Evolutionary Psychology | Literature lecture 5

Paper: Human cooperation

A simple definition of cooperation is that one individual pays a cost for another to receive a benefit. Cost and benefit are measured in terms of reproductive success, where reproduction can be cultural or genetic. In a well-mixed population in which each individual is equally likely to interact and compete with every other individual, natural selection favors defection in the PD: why should you reduce your own fitness to increase that of a competitor in the struggle for survival? Defectors always out-earn cooperators, and in a population that contains both cooperators and defectors, the latter have higher fitness. Selection therefore reduces the abundance of cooperators until the population consists entirely of defectors. For cooperation to arise, a mechanism for the evolution of cooperation is needed. Such a mechanism is an interaction structure that can cause cooperation to be favored over defection. These interaction structures specify how the individuals of a population interact to receive payoffs, and how they compete for reproduction.

Previous work has identified five such mechanisms (I will include only 4, spatial selection is not exam material): direct reciprocity, indirect reciprocity, multilevel selection and kin selection. It is important to distinguish between interaction patterns that are mechanisms for the evolution of cooperation and behaviors that require an evolutionary explanation (such as strong reciprocity, upstream reciprocity, and parochial altruism).

Five mechanisms

Direct reciprocity

Direct reciprocity arises if there are repeated encounters between the same two individuals. Because they interact repeatedly, these individuals can use conditional strategies whereby behavior depends on previous outcomes. Direct reciprocity allows the evolution of cooperation if the probability of another interaction is sufficiently high.

Indirect reciprocity

Indirect reciprocity operates if there are repeated encounters within a population and third parties observe some of these encounters or find out about them. Cooperation is costly but leads to the reputation of being a helpful individual, and therefore may increase your chances of receiving help from others. A strategy for indirect reciprocity consists of a social norm and an action rule. The social norm specifies how reputations are updated according to interactions between individuals. The action rule specifies whether or not to cooperate given the available information about the other individual. Indirect reciprocity enables the evolution of cooperation if the probability of knowing someone's reputation is sufficiently high.

Multilevel selection

Multilevel selection operates if, in addition to competition between individuals in a group, there is also competition between groups. It is possible that defectors win within groups, but that groups of cooperators outcompete groups of defectors.

Kin selection

Kin selection can be seen as a mechanism for the evolution of cooperation if properly formulated. In our opinion, kin selection operates if there is conditional behavior based on kin recognition: an individual recognizes kin and behaves accordingly. As J.B.S. Haldane reportedly said, 'I will jump into the river to save two brothers or eight cousins.

Interactions between mechanisms

Although each mechanism has traditionally been studied in isolation, it is important to consider the interplay between them. In particular, when discussing the evolution of any prosocial behavior in

humans, we cannot exclude direct and indirect reciprocity. Early human societies were small, and repetition and reputation were always in play. Even in the modern world, most of our crucial interactions are repeated, such as those with our coworkers, friends, and family.

Experimental evidence in support of the five mechanisms

Evolutionary game theory allows us to explore what evolutionary trajectories are possible and what conditions may give rise to cooperation.

Direct reciprocity

Over half a century of experiments demonstrate the power of repetition in promoting cooperation. Across many experiments using repeated PDs, people usually learn to cooperate more when the probability of future interaction is higher. As the payoff for TFT (tit-for-tat) relative to ALLD (always defect) in a mixed population increases, so too does the predicted frequency of cooperation. Repetition promotes cooperation in dyadic interactions. The situation is more complicated, however, if groups of players interact repeatedly. Such group cooperation is studied in the context of the public goods game (PGG). an n-player PD. The PGG is typically implemented by giving each of n players an endowment and having them choose how much to keep for themselves and how much to contribute to the group. All contributions are multiplied by some constant r and split equally by all group members. The key difference from the two-player PD is that in the PGG, targeted interactions are not possible. Taken together, the many experiments exploring the linking of dyadic and multiplayer repeated games demonstrate the power of direct reciprocity for promoting largescale cooperation. Interestingly, this linking also involves indirect reciprocity: if I punish a low contributor, then I reciprocate a harm done to me (direct reciprocity) as well as a harm done to other group members (indirect reciprocity).

