RESEARCH

The Ties that Bind Us

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This paper reviews the evolutionary literature on cooperation and the mechanisms proposed to explain the differences we see in the scale, breadth, and intensity of cooperation across societies, over history, and among behavioural domains. The most well-studied mechanisms that help societies sustain cooperation include kinship, reciprocity, reputation, signalling, norms, informal and formal institutions, and the competition between stable equilibria sustained by these mechanisms. I apply each of these mechanisms to the problem of reciprocity across the lifecycle. I then discuss how these same ties also tear us apart and what policies might help tie us back together.

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1. Introduction

Why do people choose to cooperate and help each other, even when the immediate benefits of working alone are greater? Or even if they do choose to cooperate in a group, why do they choose a larger group when the immediate benefits of a smaller group are greater? These questions underlie many human interactions and are of interest across the biological, human, and social sciences. Indeed in 2005, *Science* ranked "How did cooperative behaviour evolve?" as one of its top 25 "big questions" for the coming quarter-century [1]. In a recent *Annual Review*, Joe Henrich and I [2] lay out the challenges, theory, evidence, and answers we have so far. In this paper, I briefly summarize the insights from this literature and apply them to the challenge that reciprocity between generations across the lifecycle poses.

Many Western, educated, industrialized, rich, and democratic (WEIRD [3]) societies, such as the United States, United Kingdom, Canada, Australia, and much of Western Europe,¹ are held together by the actions of millions of anonymous strangers helping each other for little gain, or even at a cost to themselves: fairly trading rather than swindling and shortchanging; making prosocial acts of charity over theft and blood spill; paying taxes that support a social welfare state over personally beneficial tax avoidance; and so on. But the world has not always been this prosocial and many parts of the world are still far less prosocial. The fact the "WEIRD people problem" is perceived to be ubiquitous stems from the fact that much research over-relies on participants from WEIRD nations and is conducted by WEIRD researchers with WEIRD life experience and is so vulnerable to all the biases that entails [3–5].

For example, most of us living in WEIRD societies have grown accustomed to prosocial behaviours. It is cooperation that seems normal and its failure the puzzle to be explained. But from a cross-species, cross-cultural, and cross-temporal perspective, the puzzle is not the failure of large-scale cooperation but how we came to achieve such a scale and how we sustain it. There are four key discrete facts that require explanation:

- 1. Human societies vary dramatically in the scale and intensity of their cooperation. Even in the smallest societies, humans cooperate more than any other mammal, including our closest primate relatives. But cross-culturally, some societies remain small bands of related kin, while others are nation-states of millions or billions, with dramatically different levels of cooperation between these two extremes [6, 7];
- 2. Human societies vary substantially in the domains of their cooperation. Some societies cooperate only in extremis, such as at times at war, while other societies, some even nearby, may cooperate more prosaically, such as in housebuilding and communal rituals. In modern nation-states, some societies cooperate more on education, healthcare, defense, or relevant to this issue, reciprocity across the life-cycle;

¹ WEIRD refers to a cluster of countries that share ancestry, education-levels, modes of production, wealth, and other institutions, but because cultural differences exist along many different dimensions, it is more useful to measure cultural distance along the dimension relevant to the research question (e.g., politics, social relationships). Where an aggregate cultural distance is useful, distance from the United States serves as a "WEIRD scale" and is predictive of many cross-cultural and psychological and behavioral differences (see [4]).

- 3. Human societies rapidly expanded in the scale of their cooperation over the last 12,000 years, but this expansion differed dramatically by region and society; and
- 4. Human societies use the same mechanisms, such as sanctioning, signalling, and norms, to support both costly cooperative and non-cooperative maladaptive behaviors. Prominent examples that harm health include female foot binding, female genital cutting, or ritual consumption of dead relatives (see [8, 9]).

In the next section, I briefly summarise the ties that bind us—the main mechanisms that stabilize cooperation at different scales—and how they relate to the facts above and the problem of reciprocity across the lifecycle. Sometimes these mechanisms can work in coordination to strengthen cooperation, but they can also sometimes undermine one another. These ties and the relationship between them can help guide policy decisions.

2. The Ties that Bind Us

2.1. Inclusive fitness

At the most base level, inclusive fitness—or kin selection—helps explain cooperation between related individuals. From a genetic perspective, genes that can identify and preferentially favour copies of themselves will spread at the expense of those that do not. We see cooperation among kin across the entirety of the animal kingdom, with humans most obviously showing reciprocity across the lifecycle within families, such as with economically productive children supporting their parents in retirement and grandparents caring for their grandchildren. But changes within societies, particularly Western societies, mean that this reciprocity is no longer as strong as it was, while these changing patterns continue to contribute to the present challenge reciprocity poses. For example, individuals now take a longer time to reach peak economic productivity due to longer periods in education or completing job training [10], while the demographic transition has seen a reduction in family size [11]. But inclusive fitness only gets us to the scale of cooperation among related individuals.

