

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

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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.

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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**].

Social competence

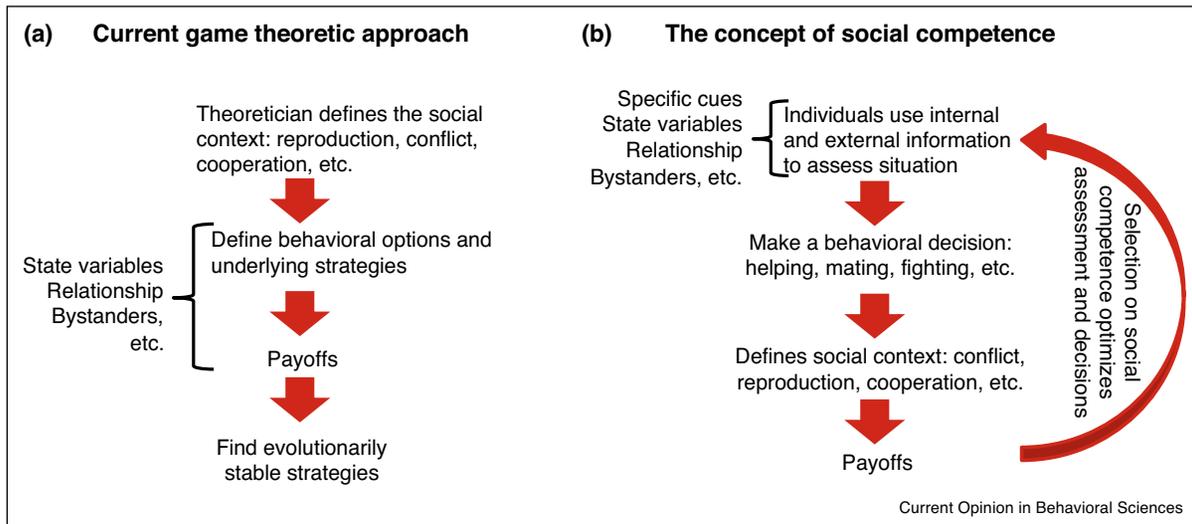
Social competence has been defined as the ability of an individual to adjust the expression of its social behavior

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.

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

Figure 1



How to conceptualize social interactions. **(a)** Current game theory approach: the type of social context is assumed to be known by all individuals. Behavioral options as well as the corresponding payoffs are defined as a function of various factors like state, the relationship with the partner and/or the presence of bystanders. The goal is to determine evolutionary stable strategies that apply specifically to the social interaction investigated. **(b)** The concept of social competence differs in that situation-specific cues (presence of food, among others) together with various other factors allow individuals to assess the situation in order to make behavioral decisions. The combined choices define the social context and the corresponding payoffs (context and payoffs are the consequences of combined decisions rather than given). Selection on social competence allows an animal to maximize payoffs across a variety of social interactions within the constraints set by the circumstances like state or position in a rank hierarchy. Note that a proper theoretical analysis of the social competence concept will need game theoretical modeling.

component, and social competence to be itself a trait with a high capacity for adaptive evolution (i.e. evolvability) as flexibility optimizes the response to social stimuli. A linked issue is that individuals need to be competent in identifying the relevant stimuli in the environment for correct assessment of the situation [24**]. Importantly, since social competence must operate across different functional contexts of sociality (e.g. resource acquisition and defense, mating, among others), it should be seen as an organismal trait composed of lower-level behavioral traits (e.g. variation in aggression, variation in courtship, among others), which would be linked within each individual, such that individual social performance is predicted to be correlated across functional contexts [19**]. Indeed, the empiric evidence available in this respect supports this view, as illustrated by suites of social behaviors across functional contexts being set by early social experience in different animal species (e.g. fish: [25,26*,27,28]).

The conceptual framework of social competence outlined above views helping behavior as part of a wider repertoire of behaviors that can be flexibly expressed in response to the perceived social environment. The difference between this way of thinking and current game theory is illustrated in Figure 1. Viewing helping as part of a broader 'whole-social behavior' trait (i.e. social competence) has a number of conceptual consequences for the game theoretic approach that provide new perspectives

on the evolution of helping behavior, which are outlined below.

