Cooperative Relationships

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Abstract

Cooperative relationships arise from a history of mutually beneficial interactions between individuals, and they enable cooperation among a range of entities, including biological organisms, business firms, and nation-states. As one of the simplest of emergent social forms, cooperative relationships can possess higher level properties (e.g., common expectations and rules of interaction, shared communication protocols) that are more than the sum of individual interactions. As such, cooperative relationships can become "things" in their own right, shaping how partners treat each other and how others treat partners within a relationship. Many open questions remain about how the emergent properties of cooperative relationships arise and how they foster future beneficial interactions while mitigating the risk of exploitation. Here, we frame these diverse findings and emerging questions in terms of the inputs and algorithms that partners use in forming models of each other and in guiding behaviors toward each other. We finish by outlining areas ripe for future exploration.

INTRODUCTIONS

Cooperation is pervasive in the biological world. It has played a key role in the major evolutionary transitions from prokaryotes to eukaryotes, from eukaryotes to multicellular organisms, and from multicellular organisms to social animal colonies (West, Fisher, Gardner, & Kiers, 2015). Cooperation at multiple scales is also a crucial ingredient in the meteoric rise of humans on Earth (Boyd & Richerson, 2009). While cooperating with others can confer benefits, it can also place cooperators at risk of exploitation by selfish partners who might try to enjoy the benefits of cooperation without paying any of the costs. Cooperative relationships are one mechanism for mitigating such risk by increasing the probability of beneficial interactions in the future and by increasing the efficiency of these interactions. These changes in turn give partners additional incentives to continue cooperating and to maintain their relationship into the future.

Emerging Trends in the Social and Behavioral Sciences.
Robert Scott and Marlis Buchmann (General Editors) with Stephen Kosslyn (Consulting Editor).
 ISBN 978-1-118-90077-2.

Cooperative relationships arise from a history of interactions, but they are not a simple sum or description of those interactions (Hinde, 1976; Kummer, 1978). They also rely on emergent properties that can in turn shape future interactions. These include expectations, rules of coordination, shared modes of communication, commonly understood consequences for defection, and partners' valuation of each other and the relationship (Delton & Robertson, 2016; Hruschka, 2010). Such properties rely on a range of capacities permitting organisms to set up common expectations and protocols, to resist the temptation to exploit a partner, to recognize good partners, to evaluate the long-term benefits of a relationship, and to modulate behaviors toward friends, strangers, freeloaders, and enemies based on these evaluations (Brent, Chang, Gariépy, & Platt, 2014; Hruschka, 2010).

As these capacities extend the possible length of relationships far into the future, it becomes increasingly difficult to assess the long-term value of any given relationship based on past behaviors. This can complicate decisions about staying with existing partners versus leaving them for others who might be more beneficial relationship partners in the long run. It can also increase the salience of cues and signals of a partners' commitment to continuing the relationship in the long term (Hruschka, 2010). The spiraling complexity required to orchestrate these decisions and behaviors may be one reason that cooperative relationships do not arise more often in the biological world. It also raises fascinating questions about the evolution and development of such relationships. In this essay, we review some of the best studied questions in this area and outline directions for future work.

FOUNDATIONAL

In the last two decades, researchers have shown that organisms from a wide range of taxa selectively cultivate enduring relationships with conspecifics, and that past histories of mutually beneficial interactions with a partner predict future behaviors toward that partner (Seyfarth & Cheney, 2012). These results parallel long-standing findings in the social sciences about cooperative relationships between individuals as well as higher level social organizations, such as business firms and nation-states (Hruschka, 2010; Leeds, 2003; Ring & Van de Ven, 1992; Uzzi, 1997). In many cases, individuals also appear to gain long-term benefits from their social relationships. These include improvements in individual health and well-being and, for organizations, increased profits or greater success in accomplishing key missions (Berkman & Glass, 2000; Dyer & Singh, 1998). Among organisms there is also emerging evidence that social relationship can contribute to individual fitness, suggesting that the ability to cultivate and maintain such relationships can give a selective advantage (Silk & National Research Council, 2014).

These common findings across a range of disciplines have given rise to questions and debates about the origins and design of such cooperative relationships. One can productively frame many of these questions in computational terms using the related concepts of *inputs* and *algorithms*. *Inputs* are cues and signals that individuals pay attention to when forming models of a partner and a relationship. These can include the duration of the relationship, the balance of past favors, information about genetic relatedness, and cues of how much a partner wants to continue the relationship into the future. *Algorithms* are computational systems for transforming these inputs into actions. These can involve evaluations and models of the relationship that have been shaped over a long history of interactions (Delton & Robertson, 2016; Hruschka, 2010; Hruschka, Hackman, & Macfarlan, 2015; Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). Importantly, these algorithms may change over the course of a relationship as partners begin to pay attention to different inputs or integrate those inputs in new ways (Xue & Silk, 2012).