2.2. Direct reciprocity

Direct reciprocity allows us to cooperate beyond family to friends and colleagues. This includes reciprocated benefit ("you scratch my back, I'll scratch yours") and reciprocated harm ("an eye for an eye, a tooth for a tooth"). Direct reciprocity requires knowing your reciprocators and for there to be ongoing interaction with them to ensure that people do not gain a benefit and then leave before returning it. It is here that the analogy of reciprocity across the lifecycle first breaks down in contemporary WEIRD society. Rather than "pay-it-back bi-directional reciprocity", we face a "pay-it-forward onedirectional reciprocity", where the younger generation bear the costs of the older generation, to be paid back in benefits by the next generation, rather than reciprocated by the older generation about to leave the population.

This is a relatively recent phenomenon, with grandparents having traditionally reciprocated by offering wisdom and information to their children and grandchildren in return for social and economic support, the Wikipedias of their time. Thus, in their post-fertility and post- economic peak period, they played a valuable role in teaching and caring for their grandchildren as alloparents. Indeed, it is this role that may explain the long lifespans and the lengthy post-menopausal life period of our species, which is unusual in the animal kingdom [12–14]. As per this "Information Grandmother Hypothesis", transmission of cultural knowledge from the elderly to children may have "paid" for their consumption of resources, given how much our species relied on a lifetime of socially acquired and transmittable information to survive and thrive. In contemporary society, however, rapid technological changes render that accumulated experience and expertise less valuable or even obsolete, reducing the traditional evolutionary value of a second living generation. Contemporary society's tendency for grandchildren to live apart from grandparents further reduces their ability to alloparent, further causing them to be perceived as a burden rather than a benefit.

2.3. Indirect reciprocity

Indirect reciprocity, or reputation, enables cooperation with those beyond which we *know* to those we *know of*. We prefer to help those with a good reputation, such as those known to be good reciprocators, over those with a poor reputation. In some cases, we may even harm those with a poor reputation, such as through ostracism or, in the case of some small societies, seizing their property or not punishing those who harm them [15]. The obvious limit to indirect reciprocity is the reliability of the reputational information. However, there are ways for our society to supplement this information, such as through norms, rewards, punishments, and signals that form part of our social compact. We can informally track and assess what people do and don't do (descriptive norms) and what people approve of and disapprove of (injunctive norms), rewarding those who comply with these norms and punishing those who do not. Reputation can also be formally tracked through institutions where we can rely on institutional trust for the accuracy of reputational information rather than the aggregate of individual sources.

2.4. Social norms

Social norms combined with reward and punishment significantly expand the range of behaviors that are evolutionary stable strategies (ESS)—sets of strategies (in this case norms, such as particular professed beliefs and practiced behaviours) unable to be displaced by any one individual deviating with a different set of norms. This individual would be

punished for violating the norms particular to the population they live in. Because we can track social norms, including rewards for punishing norm violators, different norms can become ESS in different groups [16–20]. For example, when asked "would you lie under oath to protect a friend", most Swiss would not, but most Venezuelans would. The hierarchy of norms in these two societies places the rule of law and loyalty to friends in contrasting positions [21]. In terms of reciprocity across the lifecycle, we can track different normative expectations for different people and different groups at different times, such as the cross-cultural differences we see in attitudes toward the elderly. Of course, greater rewards or greater punishment may be required the more desired normative behaviours deviate from other incentives. For example, a norm of regular attendance at public prayer would require a larger social sanction or a greater social reward the more such a norm prevented employment. It is through such systems of reward and punishment that a much wider range of arbitrary behaviours can become evolutionarily stable. These in turn create two new ties to bind us: informal and formal institutions and competition between stable equilibria.

2.5. Informal and formal institutions

Norms can be hardened through becoming incorporated into informal institutions of connected norms, such as those associated with marriage (e.g., obligations to in-laws, expectations of monogamy, child-rearing practices, etc.). These in turn can be hardened further through transforming into formal institutions, such as through rules, laws, or constitutions (e.g., laws against polygamy or enforcing financial support for children after divorce) [10, 22]. These formal institutions remain entwined and supported by any non-formalised norms that they co-evolved with—the cultural pillars that support institutions. Let us consider cross-cultural differences in rule of law or attitudes toward what constitutes fair taxation. Penalties for tax avoidance reflect the degree to which there are norms against tax avoidance—the psychology of norm violation is doing some of the work in enforcing behaviour. Were there less stigma against tax avoidance, penalties would need to increase to maintain the same level of compliance. It may be that transplanting formal institutions is therefore easier than transplanting the norms on which they rest, with the hope that the norms follow the institutions.