Toward a game theoretic approach based on the social competence framework

Although the game theoretic approach has been hugely successful in reconciling helping with evolutionary theory, we are currently far from understanding how animals decide to help or not. Counting rules like Tit-for-tat do not seem to be used [29], demanding a better understanding of how rules-of-thumb are developed [24**,30], what cooperative rules exist in nature [31], and in how far they are domain specific or used in a variety of social contexts. As we see it, the current research on helping compartmentalizes social life into specific situations and typically takes the payoff matrix as a given in order to explore corresponding strategies. This approach will continue to be useful but we will need to investigate higher level performance in the future as well.

Toward a holistic approach to social behavior

As the social realm comprises multiple functional contexts, such as predator avoidance, resource acquisition, mate acquisition, and offspring care, which may co-occur in many species, the game theoretic approach is currently compartmentalizing social behavior. By contrast, the concept of social competence proposes to integrate the performance of the animal across these different functional

contexts, aiming at offering solutions to multiple simultaneous games. For example, how can a territorial male simultaneously deter rivals and court females? How do the resulting trade-offs inherent in simultaneous games affect strategies/decision rules? Compartmentalization of social behavior also reduces our ability to identify constraints due to the complexity of social life. In reality, animals are often constrained in terms of having access to the full information required for them to switch between evolutionary games in an adaptive way, for example due to the well-known trade-off between speed and accuracy in information processing [32]. As a consequence, it is much more plausible that animals have evolved heuristics to make decisions under time constraints, and hence in the absence of complete social information [24**,30,33]. Models and experiments varying game structures (i.e. mixing payoff matrices equivalent to a prisoner's dilemma, a volunteer's dilemma and by-product mutualism) offer a first step to investigate how animals deal with variation in the nature of cooperation games: would they develop a single general decision rule, would they build a heuristic based on specific cues that are correlated with each game or are they able to behave rather optimally in each game? Constraints and rules of thumb in decision-making are currently not a major topic in the game theoretical approach (see e.g. a recent edited volume in the Journal of Theoretical Biology, [5]). However, we know from animal personality research that behavioral syndromes may occur across different contexts [34]. Thus, it is well possible that in some cases variation between individuals with respect to helping tendencies could largely be due to selection on behavior in other contexts. Also, as long as we accept that behavior is often based on learning, it is known in experimental psychology that animals may not explore the full strategy space because a standard learning mechanism — operant conditioning — may make them stuck in one behavior [35]. Internal and external cues that are present across different contexts could facilitate behavioral correlations across contexts [24**]. Given recent advances in our understanding of the mechanisms underlying behavioral decisions (Box 2), it is high time to integrate mechanisms explicitly into models.

Toward flexible games and corresponding payoff matrices

The current game theoretic approach takes the game and payoff matrix as a given, which works well in cases where external cues properly define the game for all participants, like the clearly defined interspecific interactions in the context of mutualism or the approach of a stalking predator. Often, however, the game is not pre-determined but the situation is ambiguous, with individuals having to decide what game is to be played. For example, a male baboon approaching a female may want to groom, to be groomed, to mate, or to aggress her. In the social competence perspective, individuals will be under selection to choose the appropriate game, to determine the game