Indirect reciprocity

Indirect reciprocity is a powerful mechanism for promoting cooperation among subjects who are not necessarily engaged in pairwise repeated interactions. Having a reputation of being a cooperator is valuable, and cooperation is maintained: it is worth paying the cost of cooperation today to earn the benefits of a good reputation tomorrow. Indirect reciprocity relies on peoples' ability to effectively communicate and distribute reputational information. Not surprisingly, people spend a great deal of their time talking to each other (gossiping) about the behavior of third parties. In addition to this traditional form of transmitting reputational information, the internet has dramatically expanded our ability to maintain large-scale reputation systems among strangers. To remain in good reputation, you must not only cooperate in the primary interactions but also share truthful information.

Finally, there is evidence of the central role of reputational concerns in human evolution. Infants as young as 6 months of age take into account others' actions toward third parties when making social evaluations. Humans are also exquisitely sensitive to the possibility of being observed by third parties. In the opposite direction, making studies double-blind such that experimenters cannot associate subjects with their actions increases selfishness.

Multilevel selection

In the laboratory, multilevel selection is typically implemented using interaction structures in which groups compete with each other. Numerous such experiments have shown that competition between groups increases cooperation substantially. Experience with real-world intergroup conflict also increases cooperation. Critics of multilevel selection argue that empirically, the conditions necessary for substantial selection pressure at the group level were not met over the course of human history: concerns include low ratios of between-group to within-group variation because of factors such as migration and mutation/experimentation, and the infrequency of group extinction or lethal inter-group warfare. The laboratory experiments discussed above do not address these concerns: in these studies, the interaction structure is explicitly constructed to generate group-level selection.

Kin selection

Perhaps surprisingly, kin selection is the least-studied mechanism for human cooperation. Research on humans largely focuses on cooperation between non-kin. In part this is because cooperation between related individuals is seen as expected and therefore uninteresting. Furthermore, humans cooperate with unrelated partners at a much higher rate than for other species, and thus non-kin cooperation is an element of potential human uniqueness. In predicting self-reported altruistic behavior, an interaction has been found between observing your mother caring for a sibling (maternal perinatal association, MPA) and the amount of time spent living with a sibling (co-residence): MPA is a strong signal of relatedness, and thus co-residence does not predict altruism in the presence of MPA. In the absence of MPA (e.g., if you are a younger sibling who did not observe your older siblings being cared for), however, co-residence does predict altruism. This interaction suggests that co-residence is used as an indication of relatedness, rather than only as an indication of the probability of future interaction.

Cooperation in the absence of any mechanisms

How can we explain cooperation in one-shot anonymous laboratory games between strangers? Such cooperation is common, yet seems to contradict theoretical predictions because none of the five mechanisms appears to be in play: no repetition or reputation effects exist, interactions are not structured, groups are not competing, and subjects are not genetic relatives. Yet many subjects still cooperate. Why? Because the intuitions and norms that guide these decisions were shaped outside the laboratory by mechanisms for the evolution of cooperation. There are two dimensions along which scholars disagree: (i) whether cooperation in one-shot interactions is explicitly favored by evolution (through spatial or multilevel selection) or is the result of overgeneralizing strategies from settings in which cooperation is in one's long-run self-interest (due to direct and indirect reciprocity); and (ii) the relative importance of genetic evolution versus cultural evolution in shaping human cooperation.

On the first dimension, one perspective argues that multilevel selection and spatial structure specifically favor altruistic preferences that lead to cooperation in one-shot anonymous settings. Thus, although laboratory experiments may not explicitly include these effects, they have left their mark on the psychology that subjects bring into the laboratory by giving rise to altruism. The alternative perspective argues that direct and indirect reciprocity were the dominant forces in human evolution. By this account, selection favors cooperative strategies because most interactions involve repetition or reputation. Because cooperation is typically advantageous, we internalize it as our default behavior. This cooperative predisposition is then sometimes overgeneralized, spilling over into unusual situations in which others are not watching. In this view, cooperation in anonymous one-shot settings is a side effect of selection for reciprocal cooperation, rather than an active target of selection itself.

