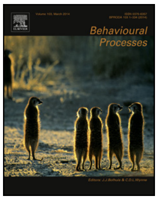
Behavioural Processes 113 (2015) 86–93

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Randomness in the evolution of cooperation

Tarik Hadzibeganovic[a], Dietrich Stauffer[b], Xiao-Pu Han[c,*]

[a] *Department of Psychology, University of Graz, A-8010 Graz, Austria*
[b] *Institute for Theoretical Physics, Cologne University, D-50923 Köln, Germany*
[c] *Alibaba Research Center for Complexity Sciences, Hangzhou Normal University, Hangzhou 311121, China*

ARTICLE INFO

Article history:
Received 25 September 2014
Received in revised form
22 December 2014
Accepted 6 January 2015
Available online 7 January 2015

Keywords:
Evolution of cooperation
Randomness
Tag-based cooperation
Altruism
Agent-based model

ABSTRACT

Tag-based ethnocentric cooperation is a highly robust behavior which can evolve and prevail under a wide variety of conditions. Recent studies have demonstrated, however, that ethnocentrism can temporarily be suppressed by other competing strategies, especially in its early evolutionary stages. In a series of computational experiments, conducted with an agent-based evolutionary model of tag-mediated cooperation, we addressed the question of whether a stochastically established and once dominant non-ethnocentric strategy such as indiscriminate altruism can stably persist and permanently outweigh ethnocentrism. Our model, simulated on various complex network topologies, employs simple haploid genetics and asexual reproduction of computational agents equipped with memory and heritable phenotypic traits. We find that in combination with an implemented memory mechanism and tags, random bias acting in favor of altruists can lead to their long-lasting victory over all other types of strategists. The difference in density between altruistic and ethnocentric cooperators increases with greater rewiring of the underlying network, but decreases with growing population size. These findings suggest that randomness plays an important role in promoting non-ethnocentric cooperation and contributes to our understanding of how other than adaptive mechanisms can initiate the design of novel behavioral phenotypes, thereby shaping surprisingly new evolutionary pathways.

1. Introduction

The ubiquity of costly cooperative behavior (Axelrod and Hamilton, 1981; Tomasello, 2009), especially when emerging among unrelated individuals in one-shot interactions (Clutton-Brock, 2009), has been puzzling researchers for many decades in a variety of fields, including behavioral and brain sciences (Bereczkei et al., 2010; Bergmüller et al., 2007; Brosnan et al., 2010; Buston and Balshine, 2007; De Dreu, 2012; Declerck et al., 2013; Kurzban and Houser, 2005; Olson and Spelke, 2008; Rand and Nowak, 2013; Silk et al., 2013; Yamagishi et al., 2014; Zaki and Mitchell, 2013). One possibility for generating cooperation between strangers is by phenotypic similarity (Krupp et al., 2008; Sigmund, 2009): I help you and you help me if we are similar enough with respect to some noticeable characteristic.

Examples of assortment by phenotypic traits such as color (Sinervo et al., 2006), sex (Lusseau and Newman, 2004), speech accent (Cohen and Haun, 2013), facial patterns (Tibbetts and Injaian, 2013), or even trivial visual markers (Efferson et al., 2008) are well documented in the literature for a variety of species. Such adaptively beneficial phenotypic features or 'tags' can lead to elevated cooperation levels if some individuals direct their benevolence exclusively towards sufficiently similar others. This so-called greenbeard effect (Gardner and West, 2009), which gives rise to tag-based 'ethnocentric' interactions, has been identified previously as a highly robust strategy (Hammond and Axelrod, 2006) surviving even under harsh conditions that are otherwise known as detrimental to cooperative behavior (Hadzibeganovic et al., 2012; for a review see Cohen, 2012).

Recent studies have shown that large-scale cooperation can emerge from simple evolutionary processes entailing similarity-based local-level interactions (e.g. Hadzibeganovic et al., 2014; Hartshorn et al., 2013; Kim and Hanneman, 2014; McAvity et al., 2013; Wu et al., 2013), even in aspatial systems (Antal et al., 2009; Colman et al., 2012) and without any advanced cognitive mechanisms (Riolo et al., 2001). Such theoretical studies have placed cooperation by phenotypic similarity on a much stronger foundation, not only by revealing minimal conditions for the emergence of elevated cooperation levels (Hales, 2005), but also by identifying specific situations in which ingroup biased behavior can co-exist with or is outcompeted by other strategies (Laird, 2011, 2012).

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* Corresponding author. Tel.: +86 15167129608.
E-mail addresses: tarik.hadzibeganovic@gmail.com (T. Hadzibeganovic), dstauff@thp.uni-koeln.de (D. Stauffer), xp@hznu.edu.cn (X.-P. Han).

http://dx.doi.org/10.1016/j.beproc.2015.01.003
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Besides its recently reported suppression by extra-tag cosmopolitan cooperation (Laird, 2011), which can dominate for a limited range of low cost-to-benefit ratios, ethnocentric cooperation can also be outcompeted temporarily by its closest competitor: indiscriminate (or pure) altruism. In fact, three distinct scenarios have been reported previously with respect to the early ethnocentrism–altruism relationship in evolutionary tag-based models (Hartshorn et al., 2013): (a) dominance of ethnocentric agents who are clearly ahead of all other strategists (including altruists), (b) strong competition between ethnocentrics and altruists, and finally (c) early but short-term dominance of pure altruists, which has been attributed to a stochastic bias acting in favor of altruistic agents.