The computational perspective provides a unified way of asking a number of common questions about cooperative relationships. What inputs and algorithms do partners use in decisions to start, build, maintain, and switch cooperative relationships? How do these inputs and algorithms change as partners move through different stages of a cooperative relationship? From what physiological and cognitive building blocks did natural selection construct these algorithms? How can researchers assess these algorithms across taxa in observational and experimental settings? And what consequences do different algorithms have for the long-term robustness of such relationships?

Different fields have tackled these questions with different theoretical assumptions about how these algorithms work and what inputs they rely on. Human behavioral ecology, for example, has focused on theoretical inputs traditionally derived from evolutionary models of cooperation—genetic relatedness, spatial proximity, frequency of interaction, past helping behavior, and reproductive pair bonds—while paying less attention to proximate psychological mediators (Hackman, Munira, Jesmin, & Hruschka, 2017). This reflects twin assumptions that (i) these theoretical variables are the relevant inputs informing behavior within relationships and (ii) the algorithms translating these inputs into helping are sufficiently direct that investigating psychological mediators will likely not improve behavioral models (Hackman *et al.*, 2017).

Researchers studying nonhuman animals have also necessarily focused on observable behavioral variables—tolerance, affiliation, grooming, coalitional support, and mating—in predicting future patterns of behaviors in relationships. However, realizing that cooperative relationships often rely on partner's emergent expectations and evaluations of each other, primatologists in particular have begun to develop novel behavioral and experimental tools to assess these psychological mediators and their relationship to behaviors (Cords & Aureli, 2000; Dunbar & Shultz, 2010; Silk, Cheney, & Seyfarth, 2013).

Meanwhile, economists and psychologists have examined how different relational cues, perceptions, and evaluations guide behaviors within cooperative relationships (Aron, Aron, & Smollan, 1992; Berscheid, Snyder, & Omoto, 1989; Jones & Rachlin, 2006). While useful at reverse engineering relational algorithms, the experimental and survey methods used in these social sciences often rely heavily on human language and the manipulation of complex symbolic systems. They also frequently rely on behaviors in laboratory contexts that have unknown external validity. For these reasons, it can be challenging to extend these findings to diverse human groups with varying levels of literacy and education, much less to nonhuman organisms.

Given their complementary strengths and weaknesses, each of these approaches can contribute useful methods and findings to the study of cooperative relationships. In the next section, we outline some key advances stemming from these diverse fields of study.

RECENT RESEARCH

What Inputs and Algorithms Do Partners Use in Decisions to Start, Build, Maintain, and Switch Cooperative Relationships?

A large body of work has examined how past costs and benefits from a relationship are associated with future behaviors. This includes short-term studies of recent helping or sharing in laboratory experiments conducted on humans and several nonhuman primate species, long-term field studies of food sharing in humans and other primates, and surveys asking people to evaluate the long-term balance of give-and-take in their relationships (Brosnan *et al.*, 2009; Hruschka, 2010; Jaeggi & Gurven, 2013). Researchers have focused on these specific inputs because they are important variables in game theoretic models of cooperation and because they give some indication of the benefits one's partner could provide in the future.

However, many factors can influence correlations between a partner's past behaviors and future behaviors. Most notably, a partner can find more beneficial relationships or better outside options. Thus, paying attention to cues of such changes in a partner can also be important in helping individuals avoid exploitation. In this regard, researchers have begun to explore another set of inputs also derived directly from game theoretic models of cooperation. In such models, inequalities between three variables—the benefits and costs of cooperation and the expected duration of a series of interactions—determines when it is reasonable to cooperate with another. In most game theoretic formulations, the third variable—the expected duration of the relationship—is defined *a priori*. However, partners can often dramatically prolong or shorten a relationship by their own actions. In such cases, individuals should be particularly attuned to their partner's commitment to continuing the relationship.

This second concern about the expected duration of a relationship has led to exciting research in the last decade, showing that evaluations of a relationship depend on much more than the direct benefits one has received or the costs one has incurred. Among other things, these evaluations depend on cues that one's partner can rely on a third party to satisfy the same needs as one might provide (Niiya & Ellsworth, 2010). They can also depend on cues that a partner is giving exclusive attention to the relationship (Ohtsubo *et al*., 2014) or how a partner ranks the relationship relative to other possible relationships (DeScioli & Kurzban, 2009). What unifies these diverse cues and signals is that each gives some indication of how much a partner values *this relationship specifically* and how much that partner would work to extend it into the future. Interestingly, having a partner who wants to prolong a beneficial relationship with *you* can also make that partner more valuable to you, a process that can lead to mutually reinforcing evaluations among two partners (Tooby & Cosmides, 1996).