Institutions can combine with these other ties, securitizing trust, reciprocity, and recently, reputation. For example, instead of trusting particular people, we may trust institutions to reward and punish on our behalf, such as governments, judiciaries, and police forces. Similarly, credit scores, social credit scores, and more recently, reputational information managed by firms (e.g., online reviews and ratings) have allowed for these mechanisms to sustain larger scales of cooperation. For example, riding in a stranger's car or sleeping in a stranger's house are now safer thanks to reputations being managed by firms like Uber and AirBnB.

Returning to the topic at hand, reciprocity across the lifecycle is now managed by a combination of government pensions, legally binding monetary contributions, and personally funded accounts provided by competing firms. But support for such reciprocity relies on social norms in the form of attitudes towards the elderly and, specifically, the large cohort entering retirement. These social preferences affect public sentiment which, in turn, affect political will.

2.6. Competition between stable equilibria

Our norm psychology, including informal and formal institutions, can create multiple evolutionarily stable equilibria that explain the four key facts described earlier—the scale, intensity, domain diversity, rapid expansion, and stable maladaptive traits found in different societies. Societies may find themselves trapped in different evolutionarily stable equilibria. A policy challenge is in how to move societies between equilibria [23].

The science of cultural-group² selection describes some of the mechanisms through which these evolutionarily stable equilibria compete [2, 24–26]. It is worth noting that people can belong to multiple embedded groups (part of a city and country) or overlapping groups (part of a religion or corporation). Cultural-groups are therefore best described as a group of traits, values, or norms, rather than as a group of people [27]. In some cases, the norms and the people overlap considerably, such as in the case of ethnolinguistic groups that share both ethnicity and language. And, in some cases, who is in and not in the cultural-group is clearer, such as in the case of firms and nation-states. But this is not always the case.

These cultural-groups of stable norms compete for dominance in various arenas. There are direct encounters between different cultural-groups, as in migration and conflict. There are also indirect encounters through differential growth and through imitation of other societies (rather than specific people). The best studied of these mechanisms are

- 1. Differential migration, whereby people choose to join some groups over others. For example, top engineers working for Google over Microsoft, or highly skilled migrants moving to the United Kingdom over the United States.
- 2. Differential group survival, such as firms going bankrupt, political regimes failing, or groups dying out. This does not necessarily require conflict.
- 3. Differential growth, whereby some groups grow faster than others, such as economic or population growth. Mormons, for example, grew rapidly through high rates of fertility, leading to their relative cultural dominance in Utah.

² The hyphen in cultural-group selection emphasizes the selection on cultural-groups (groups of cultural traits) rather than a cultural form of group selection.

4. Prestige-biased cultural-group transmission, whereby groups preferentially learn from some cultural-groups over another. For example, the spread of democracy to the point that even dictators often fake elections or the many national constitutions inspired by the US Constitution [28].

Cultural-group selection is an active area of research. These four well-studied mechanisms are a small subset of potential mechanisms. Through these mechanisms, cultural-groups have competed over history trying different norms, informal institutions, and formal institutions. Cultural-groups—including companies, countries, and religions—that discover norms and institutions that allow them to better access resources, to outcompete rivals, to grow faster, to attract new members, or to grow by being copied by others thereby rapidly increase the scales, intensity, and domains of cooperation. Religion is a good example: it is not an accident that all major religions tend to be pro-fertility and prosocial toward at least in-group members. Religions that did not have these norms and institutions were outcompeted by those that did [29]. But through cultural-group selection, the very same ties that bind us serve to tear us apart.

3. Tearing Us Apart

3.1. Corruption and conflict as cooperation

In earlier work, I've argued that the mechanisms that sustain cooperation offer a framework for thinking about corruption. Corruption is one scale of cooperation undermining another [6, 22]. Helping family and friends and returning favours is natural and common, even outside our species. These tendencies are well described by inclusive fitness as well as direct and indirect reciprocity. But these mechanisms also undermine our norms and institutions. When a leader gives his relative a government contract, it is nepotism. But it's also cooperation at the level of the family, well explained by inclusive fitness, undermining cooperation at the level of the state. When a manager gives her friend a job, it is cronyism. But it is also cooperation at the level of friends, well explained by direct or indirect reciprocity, undermining the notion of meritocracy in society. Bribery is a cooperative act between two or more people [6], and so on. It is no surprise that family-oriented cultures like India and China are also high on corruption, particularly nepotism. In the Western world, we might expect to see more cronyism than nepotism due to the ability to more easily make and break friendships and other relationships (relational mobility [30]). Or, as Joe Henrich and collaborators have argued, the Medieval Catholic Church's decisions around marriage (e.g., banning cousin marriage) helped weaken inclusive fitness, creating many aspects of WEIRD psychology and allowing Europe to develop stronger state and democratic institutions [21, 31, 32].