However, since the effect of this stochastic bias is usually only short-lived in tag-based systems (Hartshorn et al., 2013), the question arises as to whether (and under what conditions) an early established dominance of a non-ethnocentric strategy such as altruism can also persist in later evolutionary stages and thereby permanently outweigh ethnocentrism? Here, we address this question in the context of an agent-based evolutionary model studied on a set of large-scale complex networks comprising millions of interacting agents equipped with memory and discernible phenotypic traits. Agent-based modeling and simulation (Railsback and Grimm, 2011), which constitute the foundation of our approach in the current paper, have recently attracted considerable attention in behavioral sciences (Colman et al., 2012; Conte and Paolucci, 2014; Goldstone and Janssen, 2005; Goldstone et al., 2008; Gray et al., 2014; Kopps et al., 2014; Muro et al., 2011; Pratt et al., 2005; Rand and Nowak, 2013; Smith and Conrey, 2007).

Previous behavioral studies of randomness have largely dealt with animal motion (e.g. Bartumeus, 2009; Reynolds et al., 2013), mating success (Barreto and Avise, 2011; Focardi and Tinelli, 1996), the generation of random behavior in humans (Neuringer, 1986; Nickerson and Butler, 2009) and the associated assessment of executive functions (Jahanshahi et al., 2006; Towse and Cheshire, 2007), or with the perception and judgment of random events and patterns (Matthews, 2013; Sun and Wang, 2010; Williams and Griffiths, 2013). However, the exact role and the influence of randomness on the evolution of human and other animal behavior is less well understood (Bonner, 2013).

For example, recent theoretical studies (Bausch, in press; Zhu and Wei, 2014) have shown that random (relative to deterministic) interactions among connected agents can substantially boost total cooperation levels in the studied population. Similarly, later extensions of Schelling's segregation model (Schelling, 1971; also see Krieger, 1971), which introduced more randomness into the modeling algorithms, have revealed the emergence of much clearer segregation patterns relative to the performance of the original model (Jones, 1985; also see Clark and Fossett, 2008). Thus, the presence of certain random features can often produce order out of disorder and promote unexpectedly new evolutionary paths. For instance, randomness can variably influence developmental processes which in turn, jointly with cognitive capacities, may instigate the design of behavioral neophenotypes whose generation is independent of the standard evolutionary mechanisms (Gottlieb, 2002).

Here, we expect that in combination with advanced cognition and phenotypic tags, stochastic bias can promote the stability of not only the early established altruism, but it can also switch the equilibrium from the dominant ingroup favoritism towards the more global altruism and intergroup harmony. Moreover, it is expected that these random victories of indiscriminate altruism, typically observed in the early evolutionary stages, can later lead to its permanent dominance over all other competing strategies, including egoism and ethnocentrism. Such reduction of elevated ethnocentrism is relevant for promoting socially desirable intergroup cooperation (Masuda, 2012; Yamagishi et al., 1998), but it may also be necessary for the global transition to pure altruism as the population is evolving towards ever higher levels of organization.

2. Methods

To study individual differences across simulated systems in their early evolutionary stages, we first replicated the standard agent-based model of tag-mediated ethnocentrism (Hammond and Axelrod, 2006). We then introduced an extension of this model to specifically investigate the randomness effects on the competition between the two dominant strategies (ethnocentrism and altruism) throughout their evolution.

In our models, agents populated a large complex network with interactions occurring among connected agents. The underlying spatial structure of the employed networks ranged from regular square lattices to small-world networks (Watts and Strogatz, 1998). Network nodes were initially empty and then at each time step invaded by one individual agent with randomly distributed traits (i.e. tag and strategy). The phenotypic tag was represented through a single color displayed by each agent and visible to all connected neighbors (a total of four different colors was used in the model). Each strategy included an instruction for the execution of the behavior when an agent was encountering (i) identical tag-mates (i.e. agents of the same color) and (ii) dissimilar agents, displaying differently colored tags. Four strategies were implemented in the model: Indiscriminate (or pure) altruistic cooperation (i.e. 'always cooperate'), egoistic unconditional defection ('always defect'), ethnocentric or in-group cooperation ('cooperate with similar, defect with dissimilar'), and cosmopolitan out-group cooperation ('defect with similar, cooperate with dissimilar').

Equipped with these traits, agents played simultaneous Prisoner's Dilemma-like games with their linked neighborhood (in lattices, this was always the von Neumann neighborhood). During their encounters, agents always considered their own displayed color, the color of their co-player's tag, and the associated behavioral strategy. In combination, these three features determined whether an agent cooperated or defected with the surrounding neighbors. In one time step each agent interacted with all its neighbors (i.e. cooperated or defected), and each cooperative action was costly for donors, reducing their reproductive potential α by the cost c, while simultaneously increasing the α of all donation receivers by the benefit b. Thus, cooperation in our model is defined as a donation of benefit b to another party that incurs a cost c to the donor (Nowak, 2006); for further (re)definitions and misconceptions frequently arising around the meaning of terms cooperation and altruism, see West et al., 2011.

Following the interaction stage of each time step, an offspring of each occupied node is produced with probability α and placed onto an empty node in its vicinity. Newborns then inherit the traits of their progenitors, but with probability μ, inherited traits can take new values. At the end of each time step, with probability δ, each individual is randomly selected to die. One time step always meant one update per each individual node of the simulated network. The simulated systems were always static (i.e. the networks did not dynamically grow or shrink during the simulation) and agents were not able to migrate across network nodes. When clusters or larger groups of same-colored agents emerged, they did not obtain special behavioral features at the collective level and could therefore not act as distinct entities (thus, multi-level selection was disabled in the model).

Besides studying much larger systems and different network topologies, in the extended version of this model we equipped our agents with a more advanced cognitive mechanism: When encountering a neighboring co-player, an agent was able to memorize