Turning to the second dimension, all of the mechanisms for the evolution of cooperation can function via either genetic or cultural evolution. In the context of cultural evolution, traits spread through learning, often modeled as imitation of strategies that yield higher payoffs or are more common. It has been argued by some that multilevel selection promotes cooperation through genetic evolution, whereas others posit an important role of culture. The same is true for reciprocity. We might have genetic predispositions to cooperate because our ancestors lived in small groups with largely repeated interactions. Or we might have learned cooperation as a good rule of thumb for social interaction, because most of our important relationships are repeated and thus cooperation is typically advantageous, as per the 'social heuristics hypothesis'.

Intuitive reciprocation

Experiments using economic games have shown that automatic, intuitive processes support cooperation in one-shot games, whereas reflection and deliberation lead to selfishness. Faster decisions in the PGG tend to be more cooperative. We now evaluate a further prediction of this line of reciprocity-based reasoning: cooperation should not always be intuitive. A key element of direct and

indirect reciprocity is conditional cooperation. As exemplified by the TFT strategy, reciprocal interactions should lead to intuitions that favor cooperation at the outset of a relationship, and cooperation in response to a cooperative partner. However, in response to a selfish partner, the automatic response should reverse to selfishness.
Put differently, reciprocity-based hypotheses for the evolution of human cooperation predict intuitive reciprocation. As predicted, we find that if the partner cooperated in the previous round, faster decisions are significantly more cooperative but if the partner did not cooperate in the previous round, faster decisions are significantly less cooperative. When responders are confronted with unfair offers (in the Ultimatum Game), the intuitive decision is to reject, whereas reflection leads to increased acceptance. Thus, intuition again favors reciprocation (in this case, paying a cost to retaliate against selfishness). Are these intuitions the result of genetic hard-coding or of learning and experience? Several additional results support the latter hypothesis. Intuitions are malleable rather than hard-coded. We find support for the social heuristics hypothesis, and for the importance of learning and culture in human cooperation.

Paper 2: Review: A dual model of leadership and hierarchy: Evolutionary synthesis

The nature of leadership

Leadership, which we define in terms of having a disproportionate influence on collective actions and group decisions, has been widely studied in the social and biological sciences, generating proximate and ultimate explanations for its emergence. Recently, cognitive scientists have also shown an interest in the neural mechanisms by which particular leaders attract and exercise influence on followership.

Here we argue that that there are two leadership styles: prestige style and dominance style. The first type of leader exercises influences by conferring (or promising to confer) benefits on followers and the second by inflicting (or threatening to inflict) costs on nonfollowers. The prestige–dominance model has been influential in the evolutionary behavioral sciences, mainly in distinguishing the ways in which people accumulate status in groups. One manifestation of status is the relative influence of different individuals on group decisions – thus, leadership. However, not all leaders are necessarily high-ranking individuals, such that leadership and status are not identical. This dual model contributes to evolutionary theory because it raises the possibility that natural (and sexual) selection has shaped

> Box 1: Evolutionary theories of leadership offer a unifying framework
> Evolutionary theory offers a unifying framework to understand the selection pressures favoring leadership and followership, both of which are supported by theoretical models and data. First, across mammalian societies, leaders, on average, gain a disproportional (direct) benefit from their influence on collective behaviour. Second, some forms of leadership emerge because of kin-directed benefits. For example, costly leadership is favored by indirect benefits to lionesses; individuals lead in protecting relatives from intruders within their egalitarian family groups. Third, reciprocity may compensate leaders who may claim a 'fee' for their services through a greater share of the spoils. Although taxation is typical in more complex traditional societies, leaders may instead accrue alternative currencies, such as increased status, power, and political support. The service-for-prestige theory asserts that these reciprocated benefits accrue principally during times of need, such as a food shortage, whereby good leadership (e.g., in hunts) acts as a form of collective insurance. Fourth, effective leadership may act as a costly signal of personal qualities, which motivates followers to reward leaders in terms of deference, friendships, or mating opportunities. In small-scale societies, leadership in hunting and conflict resolution is positively associated with reproductive success

these two proximate leadership mechanisms independently.

