The Origins and Psychology of Human Cooperation

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ABSTRACT

Humans are an ultrasocial species. However, several aspects of this sociality are not easily explained by the canonical approaches found in evolutionary biology, psychology, or economics. Understanding our unique social psychology requires not only accounting for the breadth and intensity of human cooperation but also for the variation found across societies, over history and among behavioral domains (within societies). Here, we introduce an expanded evolutionary approach that considers how genetic and cultural evolution, as well as their interaction, may have shaped both the reliably developing features of our minds and the well-documented differences in cultural psychologies around the globe. We review the major evolutionary mechanisms that have been proposed to explain human cooperation, including kinship, reciprocity (partner choice), reputation, signaling and punishment, discuss key culture-gene coevolutionary hypotheses, such as those surrounding self-domestication and norm psychology, and consider the role of religions, rituals and marriage systems. Empirically, we bring together experimental, observational, and anthropological evidence from studies of children and adults from diverse societies and from non-human primates.

The origins and nature of our species' cooperative psychology and prosocial behavior has been a major scientific challenge since at least the time of Darwin. Recently, however, progress on this question has accelerated with the rise of a highly interdisciplinary version of evolutionary psychology, one that takes seriously our primate heritage, but also recognizes that humans have become a uniquely cultural species. Here we chart progress in this endeavor with the aim of directing ongoing research, clarifying key debates, and connecting psychology to the broader scientific exploration of cooperation.

SIDE BAR: Substantial progress has been made on the problem of cooperation by integrating four converging lines of inquiry: (1) P*hylogeny*: what features of cooperation or social psychology might the genus *Homo* have inherited from our primate ancestors? (2) *Selective processes*: what evolutionary processes, considering both genetic and cultural inheritance, are responsible for the array of cooperative psychologies observed? (3) *Proximate psychology*: how can we best describe the psychological mechanisms involved in cooperative behavior at the population or species' level? And, (4) *Ontogeny*: how, where and when do these psychological mechanisms develop. These, Tinbergen's Four Questions, have catalyzed efforts to understand human cooperation, driven much cross-cultural, developmental, and comparative research, and permitted our species to be seated within the natural world.

The question of cooperation focuses on how and why individuals make choices that help others (or avoid hurting them) at a personal cost. Viewed from a comparative perspective, our species presents an immediate puzzle: both the scale and intensity of human cooperation is substantially greater than that found in other mammals, a fact that has led psychologists, economists and evolutionary theorists to label our species "ultrasocial" (Campbell 1983; Gowdy & Krall 2016; Richerson & Boyd 1998; Turchin 2013). Field studies show how humans cooperate more than other mammals at both small-scales, such as within hunter-gather bands or families, and at larger scales, such as within ethno-linguistic populations or nation-states (Gurven et al. 2012; Handley & Mathew 2020; Jaeggi & Gurven 2013; Mathew & Boyd 2011a). Experimental studies, done cross-culturally, developmentally and comparatively, reveal that humans—usually by middle childhood—are substantially more inclined toward food sharing than our primate cousins (Ensminger & Henrich 2014; House 2017; House et al. 2013b,a, 2019; Jaeggi et al. 2010; Jensen et al. 2007a; Silk et al. 2005; Silk & House 2016). Interestingly, while the cooperation observed in experiments with non-human primates can often (but not always) be explained by rational choice models rooted in self-interest, humans almost always look too prosocial for these models, a fact that has led economics to incorporate notions of "social" or "other-regarding" preferences into their utility functions (Camerer 2003).

To explain this human anomaly, many intuitively point to our linguistic capacities or superior cognitive abilities (Wrangham 2019). However, while these now play a role, neither favors the evolution of greater cooperation in the first place. Instead, such cognitive traits often make lying, cheating, stealing and exploiting others easier to pull off—con artists use persuasive language and ingenious tactics to deceive us (Boyd & Mathew 2014; Lachmann & Bergstrom 2004; McNally et al. 2012; McNally & Jackson 2013). To the contrary, we argue that the door to the evolution of cooperative communication systems (e.g., spoken language) was opened by the emergence of greater sociality in our lineage. Similarly, regarding our cognitive abilities, the question should focus on explaining how our social environments have become structured such that the smart move is often to cooperate and help instead of exploit and harm.

Unraveling the puzzle of human ultrasociality requires more than just accounting for our species' unusual levels of cooperation. The standard evolutionary and economic explanations for cooperation, based on kinship and repeated interaction, not only struggle to account for the degree of cooperation observed in our species, but provide little account for four more stylized facts about human cooperation (Chudek & Henrich 2010):

1) **Scale and intensity differences:** The scale and intensity of cooperation vary dramatically among societies, from groups where the scale of cooperation is limited to small hamlets or extended families (Johnson 2003) to modern nation-states that routinely cooperate on the order of thousands or even millions of individuals. Over two decades of research, using behavioral experiments, survey measures and ecologically-valid observational techniques, have repeatedly documented this ample and important variation (Algan & Cahuc 2013; Balliet & Van Lange 2012; Henrich et al. 2001, 2010; Hruschka et al. 2014; Purzycki et al. 2016; Schulz et al. 2019).
2) **Domain differences:** The domains of cooperation vary substantially from society to society? Comparative ethnography shows that different social groups inhabiting the same ecology cooperate in different domains. Some cooperate only in warfare and fishing, while others, just downstream, cooperate only in house-building and communal rituals (Curry et al. 2019; Henrich & Henrich 2007).
3) **Rapid expansion:** Over the last 12,000 years, human societies scaled up from relatively small-scale communities to vast states (Turchin 2015)? Theories of human cooperation need to explain this rapid process, and why it proceeded at different rates in different populations and on different continents.
4) **Non-cooperative and maladaptive behavior:** The same sanctioning and other incentivizing mechanisms that support cooperation in some human populations, such as those based on punishment, reputation, and signaling, also enforce costly behaviors that are unrelated to cooperation, such as ritual practices, food taboos, sexual prohibitions and clothing customs. Why do these same mechanisms sometimes also sustain maladaptive practices, like the consumption of dead relatives (spreading prion diseases), female foot-binding, and female genital cutting (Durham 1991; Mackie 1996; Vogt et al. 2017)?