Another area of active research aims to understand how individuals encode the value of their partners and relationships and how these encodings, sometimes known as *internal regulatory variables*, shape future action. Modeling work suggests that long-run encodings of a partner and the partner's contribution to one's well-being can facilitate the emergence of cooperative relationships (Hruschka & Henrich, 2006; Roberts, 2005). There is also considerable theoretical work on what specific inputs should contribute to these encodings, what "bookkeeping" styles transform these inputs into encodings, and how these encodings interact with other information to guide decisions (Delton & Robertson, 2016; Hruschka *et al*., 2015; Lieberman, Tooby, & Cosmides, 2007; Silk, 2003).

One concept that researchers from a range of fields have begun to explore is perceived closeness, an assessment of relationship quality that in many (but not all) cultures relies on a metaphor of spatial proximity (Aron *et al*., 1992; Curry, Roberts, & Dunbar, 2013; Hackman *et al*., 2017; Jones & Rachlin, 2006). It is important to point out that perceived closeness is only loosely correlated with actual spatial proximity. Rather, it is a general way of ranking relationships in terms of their positive value to an individual. Research across neuroscience, economics, psychology, and anthropology has shown that perceived closeness increases over a series of cooperative interactions (Krueger *et al*., 2007), that cues that a partner devalues a relationship can reduce feelings of closeness (Niiya & Ellsworth, 2010), and that perceived closeness is associated with greater helping and sharing in experimental and observational settings (Aron *et al*., 1992; Curry *et al*., 2013; Hackman *et al*., 2017; Hruschka, 2010; Jones & Rachlin, 2006).

Although perceived closeness does somewhat correlate with a range of other cues, such as genetic relatedness, past help, and frequency of interaction, there is little evidence that perceived closeness can be reduced to a simple mediator of other commonly studied variables. For example, the associations of perceived closeness with helping are independent of other important variables, such as genetic or affinal kinship, spatial proximity, and help received from one's partner (Hackman *et al*., 2017). Moreover, a number of studies have shown that other important predictors, such as genetic kinship and participation in a mating tie, have associations with helping and sharing that are independent of perceived closeness (Curry *et al*., 2013; Hackman, Danvers, & Hruschka, 2015). Thus, perceived closeness appears to open a window to psychological mediators having independent associations with cooperative behaviors.

Perceived closeness is one of the most thoroughly and widely studied ways of encoding the value of a partner and relationship, but there are many others, including judgments of competence, trustworthiness, genetic kinship, mating and pair-bonding potential, and relative need, that likely interact with closeness in guiding decisions about behavior toward partners (Fiske, Cuddy, & Glick, 2007; Hackman *et al*., 2015; Rousseau, Sitkin, Burt, & Camerer, 1998).

How can Researchers Assess these Algorithms across Culture and Taxa?

Taking an algorithmic approach to cooperative relationships has traditionally required inferring relevant inputs and internal computations from observed behaviors—attention, tolerance, affiliation, helping, and sharing (Silk *et al*., 2013), and among humans, self-reports of internal states (Aron *et al*., 1992; Hackman *et al*., 2017; Jones & Rachlin, 2006). Using averages and correlations among these behaviors over time and behavioral responses to experimental stimuli, researchers attempt to reverse engineer the relevant inputs, encodings, and algorithms that guide actions with relationship partners.

Among humans, self-reports about perceptions and evaluations provide some window into the ways that individuals encode important information about partners and relationships (Aron *et al*., 1992; Berscheid *et al*., 1989; Jones & Rachlin, 2006). However, it is difficult to verify self-reports about mental states. Moreover, it is not straightforward to elicit these self-reports across diverse languages and cultures. For example, the increasingly popular perceived closeness paradigm often uses spatial metaphors to elicit rankings of relationships, but not all languages and cultures use spatial metaphors to rank their relationships. And even when individuals may be able to respond in terms of spatial metaphors, common two-dimensional tasks on paper may not be immediately meaningful to respondents. In the last 15 years, researchers have been developing and adapting different approaches to tackle these problems and to develop a richer view of relational decision-making. These include experiments that probe attention, processing speed, and decision-making about partners and relationships (Karremans & Aarts, 2007; O'Gorman & Roberts, 2017; Wiltermuth & Heath, 2009), new methods for mapping brain networks involved in relational decision-making (Krueger *et al*., 2007), and the development of locally appropriate tools for assessing concepts such as emotional closeness and their relationship with behavior in diverse cultural settings (Hackman *et al*., 2017).