Box 2 Proximate mechanisms of social behavior

Social behavior has been classically classified according to its consequences for the lifetime direct fitness of the actor and the recipient (i.e. cooperative, when the outcome is beneficial for both; selfish, when the actor benefits at the costs of the recipient; altruistic, when the recipient benefits at the costs of the actor; or spiteful, when the outcome is detrimental for both [1,2]. By contrast, when studying its proximate causes behavior is usually classified according to its form (e.g. fixed action patterns), as it is easier to relate brain activity to the movement pattern of an organism than to its function [58]. Importantly, the same action patterns can serve different functions by being used in different contexts, like aggressing a predator (cooperative in group defense) versus aggressing a group member in competition for resources. This scenario suggests that the same neural circuits are at least partially shared between functionally different behaviors. Indeed, evolutionary conserved neural circuits responsible for action initiation and action selection explain to a great extent the patterns of behavior in clades as diverse as insects and mammals (central complex/basal ganglia, [59]). However, given that these behavior patterns can be expressed in different functional contexts other upstream circuits must exist that provide a functional mode to the expressed actions (e.g. competition vs. cooperation), which would define the space of the behavioral repertoire to be expressed. Such circuits for social decision making have also been identified, and are also evolutionary conserved across vertebrates [60,61**]. Supporting the social competence hypothesis these social decision making networks are shared by multiple social behaviors (e.g. mating, aggression), such that what better explains behavior is the overall activity pattern of the network rather than the activity of one of its nodes (i.e. brain nuclei). The nodes of this network express receptors for neuromodulators such as sex hormones and neuropeptides of the vasopressin/oxytocin family, which can specify the functional mode. For example, sex hormones provide a mating mode, eliciting mode-specific behavioral repertoires in the network [62*].

structure and corresponding pay-off matrix as well as to adjust behavior between games with different pay-off matrices. The problem occurs both within the life span of individuals and over evolutionary time periods. As it stands, we have to consider that positive feedback loops between sociality and social competence would potentially lead to the emergence of new (and more elaborated) patterns in the social repertoire, and both cooperative and deceptive behaviors may emerge this way [36**,37]. This scenario assumes that variation in social competence is present in a population and that individuals with higher competence would engage more in social interactions, since they are more efficient and potentially get higher fitness benefits from them [19**]. As a consequence of the resulting increase in sociality, the strength of selection for social competence would be increased. For example, the obligate cleaner wrasse *L. dimidiatus* — but not a closely related wrasse — has been selected to fine-tune service quality to the specifics of the situation [38], and to manipulate client decision with the application of tactile stimulation [39], while larvae of few lycaenid butterfly species that are dependent on ant tending for survival have evolved into parasites [40]. To give another example, the evolution of the ability to form coalitions has important consequences for the game structure and payoffs [41], and

hence the evolution of characters: male–male coalitions to gain access to females change the distribution of male reproductive success from ‘the winner takes all’ to a more equal share among the socially most competent rather than strongest individuals. Thus, early attempts to let payoff matrices evolve [42] should be expanded and linked to social competence.

Concluding remarks

We are at a stage where future progress will strongly depend on the integration of Tinbergen’s four ‘whys’, that is, the integration of ultimate and proximate questions [43,44,45,46,47], and we see a game theory based on the insights provide by the social competence hypothesis as an important step in this direction. The social competence perspective emphasizes the importance of studying the behavior and underlying decision rules/strategies of individuals across different social contexts. Cross-correlations may indicate general decision rules that may either represent alternative strategies or constraints in the ability to fine-tune behavior. Distinguishing between these two alternatives will be a main challenge for empiricists. The increased complexity in the research question warrants close interactions between empiricists and theoreticians. As the social competence concept has been built on the recent expansion in our knowledge about mechanisms underlying behavior (Box 2), it is bound to provide useful information to theoreticians interested in the incorporation of mechanisms into models on the evolution of helping. Only empirically informed models will be able to incorporate biologically meaningful mechanisms/trade-offs/constraints and decision rules in order to produce mathematical analyses of helping as part of a large social decision making process. Such a new approach will lead to an evolutionary game theory of physiology and cognition, which is bound to yield a better understanding of differences between species in the helping tendencies and the sophistication of decision rules underlying their social behavior.

Thus, according to the social competence hypothesis helping should correspond to a social mode and therefore should not be expected to have a dedicated neural circuit but rather to be specified by a specific set of neuromodulators, which provide the specific functional mode. Indeed, recent work has implicated different neuromodulators on the regulation of cooperative behaviors in cleaner fish, namely the neuropeptides vasotocin and isotocin and cortisol [63–65]. Importantly, the occurrence of helping in different social contexts may be achieved by different combinations of neuromodulators, which would elicit a specific state of the network, thus specifying the functional mode to a great detail. For example, hypothetically sex steroids together with oxytocin would provide a network state that would promote the expression of helping within a reproductive mode.

Conflict of interest statement

Nothing declared.

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