Ongoing efforts to explain cooperation in our species will need to confront these puzzles. However, some psychologists may react to these explanatory challenges by seeing them as questions that reside outside of their discipline. Here, by introducing readers to an evolutionary framework that incorporates culture, we'll show how fundamental questions about human nature, psychological diversity, social structure, and child development can be addressed in a cumulative fashion (Muthukrishna & Henrich 2019). As we'll see, the current evidence supports the view that our psychology coevolves culturally with our institutions, so any account of "human cooperative psychology" requires a theory that integrates the cultural evolution of social norms and institutions.

We'll begin by introducing an extended evolutionary synthesis that considers the emergence of our species' capacities for cultural learning, the rise of cultural evolution, and the ensuing interaction between our genetic and cultural forms of inheritance. Then, using the extended synthesis as a theoretical menu of the major evolutionary mechanisms that have been proposed to explain human cooperation, we'll review key results related to kinship, direct reciprocity, reputation, punishment, and signaling. For each of these mechanisms, we'll consider the potential role for both genetic and cultural evolutionary processes in light of research from diverse populations, as well as from other primates. After highlighting the limitations of these mechanisms for explaining human cooperation, we'll consider how intergroup competition in cultural evolution interacts with these within-group mechanisms to provide a more complete account. Next, having illustrated various ways that cultural evolution produces social norms, we'll discuss three interrelated culture-gene coevolutionary hypotheses that consider how social norms, as a recurrent feature in our lineages' ancestral environments, may have driven the genetic evolution of various aspects of our social psychology. Finally, we'll close by presenting research that anchors our cultural evolutionary psychology in history, and analyze how the diffusion of specific institutions, including those related to kinship and religion, have shaped our cooperative psychology.

A CULTURAL SPECIES

Whether they were stranded in Australia, Panama, or the Arctic, numerous cases of "lost European explorers" illustrate that our huge primate brains are singularly ill-equipped to helping us to survive as hunter-gatherers (Henrich 2016). We don't innately know, and usually can't individually figure out, how to detoxify plants, fashion tools, make clothing, start fires, or locate water. Unlike other animals, we are entirely dependent on learning from other people for our very survival, even for our survival as foragers; as a species, we are addicted to culture—on acquiring a substantial portion of our phenotype by tapping into a large body of non-genetic information that has been filtered and accumulated over generations. This process, termed *cumulative cultural evolution*, creates a storehouse in the form of strategies, attentional biases, motivations, tastes and cognitive heuristics that are necessary for us to accomplish even the basics of survival (e.g., finding food), which most other species manage with little to no cultural input (Dean et al. 2014; Henrich 2016). Without access to this non-genetic inheritance, we are virtually helpless. While many species rely on social learning to some degree, little or no cumulative cultural evolution has been found outside of the genus *Homo* (Henrich & Tennie 2017; St Clair et al. 2018). How can we apply an evolutionary approach to a species that is so heavily reliant on culture?

Beginning in the 1970s, a few evolutionary researchers began to apply the logic of natural selection to the evolution of our capacities for culture and to think systematically about how to model cultural transmission over generations (Boyd & Richerson 1976; Feldman & Cavalli-Sforza 1976). The evolutionary framework that blossomed from these intellectual roots can be partitioned into three categories of inquiry: (1) the genetic evolution of our species' capacities for culture, (2) cultural evolution and the emergence of institutions, and (3) the process of culture-gene coevolution.

Evolved Capacities for Culture

This enterprise begins by asking: how has natural selection shaped our minds and brains to allow individuals to most effectively extract adaptive practices, know-how, strategies, preferences and decision-heuristics from the minds and behaviors of those around us? This leads to the 'who', 'what' and 'when' of cultural learning (Rendell et al. 2011).

1) **'Who'** should individuals learn from? Both experimental and field observations show that adults, children and often even infants preferentially attend to and learn from individuals based on cues of competence, skill, success, prestige (receiving deference or attention from

others) and similarity to the learner on sex and ethnicity as well as other traits (Chudek et al. 2013; Harris & Corriveau 2011; Wood et al. 2013).

2) **'What'** sorts of content should learners attend to and how should they process it (Sperber 1996)? A diverse portfolio of research looks at how the content of cultural traits differentially influences attention, memory and inferences across a wide range of domains including artifacts, living kinds, social norms and ethnic groups (Barrett & Broesch 2012; Casler et al. 2009; Greif et al. 2006).
3) **'When'** should individuals rely on cultural learning over their own experience or intuitions (Aoki & Feldman 2014)? Experimental work with infants, children and adults suggests that people shift to weight more heavily what they acquire from other people, even over their own direct observations, especially as situations become more uncertain and problems get more difficult (Morgan et al. 2012; Muthukrishna et al. 2016).

Together, this ensemble of cultural learning abilities and biases provides a psychologically-rich account of cultural transmission that can not only explain the generally adaptive character of cultural evolution, but can illuminate a broad range of otherwise puzzling patterns, including phenomena such as food taboos (Henrich & Henrich 2010) and rituals (Legare & Souza 2014).