3.2. Scaling up cooperation

In recent work, Eric Schnell, Robin Schimmelpfennig, and I [33] model competition between different scales of cooperation using a stag hunt game (also known as the assurance game). The game is not specific to stags or hunting but simply describes scenarios that lead to potentially higher returns through cooperation. In contrast to the more familiar prisoner's dilemma, the stag hunt game has two equilibria: one with higher returns that requires trust that others will cooperate (a share of the "stag") and one with lower returns irrespective of the other players' decisions (a "hare").

We extend recent work on the N-person stag hunt game [34] and competition for the stag [35] to model multiple stags of larger sizes, the competition for these stags, and the population dynamics, with larger stags increasing the carrying capacity of the population. Consistent with the insight that we cooperate because the rewards per cooperator from cooperation at a higher scale are sufficiently larger than the rewards for cooperating at a lower scale, we predict that societies under resource threat will fracture, reducing them to lower scales of cooperation. Such reduction can create a negative multiplier effect, leading to more antisocial, destructive behaviour, whereby individuals have a greater incentive to compete by harming others to maintain relative status, the harm spilling over to others in the group [36–38].

We also predict that it is difficult to go from a lower stag to a higher stag without first going through an intermediary stag, or rather, making dramatic jumps in the scale of cooperation is unlikely. For example, coal, oil, and gas have long existed, but it requires a certain level of cooperation, mass of people, and technology in order to receive, for example, (EROI [39, 40]) to access and use such resources effectively. That is, tapping, refining, and shipping oil is difficult using horses, carts, and wood-based energy alone, creating a bootstrapping problem. Each energy source has some minimum energy required to access it, requiring overlap between EROI. Similarly, larger cooperative groups (such as more developed countries and large corporations) can outcompete less-developed countries in accessing those countries' own resources, helping to explain the resource curse—or the history of colonization.³ This is particularly the case if the smaller groups here struggle to sustain cooperation, such as if there are different ethnolinguistic groups in the same nation-state.

4. Conclusion: Tying Us Back Together

Returning to the topic at hand, reciprocity across the lifecycle may ultimately depend on levels of production and the division of consumption between workers and pensioners, as Nick Barr explains in his paper in this issue (CITE). But both production and attitudes towards this decision are shaped by the ties that bind us, the ties that tear us apart, and

³ Though, of course, these are interpretable from the model only in very general terms that ignore many important, specific factors.

the competition between cultural-groups of different norms and institutions. Policy decisions can shape these norms, and there are guiding lessons from this literature.

4.1. Increasing the sense of "we"

The sense of "we" becomes weaker when society is fractured along ethnic, religious, and cultural lines. Immigration brings diversity that is a fuel for both innovation and economic growth, but it can also be a source of division and cooperation at subnational scales. Resolving this paradox of diversity [41] requires taking seriously cultural differences, measuring them [4], sustainably managing migration (or investing in infrastructure to reduce competition over resources), and investing in resources to help facilitate common language and common culture that reduce coordination and communication costs while retaining cultural diversity. There are difficult practical and ethical challenges in attempting to resolve the trade-offs diversity poses, but new innovations in simply measuring diversity along different dimensions is a first step toward tackling these challenges.

4.2. Moving from burden to benefit

Reinstating the traditional role of the retired as carers, if not also as sources of information, may also offer a model to move public perception from burden to benefit. Intergenerational care home-cum-childcare centers, such as South West London's Nightingale House, offer a potential model [42] with reported benefits for both children and the elderly.

4.3. Reducing perceptions of zero-sum

Perceptions of zero-sumness can create a reality through psychological traps. If we assume that the world is more zerosum, or that others are not trustworthy, it can be difficult to reach that next cooperative threshold or to take advantages of the present positive-sum opportunities. This in turn can lead to anti-social competitive behaviour. As research on the Joy of Destruction (JoD) game shows, people are more likely to engage in destructive competition versus productive competition [37, 38, 43–45]. In this game, people are presented with an opportunity to harm another player at some cost to themselves with no other interaction between the two parties. For example, taking £40 away from another player at a cost of £20 to themselves. Participants living in Namibia have shown a higher willingness to voluntarily harm themselves to cause greater harm to another than those living in Ukraine, while within Namibia, those in low rainfall regions compared to high rainfall regions show the same tendency to embrace harm, provided more harm is done to another. It has been argued that this is a function of zero-sum contexts where relative status can be maintained more easily by harming others than by working hard to access a scarce resource. Cultural evolution and behavioural science offer tools for shaping public perception under times of resource stress and slowed growth [8].

Competing Interests

The author has no competing interests to declare.

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