Researchers working with nonhuman animals have necessarily focused on reverse engineering relevant inputs and algorithms from observable behaviors and vocal signals. These include social proximity, social grooming, the amount of time spent in interactions, responses to separations and reunions, reconciliation, behavioral synchrony, directed vocal exchanges, and social monitoring, as well as researcher-derived indices of relationship quality based on these behaviors (Cords & Aureli, 2000; Dunbar & Shultz, 2010; Silk *et al*., 2013). The challenge with many of these measures is that they are both potentially inputs to and outcomes of decision-making algorithms. Thus, it can be difficult to determine whether these measures are correlated with other relational outcomes because they are something that individuals use as inputs to their future behaviors or simply because they are both outcomes of underlying and unmeasured relational processes. For example, Dunbar and Shultz argue that relationship longevity may not be a good measure of relationship quality because it is a functional outcome of relational processes (Dunbar & Shultz, 2010). However, it is also possible that relationship longevity is a salient input in an individual's evaluation of a relationship that influences future decision-making. This may very likely be the case in many human friendships (Hruschka, 2010). Unfortunately, focusing solely on the correlations of relational length with other behavioral outcomes cannot adjudicate between these two possibilities. Experimental manipulation of social situations and partner behaviors, such as experiments playing back calls from known partners, may provide one path forward in determining what informs future decision-making in relationships and what simply arises as an outcome of relational processes (Silk *et al*., 2013). Such experimental approaches have been quite successful in human studies. And in both human and nonhuman studies assays of hormonal mediators can shed light on the internal processes underlying behaviors with relationship partners (De Dreu, 2012).

PROMISING NEW DIRECTIONS

Progress in answering the broad questions outlined above will benefit from greater cross-talk between the diverse biological, social, and behavioral fields that have developed theories and methods for studying cooperative relationships. Among the many avenues for future research, we outline several that should lead to novel insights into the origins, development, and persistence of cooperative relationships.

The Transition to a Relationship

Numerous studies have shown that partners in long-term cooperative relationships interact in very different ways than acquaintances. These differences appear to rely on different inputs and algorithms for dealing with a specific partner—for example, increasingly complex models of one's partner, common expectations and tools of coordination, increasing preferences for the partner's well-being, more concern about partner intent, and less concern about individual acts of helping and reciprocation (Clark & Mils, 1993; Hruschka, 2010; Xue, 2013; Xue & Silk, 2012). They can also lead to different weighting of inputs. For example, partners in close relationships might weight their own costs less and their partner's benefits more than strangers (McGuire, 2003). These changes involve a shift toward the relationship becoming an independent "thing" with emergent properties that guide partners' behaviors in the relationship. But what meta-inputs lead to such a transition, and how does this transition take place? What cues and signals do partners use to determine that their relationship is in a new state and that they would benefit from different modes of decision-making? Some research has shown, for example, that starting small and gradually raising the stakes can be an effective route to increasing the levels of cooperation in a relationship (Roberts & Renwick, 2003). However, it is not clear that this captures the apparently qualitative changes that can occur in some kinds of cooperative relationships (e.g., close friendships among humans) (Hruschka, 2010; Xue & Silk, 2012).

The Ontogeny of Cooperative Relationships

In addition to the changes that occur *within* developing relationships, individual organisms must also develop the capacities to cultivate and maintain these relationships. Some evidence suggests that human children across a range of settings follow similar trajectories between the ages of 7 and 15 in developing key understandings of shared expectations and relational norms (Gummerum & Keller, 2008). At the same time, there can be quite substantial variation in individual views about expectations for a good friendship even within cultures (Hruschka, 2009). While studies assessing actual relational behavior either experimentally or observationally have mainly been restricted to populations in the United States, Europe, and a few other high-income countries, this is now beginning to change. Experimental work conducted in six different cultures, including several small-scale societies, showed that children's behavior in situations that require self-sacrifice changes as children mature and varies across cultures. Population-specific variation in altruistic behavior emerges during middle childhood, and children converge toward the behavior of adults within their groups (House *et al.*, 2013). This raises important questions about the generalizability of existing findings, and the degree to which the development of capacities for cooperative relationships relies on culturally specific inputs.