Crucially, despite the existence of content-based 'what' mechanisms, human cultural learning abilities nevertheless influence an incredibly wide range of behavioral domains. Of course, people of all ages culturally acquire linguistic labels, pronunciations, tool uses, new technologies, social rules, food taboos and beliefs in invisible things like gods, ghosts, fairies, germs, and vitamins (Harris 2012). But, going deeper, cultural learning can also modify our motivations, preferences, biases and self-confidence to more closely match those of our preferred models in ways that influence our judgments and decision-making (Rosenthal & Zimmerman 1978). Experimental studies reveal that exposure to the choices of others shape our preferences for particular foods (Birch 1987), songs (Berns et al. 2010), overconfidence (Cheng et al. 2017), and mates (Zaki et al. 2011). Most important for our goals here, cultural learning influences costly behaviors, including charitable giving (Rushton 1975), blood donations (Rushton & Campbell 1977), cooperative contributions (Fowler & Christakis 2010; Gächter et al. 2012), fairness (Blake et al. 2016), helping (Eisenberg & Mussen 1989), patience (Garvert et al. 2015), aggression (Bandura 1977), standards for self- and other-rewarding (Bandura & Kupers 1964), and a willingness to engage in third-party punishment (Salali et al. 2015).

Marginal box definition: **Third-Party Punishment:** punishment administered to a norm-violator or non-cooperator by an uninvolved individual, someone not directly impacted by the errant action—a third-party. See Box 1 for the Third-Party Punishment Game.

Cultural evolution: the emergence of social norms and institutions

To understand how culture shapes our behavior and psychology, and ultimately our genetic evolution, we need to go beyond the psychological foundations of our reliably developing capacities for learning from others to consider what happens as individuals adaptively learn from those around them and interact repeatedly over generations. Using this approach, theorists have constructed mathematical models, rooted in what's known about learning, to examine the cultural evolution of technology (Creanza et al. 2017), social stratification (Henrich & Boyd 2008), honor cultures (McElreath 2003) and the formation of symbolically-marked ethnic groups (McElreath et al. 2003). Here, drawing on the largest segment of this literature, we focus on the emergence of costly social norms, where individuals engage in costly behaviors that are monitored and incentivized in some way by their groups or communities. Interestingly, many of these models were originally constructed to study the evolution of large-scale cooperation, but it turned out that the mechanisms involved—related to reputation, punishment and/or signaling—can sustain any equally costly action regardless of whether it delivers benefits to anyone. So, to understand cooperation and human social life more generally, evolutionary models of cooperation have told us to focus on the more general category of social norms. Institutions, by this account, are simply packages of social norms that interlock to govern some domain of life, such as marriage or exchange. Formal institutions arise when decision-makers, often aided by writing, clarify and standardize the informal institutions generated by social norms.

SIDEBAR: Dual Inheritance Theory

Since the mid-1970s researchers have been developing evolutionary models that consider the inheritance of both genetic and cultural traits (Boyd & Richerson 1976, 1985; Cavailli-Sforza & Feldman 1981; Feldman & Cavalli-Sforza 1976). Genetic and cultural evolution are similar in that they can be modeled by tracking how the information carried by individuals changes over time and is transmitted across generations. Genetic evolution, for example, is influenced by natural selection, drift, mutation and recombination. In humans, individuals recombine their genes from only two parents, transmission is high fidelity, mutation rates low and natural selection weak. By contrast, in cultural evolution, individuals often acquire and recombine their cultural traits from many models ('cultural parents'), transmission fidelity is relatively low at the individual level (but may be high at the group level), and selective processes are often strong, generated by a wide array of psychological processes that impact attention, memory and retransmission. This often makes cultural evolution fast relative to genetic evolution (Boyd et al. 2011; Henrich & Boyd 2002; Henrich et al. 2008; Mesoudi et al. 2006; Perreault 2012). These differences, and others, mean that cultural and genetic evolution often favor different outcomes and interact in unexpected ways, which we explore below.

In the next section, we'll explore the evolution of cooperation by considering the major evolutionary mechanisms that have been proposed for explaining human cooperation including those that can sustain costly social norms via cultural learning. To lay the groundwork for this, we'll first consider the origins of social norms at a more abstract level: once individuals possessed sufficiently sophisticated cognitive abilities to reliably culturally learn both (1) how to behave in particular contexts and (2) the standards for judging others in these contexts, stable patterns of costly behavior will emerge and can be sustained for long periods within a community. These patterns are social norms because anyone who deviates—doesn't pay the cost—will be sanctioned or otherwise incentivized to conform in some way. Below, we'll review the empirical evidence suggesting that the cultural evolution of social norms in human societies over tens or even hundreds of thousands of years has shaped the genetic evolution of our minds, including by producing a *norm psychology* (Chudek & Henrich 2010). However, for now, let's begin by considering evidence indicating that social norms do indeed matter for individually costly behaviors and that this is associated with variation across societies.

Deploying a simple dictator game (see Table 1's description) among both children (n = 833) and adults (n = 255) across eight populations (Figure 1), ranging from hunter-gatherers in Tanzania to urbanites in Berlin, House et. al. assessed people's willingness to share equally with an anonymous partner. Participants had to pick one of two possible allocations: (A) two rewards for themselves or nothing for their partner (2/0), or (B) one reward for themselves and one for their partner (1/1). Before making their decision, participants were randomly assigned to see one of three videos in which an adult from their community states either that (1) the 1/1 option is 'good' and the 2/0 'bad' (Fair condition), (2) the 2/0 is 'good' and the 1/1 'bad' (Selfish), or (3) both are ok (Neutral). After making their choices, many participants were then shown both the Fair and Selfish videos and asked which makes the 'more correct' statement about the decision—a normative assessment.

For adults across these populations, Figure 1a shows the estimated average frequencies of costly 1/1 choices (the horizontal bars) and 'more correct' judgments of the Fair videos (triangular points). Unsurprisingly, adults were more likely to make 1/1 choices in places where this was judged as 'more correct.' Analyses revealed that adult's choices are influenced by both their own preferences regarding which choice is more correct and the normative judgments of their communities. These findings indicate a role for normative concerns in adults' decisions.

