Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Behavioral Sciences

Cooperation in animals: toward a game theory within the framework of social competence

Redouan Bshary[1] and Rui F Oliveira[2,3,4]

Standard approaches to study the evolution and stability of helping either investigate how life history features like longevity and migration may yield conditions that select for rather unconditional helping or how specific game structures yield conditional helping strategies. Although the latter approach is more apt at explaining variable behavior within and between individuals, applicability seems limited due to strong compartmentalization of situations. Instead, recent evidence suggests that individuals are primarily under selection to display general social competence, that is, the ability to choose among the full range of available social behaviors the one that is appropriate to maximize fitness within the constraints of given circumstances. This view shifts the emphasis to general decision rules and the evolution of developmental mechanisms.

Addresses
[1] University of Neuchâtel, Institute of Biology, Emile-Argand 11, 2000 Neuchâtel, Switzerland
[2] Unidade de Investigação em Eco-Etologia, ISPA – Instituto Universitário, Rua Jardim do Tabaco, 34, 1149-041 Lisboa, Portugal
[3] Instituto Gulbenkian de Ciência, Rua da Quinta Grande, 6, 2780-156 Oeiras, Portugal
[4] Champalimaud Neuroscience Programme, Champalimaud Centre for the Unknown, Avenida Brasília, 1400-038 Lisboa, Portugal

Corresponding author: Bshary, Redouan (redouan.bshary@unine.ch)

Current Opinion in Behavioral Sciences 2015, **3**:31–37

This review comes from a themed issue on **Social behavior**

Edited by **Molly J Crockett** and **Amy Cuddy**

For a complete overview see the Issue and the Editorial

Available online 20th January 2015

doi:10.1016/j.cobeha.2015.01.008

Introduction

Helping — a behavior that increases the direct fitness of another individual — is frequently observed in nature. As it was seen as a challenge to natural selection with its emphasis on egoistic behavior, a large body of literature has emerged that reconciles helping with evolutionary theory. In brief, unilateral helping where the helper reduces its own direct fitness (termed 'biological altruism') is explained by kin selection: biological altruism may evolve if the costs of helping (c) are outweighed by the benefits for the receiver (b) times the degree of genetic relatedness (r) between helper and receiver ($r \times b > c$; [1]). Alternatively, helping is mutually beneficial where partners increase their direct fitness (termed 'cooperation' within species and 'mutualism' between species; for terminology see [2,3]). Two largely complementary frameworks have been developed to study helping. The ecological approach determines under which conditions key life history features like longevity and migration patterns may select for unconditional helping (typically without investigating the relative contributions of direct and indirect benefits [2]). By contrast, the game theoretic approach aims at capturing the conditions of a social interaction in order to provide a parameter space that allows conditional helping to persist. Thus, evolutionary game theory embeds helping behavior into underlying *strategies* and decision rules [4,5]. In this paper, we will first present the philosophy of the current evolutionary game theory approach to helping in more detail. In the second part we will introduce the recent, and as we see it more holistic conceptual approach of social competence. This latter concept does not compartmentalize the evolution of social behavior into particular domains like altruism, cooperation, reproduction, fighting, among others, but acknowledges that any social individual has to cope with all these different aspects. In the final part we will discuss how an integration of the social competence framework into game theoretic modeling may further our understanding of social behavior, in particular through an integration of mechanisms underlying decision making into the theoretical framework (Table 1).

The game theoretic approach

The classic example that links conditional helping to the specifics of a social interaction is Hamilton's rule [1]. Cooperation between unrelated individuals can be explained either by rather self-serving conditions (by-product mutualism and positive pseudoreciprocity) as well as by a variety of concepts with specific partner control mechanisms like Tit-for-Tat like reciprocity, punishment, sanctions, reputation or partner switching [2,5–7]. Such partner control mechanisms are necessary in cases that involve investments that would be withheld unless the partner or a third party responds negatively.

One of the great empirical challenges is to understand the observed variation within and between individuals with respect to expressed levels of cooperation [8,9]. The game theoretic solution so far has been to decompose a chain of social interactions into different games and/or

Table 1

A black and white presentation of current game theory focused on helping and a game theory based on social competence.