We argue that these two opposing views are both partially supported by the available evidence but each one on its own offers an incomplete view into the complex and dynamic processes of leadership. That is, the two constructs suffer from the same problem: they wrongly treat leadership as a single behavioral construct. The distinction between prestige-style and dominance-style leadership enables

cross-species comparisons that seek to reveal the selection pressures shaping these leader types in human evolution. To biologists, leadership and dominance are two distinct concepts; the latter is a concept largely reserved to describe an individual's ability to win dyadic fights (with a second individual) to gain priority of access to resources. Further, prestige-based influence emerges in non-human societies as individuals, regardless of rank, coordinate group movement and followers are attracted to these individuals as they provide coordination benefits. Finally, to social scientists the prestige–dominance leadership distinction delineates that prestige may not be the only route to human status; dispositionally dominant individuals may be effective group leaders, thereby enhancing their status in groups.

In small-scale human societies, women – who are often lower ranking than men – can exercise influence over collective activities such as the distribution of food or conflict mediation (female leadership is more likely when societies experience low levels of intergroup conflict). Although true gender equality – with respect to political influence in group life – remains largely absent from even the most egalitarian small-scale societies of humans, women can play a more active role than men in some domains of group life. Prestige-style leaders may not need to actively recruit followers. They can lead by example and thus exercise passive influence in groups. That is, in many cases, followers voluntarily defer to these leaders and may develop emotional connections with them, including a suite of positive feelings such as liking, admiration, passion, and sometimes love, which all contribute to a leader's charisma. By contrast, dominance-style leaders use coercive strategies to exercise influence on followers and the leader–follower relationship is based on a mix of negative emotions such as fear and anger in combination with more positive emotions such as respect, trust, and relief for getting a difficult job done.

Followers are sometimes attracted to dominance-style leaders because they provide indirect, group-wide benefits by being instrumental in solving collective action problems; for instance, mediating in conflicts between group members, dealing with free-riders, and inflicting costs on aggressive outgroup. Testosterone plays a key role in the formation and maintenance of dominance-style leadership. The dual model predicts that testosterone correlates with dominance-style leadership in contexts in which conflict management is crucial but is associated with prestige-style leadership in non-conflict contexts. Recent studies on collective hormone profiles find evidence for improved leader–follower cooperation when teams comprise a mix of high testosterone and low cortisol.

Prestige vs. dominance leadership in humans

First, although both prestige and dominance are ways to exercise influence over group decisions, leaders differ in style. Some studies find no correlation between prestige- and dominance-style influence as measured through self- and other reports. There are also different links with personality. Prestige-style leaders score higher on self-esteem, agreeableness, conscientiousness, and need for affiliation. By contrast, dominant leaders score higher on traits of aggression, disagreeableness, Machiavellianism, narcissism, and psychopathy – so-called dark-triad personality traits. Prestige is associated with humility and feelings of achievement (authentic pride), whereas dominance is associated with arrogance and feelings of superiority (hubristic pride). Dominance-style leaders more often use their influence for personal gain; for instance, by excluding rivals for their power position. However, dominant leaders prioritize group interests just as much as prestige-style leaders when their power position is securely established and in interactions with other groups.

An international study found a stronger tolerance for dominance-style leaders when citizens experienced a high degree of economic uncertainty and drastic measures were needed to restore wealth. A prestige-style leader is commonly preferred, but when the cost and probability of coordination failure is substantial – such as in intergroup or intragroup conflicts – followers switch to a more dominance-style leader even if it runs against their immediate self-interest. Developmental studies add further to the distinction between the two proximate leadership styles. Young children

have a prestige bias; that is, they preferentially learn from expert models and closely affiliate with them.

Evolutionary pathways to leadership

Game theory models show that there are different types of leadership in cooperation and coordination games that map neatly onto the prestige–dominance distinction. Leadership can be enacted through being first movers in a game: initiators whose actions, when they are copied by the rest, induce followership through exemplary leadership. Models, simulations, and experimental studies show that both leader types facilitate cooperation in groups. One model showed that prestigious Big Men leaders benefit from making a first cooperative move; they attract larger numbers of followers whose contributions increase the payoffs for leaders. There are also modelling studies showing benefits of dominance-style leadership in solving collective action problems. Groups in which one individual acts as an altruistic punisher of defectors can stabilize cooperation when punishers gain direct or indirect reputation benefits. Prestige-style leadership is more effective than having no leadership but a dominance-style leader is superior in enforcing cooperation in public goods games. Coordination-failure risks increase when groups become larger and socially more complex, giving rise to the potential for exploitation by free-riders. Dominance-style leadership solves this problem, but there is a risk of exploitation by leaders.