Turning to the developmental data, Figure 1b models the age trajectories of the 1/1 choices. In all societies, as they get older, children moved toward both the behaviors and normative judgments of the adults in their societies, leading to quite different trajectories across societies. This suggest that norms not only influence adult behavior but shape child development. Notably, divergent developmental trajectories for costly social behaviors, like those shown here, are not unusual in cross-cultural studies of child development (Blake et al. 2015a; House et al. 2013b; Rochat et al. 2009); thus, the apparent size of cross-cultural differences in psychology will depend on the age at which children are compared. Clearly, WEIRD children do not provide a good approximation for *Homo sapiens*.

In contrast to this population-level variation, the data also reveal a universal pattern in response to norms. First, across populations, children responded to the video statements (Fair, Selfish and Neutral) by moving their behavior in the normatively prescribed direction. This confirms that children respond to norms in this context. Second, as children moved through middle childhood, their behavior was better predicted by the normative preferences expressed by the adults in their communities. These patterns are consistent with theories proposing that middle childhood (roughly ages 6-11), a unique period of human life history, evolved to support cultural learning and, specifically, the acquisition of social norms (Henrich 2016).

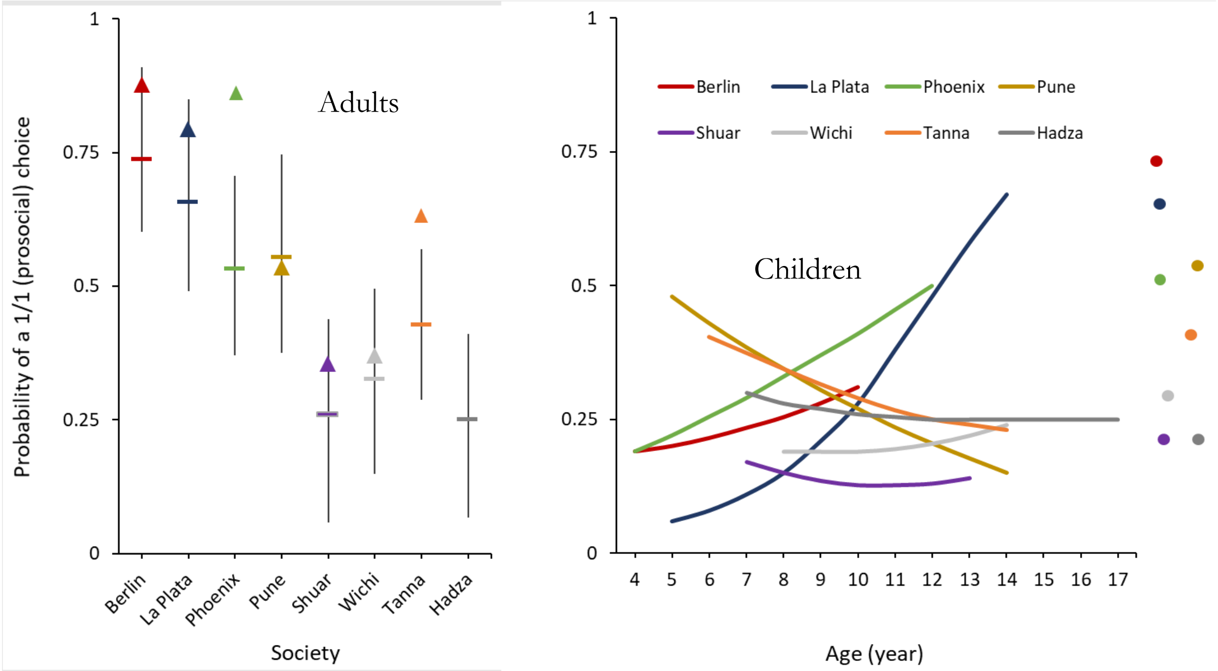

Figure 1. Binary Dictator Game results from 8 diverse populations. (A) For the adults, this figure shows the means (horizontal bars, predicted from a model) and confidence intervals (vertical lines) for making the 1/1 (fair) allocations across populations. The triangles mark the frequencies of adults' normative responses indicating that the 1/1 choice is "more correct." (B) For children, the developmental trajectories of frequencies of the 1/1 allocations (predicted from a model) for each population. The dots on the right mark the adult averages. Populations: the Shuar are Amazonian slash-and-burn horticulturalists in Ecuador; the Hadza are Tanzanian hunter-gatherers; Tanna is an island in Vanuatu where a population of hunter-horticulturalist was sampled. Pune is a city in Maharashtra, India. In Argentina, the Wichí are sedentarized hunter-gatherers and La Plata is a provincial capital. These plots are modified from House et. al. (2019).

Overall, a synthesis of evidence from across the social sciences suggests that human social behavior is heavily influenced by both cultural and genetic transmission—a dual inheritance system. To tackle this complexity, we need to think about how cultural and genetic evolutionary processes might each contribute to human cooperation and how these inheritance systems might interact in a process of culture-gene coevolution. Importantly, while cultural and genetic transmission differ in important ways, we can flesh out an approach to cooperation by considering how each can solve, or fail to solve, different kinds of cooperative dilemmas.