Conditions Favoring Cooperative Relationships

Cooperative relationships are only one of many ways to facilitate cooperation. Reputation and third-party punishment can help reinforce cooperation among a wide range of partners (Fehr & Fischbacher, 2004; Milinski, Semmann, & Krambeck, 2002). And modern markets backed by sophisticated legal systems permit individuals and organizations to cooperate in relatively anonymous and arms-length interactions (Kranton, 1996). Under what conditions do cooperative relationships become the more effective option for facilitating cooperation? In biology, a great deal of modeling and empirical work has examined these different systems in isolation, but has not examined when we should see certain systems favored over others (Hruschka & Henrich, 2006; Milinski *et al.*, 2002; Noë & Hammerstein, 1995). Some modeling and experimental work in economics, sociology, and anthropology has explored the social ecological conditions under which rational individuals would devote effort to cultivating relationships versus engaging in market-type exchanges (Kranton, 1996). Further work that assesses these and other hypotheses using cross-cultural and cross-species data should improve our understanding of the role of cooperative relationships in facilitating cooperation and also develop better integrated theories of the conditions favoring different mechanisms for facilitating cooperation.

From Cooperative Relationships to Cooperative Networks

Once cooperative relationships become emergent entities, then networks of such relationships can become important in integrating larger groups of individuals and creating novel opportunities for cooperation and exchange. For the last several decades researchers have been exploring the emergent properties of these networks and how they influence individual behaviors and outcomes. These include the advantages in accessing information, support, and economic resources by actors in specific network positions (Burt, 2009; Jackson, 2008), the ways that network structure can facilitate or discourage cooperation among dyads (Fehl, van der Post, & Semmann, 2011), and the role that network structure and density play in cumulative cultural evolution (Chapais, 2009; Hill, Wood, Baggio, Hurtado, & Boyd, 2014). Social network analyses have also become an increasingly important tool for mapping and measuring the structure of connections in nonhuman taxa (Croft, James, & Krause, 2008).

Cultural Tools and Evolved Psychology

Comparative work suggests that the capacity and motivation to cultivate and maintain long-term cooperative relationships is a human universal, and may be characteristic of the common ancestors of many primate species (Hruschka, 2010; Seyfarth & Cheney, 2012). Irrespective of whether or not this reflects psychological mechanisms that were selected specifically for the cultivation of cooperative relationships, we do know that humans often rely on cultural tools to build, regulate, and maintain these relationships. There are numerous disparate examples of such cultural tools, including formal written contracts between firms, material artifacts used as enduring symbols for a relationship, stories and memories used to remind partners of the value of the relationship, and rituals used to create community enforcement and fear of supernatural punishment (Hruschka, 2010). Conversely, research on culturally dependent relationships, such as contract-based cooperative ties between firms, also shows that such relationships frequently rely on key stakeholders who use common human capacities to cultivate friendships, loyalty, and commitment (Uzzi, 1997). Thus, particularly in the human case, a productive question is how do pre-existing capacities interact with cultural tools to permit novel cooperative relationships between individuals as well as higher level entities such as tribes, business firms, and nation-states?

In closing, the biological, social, and behavioral sciences have built promising empirical and theoretical inroads for studying the emergent properties of cooperative relationships and how these emergent properties shape future behaviors and outcomes. However, substantial progress can be made by comparing and cross-fertilizing methods and theories across these diverse fields. Here, we outline two potentially unifying concepts—inputs and algorithms—and illustrate how one can productively frame past findings and new directions in terms of these concepts. These and other tools for building bridges across the rich bodies of work on cooperative relationships should contribute to answering key questions and opening up new directions about how such relationships emerge and shape individual behavior.

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DANIEL HRUSCHKA SHORT BIOGRAPHY

Daniel J. Hruschka is an Associate Professor of Anthropology and Global Health at Arizona State University. Among other interests, he studies how humans choose to help others, how they cultivate relationships that promote cooperation, and when they choose to exclude outsiders. He is author of the book, "Friendship: Development, Ecology and Evolution of a Relationship". He directs the Laboratory of Culture Change and Behavior and his research has been funded by the National Science Foundation and the Templeton Foundation.

JOAN SILK SHORT BIOGRAPHY

Joan B. Silk. I am interested in how natural selection shapes the evolution of social behavior in primates. Most of my empirical work has focused on the behavioral and reproductive strategies of female baboons (*Papio cynocephalus*, *Papio ursinus*). Recent work documents the adaptive benefits females derive from close social bonds. I am particularly interested in questions that explicitly link studies of nonhuman primates to humans.

Experimental work conducted with chimpanzees and children focuses on the phylogenetic origins and ontogenetic development of prosocial preferences.

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