Reviews of leadership in egalitarian hunter–gatherer groups suggest that although prestige-style leadership is generally the norm in these small-scale societies, leader strategies often vary across situations like war versus peace or seasonal changes in group size. The best hunters, warriors, and diplomats have greater influence within their domains of competence, but their power is not automatically generalized to other group activities. Leadership requires competence and different people may be competent in different activities. In these societies, there is active opposition against aggressive individuals and when they become too powerful, there are levelling mechanisms in place curtailing their power. Gradual sanctions, from gossip and ridicule to exclusion and execution, are applied to deal with domineering individuals, usually males, as they undermine the egalitarian ethos of these small-scale societies.

Explanations for the persistence of leadership preferences

If dominance was actively selected against in ancestral egalitarian, small-scale societies, why do dominance-style leaders persist (and people voluntarily defer to them)? One possibility is that dominant-style leaders benefit personally from their actions. This notion has been supported by social–psychological studies showing that leaders with a dominance motivation take more than their fair share of collective resources. A second hypothesis to solve the dominance paradox is that dominance-style leaders are compensated for their role in enforcing social contracts within egalitarian groups. Examples include the use of levelling mechanisms such as punishment and homicide, which are inherently aggressive actions. Dominance-style leaders who use their physical formidability and aggressive disposition to coordinate punishment against overbearing people is a valuable public good. The availability of levelling mechanisms in small-scale societies, associated with the reversal of the dominance hierarchy, created a niche for dominance-style leaders to display aggression, especially towards antisocial males, tolerated by the rest of the group. Experiments further show that, although punishers in public goods are not as well liked as non-punishers, punishers are considered more trustworthy and group serving. This points to an adaptive solution by which dominant leaders gain status benefits from taking on punisher roles. Indirect benefits may accrue by signalling personal qualities to potential allies or sexual mate.

Finally, dominance-style leaders may gain status benefits by inflicting costs on members of outgroups through displaying aggression in combat. In favor of the warfare hypothesis, rates of war mortality and genetic differentiation among hunter–gatherer groups have been estimated to be sufficiently high for selection to favor these traits. Research on small-scale societies involved in raiding and warfare

shows that particularly brave warriors reap reproductive benefits from their dominant-style leadership displays.

The second remaining puzzle solved by the dual leadership model is the current male bias in modern society's leadership structures. Research on leadership styles, including several meta-analytical studies, suggest that men lead in a more directive, authoritarian manner whereas women are more coaching and participative. Men also score considerably higher on dark-triad and social-dominance traits. These differences can be explained by both cultural norms and the forces of sexual selection operating on men to use dominance leadership styles to compete intrasexually. Comparative studies of nonhumans suggest that females, although they have lower status than males, are more likely to emerge as prestige-style leaders, taking on leadership roles in the domains of collective movement and foraging due to greater knowledge and motivation. By contrast, males are more likely to emerge as dominant leaders in mixed-sex groups, managing conflicts within and between groups through the threat of force. These differences partly result from: (i) differences in physical formidability; (ii) age biases in leadership, as female mammals are, on average, older than the males; and (iii) the impact of reproductive physiology – pregnant and lactating females are hungrier earlier.

As human societies became larger and socially more complex, particularly in the context of intense agriculture, collective action problems and accompanying conflicts of interest intensified and therefore the degree of intergroup and intragroup conflicts has increased sharply. These pressures produced cultural adaptations for dominance-based leadership systems, whereby first headmen emerged as dominance-style leaders in small-scale societies. This was followed by more formalized authoritarian leadership structures (e.g., chiefs, kings, presidents, CEOs) aimed at galvanizing cooperation in ever-larger, more genetically diverse communities.