Box 1. Key concepts and standard behavioral experiments

Term	Explanation
Ultimatum Game	This is a two-player experimental interaction in which the pair is provided with an endowment—usually a sum of money (or other valuable items) and each participant is assigned to either the "proposer" or "receiver" role. The proposer must allocate the money between the two, from zero to the full endowment. Receivers can either "accept" or "reject" the proposed division. If they accept, the money is divided as per the proposal. If the respondent rejects the division, both players receive nothing. In its canonical form, this anonymous interaction occurs only once, which means that a receiver who cares only about maximizing their monetary returns—*Homo economicus*—

	always accepts any positive offer. Anticipating this, a *Homo economicus* proposer should allocate the smallest non-zero amount.
Dictator Game	This two-player experimental interaction parallels the Ultimatum Game except that the receiver is passive and so cannot accept or reject the allocation from the proposer, who is now called the "dictator." *Homo economicus* allocates zero.
Third Party Punishment Game	This is an interaction among three players, A, B and C. A and B play a Dictator Game in which A allocates any part of the endowment to B, the passive recipient. Player C is given an endowment equal to half of that provided to players A and B. Player C can pay any amount of this endowment to take money away from player A. Whatever amount C decides to pay is multiplied (often by 3) then subtracted from player A. In the simpler version highlighted below, player C could only choose between paying $10 (20% of their stake) to take $30 away from player A or do nothing (pay zero). In the world of *Homo economicus*, player Cs will never pay anything to punish, so player As will allocate nothing to B.
Public Goods Game	In this interaction, *n* participants are each given a monetary endowment, which they can anonymously contribute any portion of to a public good. After all *n* players have had a chance to contribute, the public good is multiplied by a factor between 1 and *n* and then divided equally among all players irrespective of contributions. *Homo economicus* always contribute zero when the interaction is one shot and anonymous.
Free-rider Problem	The free-rider problem describes the situation in cooperative dilemmas in which players derive a benefit from the contributions of other players without paying sufficient costs. E.g., a player in the public goods game above who contributes zero to the public good "free rides" on the contributions of other players.
2nd and higher order free-rider problems	One solution to the free-rider problem is to allow people to punish free-riders at some cost to themselves. However, this creates a second-order free-rider problem, whereby players derive a benefit from other players' willingness to punish free-riders, but do not themselves pay the cost of punishment. Punishing these second order free-riders creates a third-order free-rider problem and so on.
Equilibrium Selection Problem	This problem arises when evolutionary processes produce more than one dynamically stable behavioral outcome under the same conditions—e.g., both full cooperation and full defection might be simultaneously stable. Each stable state may have a different 'basin of attraction' that depends on the frequencies of different strategies or behaviors in the population. Such situations may call for additional explanatory processes, such as intergroup competition, to explain how or why rare or difficult to access equilibrium states proliferate.

EVOLUTIONARY MECHANISMS OF COOPERATION

Sustaining individually costly behaviors, including those that deliver benefits to others, requires some form of non-random interaction (Frank 1998; Henrich & Henrich 2007). Those who pay the costs of cooperation must either accrue benefits or avoid other costs, such as penalties, lost opportunities, or other sanctions. This logic holds for both genetic and cultural transmission, though in some cases certain biases in human cultural learning may permit cooperative solutions that are not accessible to natural selection acting on genes (Henrich 2009; Henrich & Boyd 2001). Even in these cases, however, one must ultimately explain how and why the relevant learning biases evolved and remain stable. Consider the simplest case (e.g. food sharing): if more cooperative individuals preferentially bestow benefits (food) on other cooperators (others who share food), a degree of cooperation can be sustained, depending on the costs of helping (*c*), the benefits delivered by helping (*b*), and the strength of the non-random association or preferential delivery (β, how much shared food is deliver to other sharers vs. non-sharers). Cooperation is sustained when $\beta \cdot b > c$. More complex mechanisms for cooperation involve sanctioning those who don't pay the required costs, such as through preferential exclusion, ostracism, exploitation or punishment (Bhui et al. 2019). Here, we'll briefly review the theory and evidence for some of the most fundamental mechanisms, considering each from both a genetic and cultural evolutionary point of view.

Kin-based altruism

Evolutionary biologists have long recognized that if individuals preferentially aid close genealogical relatives, a degree of cooperation can be sustained (Hamilton 1964). Cooperation can be stabilized with higher costs or lower benefits to relatives, the closer the genealogical relationship (*r*, the coefficient of relatedness). Here the non-random association is created by favoring relatives: $r \cdot b > c$. By directing help in accordance with *r*, individuals can preferentially deliver benefits to other cooperators. The more closely related a receiver, the higher the likelihood that they too have acquired cooperative traits via inheritance from a recent common ancestor. To take a genes eye view, genes that can identify and preferentially favor copies of themselves will spread at the expense of those that do not.

Phylogenetically, based on both field and laboratory studies with non-human primates, there's good reason to believe that humans have inherited a genetically evolved psychology for this kin-based altruism from our common ancestors. Ample evidence from both monkeys and non-human apes reveals the impact of genealogical relatedness on social patterning (who hangs out with whom) and cooperative interactions, including coalitional support, status-pursuit, and grooming (Langergraber 2012; Sandel et al. 2019; Surbeck et al. 2011). Kinship also likely plays a role in the food sharing observed in some species (Jaeggi & Gurven 2013), though in contrast to the ubiquitous food sharing across human societies, there's relatively little voluntary food sharing in non-human primates.

Like in other primates, kinship explains many of the costliest forms of human cooperation, ranging from child investment to organ donations. Kin-based cooperation is clearly a human universal (Curry et al. 2019). Researchers have documented the powerful effects of genealogical relatedness for social interactions and cooperation both across diverse societies and back into historical time (Alvard 2009; Barrett et al. 2002). Important domains of cooperation include food sharing, childcare (Kramer 2010), adoption (Silk 1987), alliance formation (Dunbar et al. 1995), residence choice (Hill et al. 2011), crisis aid and much more.

