks. For example, evolutionary graph theory studies evolutionary dynamics on static graphs, while evolutionary set theory describes individuals moving between sets thereby changing the interaction structure as part of the evolutionary process.

4) Multi-level selection operates if there is competition between individuals in a group and competition between groups. It is possible that defectors win within groups, but that groups of cooperators outcompete groups of defectors. Overall this process can result in the selection of cooperators. Darwin wrote in 1871: 'There can be no doubt that a tribe including many members who ... were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection'.

5) Kin selection can be seen as a mechanism for the evolution of cooperation if properly formulated. In my opinion, kin selection operates if there

is conditional behavior based on kin recognition. An individual recognizes kin and behaves accordingly. As JBS Haldane said 'I will jump into the river to save two brothers or eight cousins'. Unfortunately much of the current kin selection literature does not adhere to this simple definition. Instead kin selection is often linked to the concept of inclusive fitness, which is a particular method to account for fitness effects. Inclusive fitness works in special cases, but is mistakenly presented as a general concept. When studying social evolution it is best not to rely on inclusive fitness. Once fitness is calculated every aspect of relatedness is included. Kin selection requires a mathematical formulation which is not limited by inclusive fitness.

These are five mechanisms for the evolution of cooperation. There may be others. But so far all suggestions fall within these mechanisms. Often two or more mechanisms operate simultaneously, which can lead to synergistic effects. When discussing human behavior it is important to note that much of the current theory examines actions and responses to actions, but not motivation. In my opinion, human altruism can only be understood by examining the underlying motivation. An action is truly altruistic if motivated by love for the other person. This is difficult to study, but an important direction for future research.

Evolution is based on the three fundamental principles: mutation, selection and cooperation. Evolution is a search process. Every search process requires a search space, a space of limited possibilities that is being explored. Much discussion in evolutionary biology is about the search process. The molecular components of biological organisms (DNA, RNA, proteins etc) point toward the nature of the underlying search space for genetic evolution, but how exactly this search space is generated by the laws of physics and chemistry is elusive at present.

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