	Current approach	Social competence approach
Game	Given	Individuals decide
Payoff matrix (1)	Given	Consequence of individual decisions
Payoff matrix (2)	Given	Evolvable
Context investigated	Specific to helping	Placed into social interactions
Constraints	Largely absent	To be considered
Major achievement	Partner control mechanisms	Reflection on mechanisms and decision making
Decision rules	Precise	Rules of thumb

different internal states of individuals. The decomposition of social interactions into different games has worked well for example in marine cleaning mutualism involving the cleaner wrasse *Labroides dimidiatus*, where cleaners adjust service quality to the client's strategic option (cheating in return, partner switching or punishment) but also on additional features like singleton versus pair inspection or the presence/absence of bystanders [7]. Applicable models emphasize the effects of body condition, image scoring, partner choice in a biological market or frequency dependence [10–14].

Nice fits between data and models may be found in systems in which interaction partners have good *a priori* knowledge what game will be played and what the game structure is. This should often be the case in mutualisms as interactions typically serve a single purpose, that is, the exchange of specific goods/services [15], where pre-existing functions may often be adopted as partner control mechanisms [16]. Nevertheless, even under such specific circumstances current models may fail to predict the strategies/decision rules used (Box 1). Such failure seems much more likely in intraspecific cooperation that takes place in social groups, where individuals are confronted with the full range of possible social interactions and hence increased social complexity: competitors for food may also be potential mating partners, mate competitors may also be coalition partners, and dominance as well as kin relationships may affect optimal decisions. The result is a high degree of freedom with respect to individuals deciding what game is played and which behavioral decision fits accordingly. This general social complexity (rather than the specific ability to help) has been proposed to be the key selective force for the evolution of large brains [17,18]. This idea has recently been developed further in the social competence hypothesis [19••].

Box 1 on the limitations of the current game theoretical approach applied to marine cleaning mutualism.

In marine cleaning mutualism, cleaner fish and shrimps interact with a variety of client species that visit to have ectoparasites removed. In cleaner species of the genus *Labroides*, conflict arises as cleaner prefer to eat client mucus, which constitutes cheating [48,49]. In general, existing game theory has successfully predicted [10,50,51] or *post hoc* explained partner control mechanisms in cleaner–client interactions [14,52]. Cleaners adjust service quality to the client's strategic option (cheating in return, partner switching or punishment) but also on additional features like singleton versus pair inspection or the presence/absence of bystanders [7,53]. Models that emphasize the role of condition dependence [11–13] may explain why stressed cleaners use functional tactical deception to temporarily increase foraging success [54]. However, recent evidence suggests that we need to develop game theoretical models that explicitly incorporate mechanisms underlying decision making in order to take our understanding of cooperation to the next level. For example, cleaners are more cooperative after a short-term exposure to a stressor (a predatory client or a hand-net in the lab; [55]). Most recently, a location within the study area around Lizard Island was discovered that is inhabited by adult cleaners that are not sensitive to client image scoring and client partner choice options in laboratory experiments [56••]. As juveniles from this location performed similar to juveniles from neighboring reefs, ontogenetic effects seem to be a likely explanation. Indeed, the location is characterized by low interspecific social complexity, that is, low client diversity and low cleaner–cleaner competition over access to clients [56••]. The low performance of adult cleaners from the location with low interspecific social complexity was not correlated to boldness or aggressiveness [56••], while a parallel study found negative correlations between boldness and service quality within habitat [57]. The results point to various unresolved issues. On the functional level, there is the possibility that the costs and benefits of information differ between socially simple and socially complex environments, leading to the development of more or less sophisticated decision rules [36••]. On the mechanistic level, future models should consider how constraints due to physiological processes or cognitive limitations lead to the expression of more or less sophisticated decision rules.

Social competence

Social competence has been defined as the ability of an individual to adjust the expression of its social behavior according to perceived social information, in order to optimize the outcome of social interactions [20••]. Therefore, social competence is based on adaptive behavioral flexibility and is expected to have an impact on Darwinian fitness [19••]. As such social competence should be seen as a particular case of phenotypic plasticity applied to behavioral traits in a social context. Indeed, the general basic assumption is that adaptation by natural selection, which relies on heritable phenotypic variation produced by genetic variation, is not efficient when the rate of genetic change is outpaced by environmental change [21–23]. In this scenario, the need for adaptive change without genetic mutation emerges, and the ability for the same genotype to produce different phenotypes depending on environmental cues would be favored by selection. Given that the social environment is built of other behavioral agents, characterized by inherently high degrees of unpredictability, with which the individual has to interact, it is expected that it will be more complex and fluctuating than physical components of the environment [17]. Thus, plasticity is predicted to evolve more promptly in the social domain than in any other environmental