SIDE BAR (above): Paralleling our primate cousins, humans also estimate their relatedness to others using associations with their mothers, time spent together growing up, and phenotypic matching (Bressan & Kramer 2015), including both facial and olfactory similarities. Cues of kinship based on facial similarity can even increase cooperation in a public goods game (Krupp et al. 2008).

In principle, the logic of kin-based altruism can apply to cultural as well as genetic inheritance. In genetic models, knowing someone's genealogical relatedness provides the probability that you share altruism genes by recent common descent—if you have the altruism gene than there's a 50% chance (roughly and on-average) that your brother has a copy too. In theory, nothing about this logic excludes cultural evolution from exploiting the same trick (Allison 1997). In practice, however, because cultural transmission is fundamentally different from genetic inheritance, there's little reason to suspect much of a role for cultural relatedness on cooperation—where individuals would preferentially help those with the same 'cultural ancestors' (e.g., the same role models). The issue is that individuals often learn from many models drawn from a large pool. This means that the cultural relatedness between any pair goes down dramatically as the pool of potential models expands. Based on data from a small Fijian community of roughly 200 people, cultural relatedness based on common descent (i.e., learning from the same models) is 0.053 or less. This value implies that the costs of helpful actions, *c*, would have to generate benefits, *b*, that were 19 times greater than the costs. This is not promising, given that such a small, isolated island population provides perhaps the best possible conditions for cultural relatedness to favor cooperation (Boyd et al. 2011).

Nevertheless, theorists have identified one set of conditions in which cultural kinship can favor cooperation: in groups dominated by a single highly prestigious individual, where individuals look to this person for cues of how to behave, cooperative actions can invade and remain common (Henrich et al. 2015). Predictions derived from this model find support in both experiments and field observations (Gächter & Renner 2018; Henrich 2016). Notably, this mechanism cannot explain the parochial forms of cooperation observed within tribal or ethnic groups, but other cultural evolutionary processes that harness observed 'ethnic markers', such as dialect or dress, have been proposed to solve coordination problems and account for this widespread empirical pattern (Henrich & Henrich 2007; McElreath et al. 2003).

Direct Reciprocity

As with kinship, theorists have also long considered how psychological mechanisms rooted in reciprocity—also termed reciprocal altruism—might generate a sufficient degree of non-randomness in the distribution of costs and benefits to create conditions favorable to cooperation (Axelrod & Hamilton 1981; Trivers 1971). Reciprocity-based strategies, which often incorporate a tit-for-tat logic ("you scratch my back, I'll scratch yours") can operate through mechanisms based on (1) partner choice, (2) partner fidelity, or both. Under *partner choice*, individuals build relationships with those who deliver benefits to them (Barclay 2011; Hruschka & Henrich 2006). Those who fail to provide sufficient benefits to a partner lose that partner. By contrast, under *partner fidelity*, individuals attempt to persuade recalcitrant partners into greater cooperation by withholding benefits (Schino & Aureli 2017).

Phylogenetically, the evidence for reciprocity is mixed. Both experimental and observational data from non-human apes suggests a role for partner choice in some forms of cooperation (Engelmann & Herrmann 2016; Gomes et al. 2009; Samuni et al. 2017; Schino & Aureli 2010; Schweinfurth & Call 2019). However, evidence for the contingent cooperation necessary to support reciprocity based on partner fidelity is quite limited (Brosnan et al. 2009; Melis et al. 2016). Though clever experimentalist have managed to design tasks that permit chimpanzees to respond contingently to help received (Engelmann et al. 2015; Melis et al. 2008; Schmelz et al. 2017), consistently getting chimpanzee pairs to initiate and sustain tit-for-tat style reciprocity in plausibly real-world conditions remains largely elusive (Warneken 2018). Taken together, the diverse body of mixed results regarding reciprocity in other primates suggests that humans have probably inherited some capacity for reciprocity based on partner choice from our shared ancestors but likely only the rudiments of partner fidelity.

In contrast to kinship, our dual inheritance system complicates matters because cultural transmission is particularly well suited to produce, or enhance, both the partner choice and partner fidelity forms of reciprocity. There are at least three reasons for this. First, human cultural learning often involves the copying of other people's goals, actions, and strategies. If individual A helps individual B, and B copies A's action, then tit-for-tat style reciprocity is off and running. Similarly, if A is a tit-for-tat strategist and B copies A's strategy or even learns some rough version of it, then A and B can potentially begin reciprocal helping with compatible strategies. This tendency to copy an opponent's or partner's strategy is empirically well documented, even in interactions where it reduces payoffs (Belot et al. 2013; Naber et al. 2013). Second, theoretical work on reciprocity demonstrates that a strategy's success depends heavily on the other strategies active in a particular population (Lorberbaum et al. 2002; van Veelen et al. 2012). This fact makes it difficult for genetic evolution to pre-program one, or even an ensemble, of successful strategies. Cultural learning can tackle this dilemma by allowing individuals, via copying the most successful strategies currently in use, to rapidly adapt their behavior to the local distribution of strategies and thereby prevent the collapse of cooperation. Finally, theoretical work shows that adding social norms, which allow third parties to adjudicate disagreements about who did what during unsuccessful interactions, can dramatically increase the range of conditions under which direct reciprocity can emerge (Mathew et al. 2013). For these reasons, culture may have created conditions favorable to the emergence of reciprocity-based cooperation, and the interaction between culture and genes may create conditions favorable to a reliably developing reciprocity psychology.

Empirical support for this culture-gene coevolutionary view emerges from several patterns. Reciprocity-based cooperation in some form is clearly a universal (Fiske 1991; Jaeggi & Gurven 2013). Yet, while evidence from WEIRD toddlers suggests an early emergence for the rudiments of partner choice (Kuhlmeier et al. 2014; Olson & Spelke 2008), the development of actual reciprocity-based cooperation and contingent helping doesn't robustly emerge until middle childhood (Chernyak et al. 2019; House et al. 2013a; Warneken 2018)—just when children begin to adhere to costly norms (Smith et al. 2013).

The relatively late and gradual development of positive reciprocity ("you scratch my back, I'll scratch yours") contrasts with negative reciprocity ("an eye for an eye and a tooth for a tooth"). Using a computer-based experimental setup, Chernyak et. al. (2019) tested children from ages 4 to 9 in Boston by permitting them to interact with four other children who were represented by avatars. In one condition, participants received a sticker from one of the avatars (positive reciprocity) while in another condition one of the four avatars took one of the child's stickers (negative reciprocity). When given the option of whether to do anything, Figure 2A shows that children who had been given a sticker only gradually developed the inclination to reciprocate a sticker to this partner. This rising inclination towards contingent reciprocity is matched by a parallel rise in normative endorsements of reciprocity regarding what one "should" do in this context. By contrast, revenge or negative direct reciprocity appears already fully developed in four-year old children (in this population) and remains strong throughout middle childhood. This is noteworthy because experiments with chimpanzees readily reveal negative direct reciprocity (Jensen et al. 2007b), but neither positive reciprocity based on partner fidelity (Melis et al. 2016) nor third-party punishment (Riedl et al. 2012).

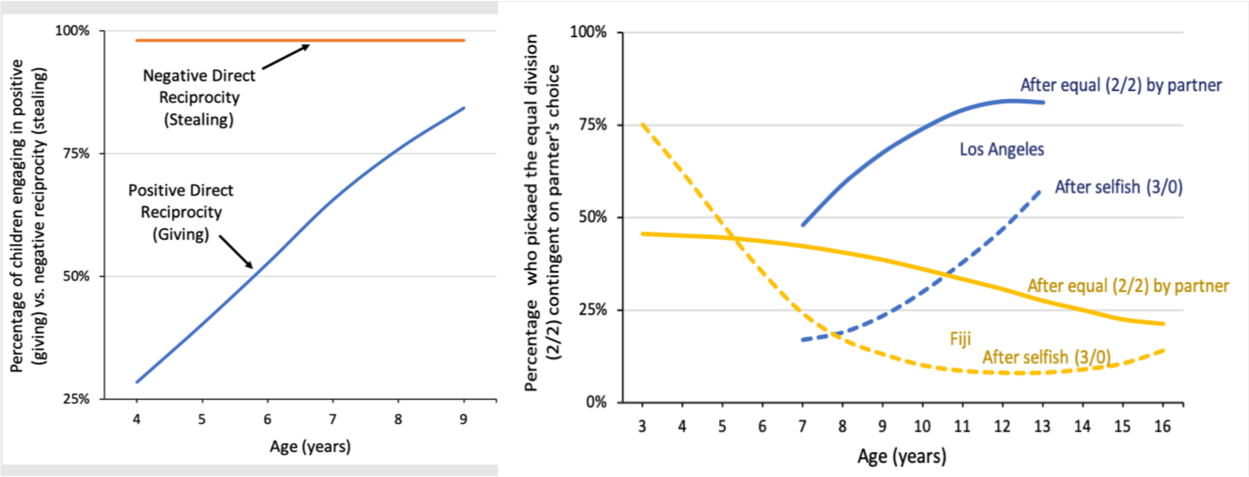

Figure 2. Developmental trajectories for (A) positive and negative direct reciprocity for children in Boston; and (B) positive reciprocity in a repeated Dictator Game with two options, a 1/1 split or 2/0, in Fiji and Los Angeles. Adapted from Cherneyek et. al. (2019) and House (2017).

Importantly, Chernyek et. al. also demonstrate that children's adoption of positive reciprocity during middle childhood is facilitated by hearing stories about characters who performed and endorsed reciprocal actions. This suggests that reciprocity may depend, or at least be enhanced by, the acquisition of reciprocity norms. Tellingly, other work suggests that the more sophisticated strategies for positive reciprocity dreamt up by theorists to contend with more complex social environments don't even begin to show themselves until after age 10, at least in WEIRD children (Blake et al. 2015b).

While developmental trajectories for positive reciprocity like that shown in Figure 2A reliably emerge in WEIRD populations (House 2017; House et al. 2012), Figure 2B permits us to compare age trajectories for the same experiment in Los Angeles and Fiji. In this experiment, children took turns selecting one of two options (A) 2 rewards for the actor and 2 for their partner or (B) 3 rewards for the actor and 0 for the other person. Children in both populations develop contingent responding, which indicates that reciprocity reliably develops in diverse social context. Yet, these populations show rather divergent trajectories—in Fiji, the older kids increasingly select the 3/0 option, so playing tit-for-tat drives cooperation down, not up.

SIDE BAR: In contrast to most societies over human history, where people experienced tight kin groups (Schulz et al. 2019) and low relational mobility (Thomson et al. 2018), WEIRD people often live in large populations and possess great freedom to pick and change their friends, spouses, neighbors, communities and business partners. As a consequence, by the time WEIRD people reach adulthood, they often maintain a portfolio of long-term friendships, where short-term tit-for-tat accounting is eschewed in favor of aggregated emotional indices, and numerous shorter-term acquaintances, where tit-for-tat style accounting is relevant (Silk 2003). In other societies, including some foragers, conditions are less favorable to partner choice and this mechanism is less important (Smith et al. 2018).

In closing this section, we note that both theoretical work and empirical evidence suggest that kinship and reciprocity can interact synergistically to increase cooperation in small, tightly knit communities (Axelrod & Hamilton 1981; Van Cleve & Akcay 2014). However, these mechanisms cannot tackle the five challenges of human cooperation; neither mechanism 'scales-up' effectively, especially in a species like humans. Genealogical relatedness cannot readily account for our (1) ultrasociality (relatedness is not sufficiently higher than other primates), (2) domain differences in cooperation (except based on the ratio of the benefits of cooperation to the costs of helping, b/c), (3) rapid expansion (genetic relatedness, r declines dramatically as groups expand), and (4) non-cooperative or maladaptive behavior (kin-altruism requires $b > 0$). When kin-based altruism does appear to play a broader role, it's usually supported by cooperative norms, such as those that prescribe prosociality towards in-laws, extended family members and stepchildren (McNamara & Henrich 2017). Similarly, while reciprocity can sustain cooperation in dyads, it tends to collapse in larger groups (Boyd & Richerson 1988). Reciprocity also cannot explain differences in the domains of cooperation (except via variation in b/c) or the existence of maladaptive behavior (reciprocity also requires $b > 0$). In fact, the intensive cooperation in smaller groups (like clans and villages), which can be enhanced by kinship and reciprocity, actually impedes the emergence of cooperation at higher levels—among many clans or ethnic groups (Schulz et al. 2019). What we call corruption, cronyism and nepotism is really just cooperation at a smaller scale, often among relatives, friends and reciprocal partners, at the expense of cooperation at a larger, impersonal scale (Muthukrishna 2017; Muthukrishna et al. 2017).

Origins of institutions: reputation, punishment and signaling

People in some populations readily give blood anonymously to strangers, recycle, help the poor, report crime and volunteer for war. To explain cooperation at larger scales, where genealogical relatedness and the potential for reciprocity necessarily declines, evolutionary theorists have developed models that can sustain cooperation based on mechanisms involving punishment, reputation and signaling as well as combinations of these mechanisms. In typical models of diffuse punishment, for example, individuals who fail to cooperate, say in contributing to a public good, will be punished (at a cost) by any punishers in the group. This can sustain cooperation by penalizing defections, but it creates what's called the *second-order free rider problem* (Box 1). Who will punish those who benefit by evading the costs of punishing free riders? One solution is to randomly designate a single punisher—if there's only one punisher, the free rider problem vanishes (Boyd & Richerson 1992; O'Gorman et al. 2009).

Alternatively, diffuse or third party punishment may be a signal of otherwise hidden inclinations toward cooperativeness or trustworthiness (Gintis et al. 2001; Jordan et al. 2016). Here, individuals signal their social-behavioral qualities by punishing non-cooperators (or any norm violator), which both sustains costly norms (including larger scale cooperation) and promotes beneficial future interactions for the signaler.

Yet a third solution proposes that, after a norm violation, punishers signal their intent to punish and then punish if enough others also signal their punitive intentions (Boyd et al. 2010). If too few individuals signal, punishers withhold their sanctions. By coordinating punishment and compelling defectors into cooperation, this system can guarantee that punishers tend to end up in cooperative groups, and when they don't, they can still avoid the costs of punishment.

Large-scale cooperation can also be sustained by reputational systems, often termed *indirect reciprocity*, that ties different kinds of social interactions together via a shared roster of who is in good standing. In the classic model (Panchanathan & Boyd 2004), individuals experience two kinds of interactions: a public good involving many individuals and a dyadic mutual aid interaction. Individuals decide whether to help based on their partner's contribution to the public good (e.g., pay taxes). If a player defects in the public good, their partner can abstain from helping them in the dyadic interaction when they are in the role of 'donor' (without themselves getting a bad reputation for it). Essentially, the withdrawal of help in the dyadic helping interaction, which benefits the person freed from the burden of helping, is used to sanction non-contributors to the public good. The model has been confirmed in laboratory experiments (Hauser et al. 2016), though the strength of this reputation-based cooperation is dependent on being able to track and verify the accuracy of reputations and may be undermined by reputations in different domains and at different scales.

Collectively, these and other similar models reveal two additional important features about the mechanisms that can sustain larger-scale cooperation. First, although all these models were initially built to examine cooperation, the mathematics reveal that—unlike kinship and direct reciprocity—they can sustain any equally costly behavior regardless of whether any benefit is delivered to the community. That is, they are models about how to sustain social norms, of which cooperative social norms are a subclass. Second, they contain what theorists call *multiple stable equilibria*. This means that under the identical conditions—same costs, benefits, group size, error rates, etc.—there are stable states for the populations in which no costly norms exist (e.g., all defection) and states in which costly norms are adhered to and cooperation can be maintained. In the language of complex systems, there are *basins of attraction* for both defection and costly norms that depend on the frequency of different behaviors or strategies in the population.

Are these models of large-scale cooperation best understood as products of genetic or cultural evolution? Unlike kinship and reciprocity, both the assumptions employed in these models and the results derived strongly suggest that they are most plausibly understood as cultural processes. And, even if they are viewed as genetic evolutionary processes, most rely on one or more key cultural products, like (1) shared behavioral standards (what counts as 'cooperation' or qualifies as 'good standing'), (2) recognized social roles (who is a 'donor'), institutions (for punishment) and (3) the ability to disseminate reputational information (Bhui et al. 2019; Leimar & Hammerstein 2001). Empirically, reputations are formed and shared primarily via cultural transmission since most people don't directly observe most social interactions—so, most reputation-based models presuppose sophisticated cultural learning abilities. The interpretation of these models as cultural evolutionary processes is underlined by the fact that none of them have been successfully applied to explain cooperation in non-humans. Consistent with this, experimental work indicates that non-human primates show no concern for their reputations (Engelmann et al. 2012), no inclination to cooperate with strangers (de Waal et al. 2008), and little tendency to engage in costly third-party punishment (Riedl et al. 2012). In contrast, by middle childhood, human children are concerned about their reputations, responsive to the normative demands of their societies (Figure 1B), and willing to engage in third-party punishment of social norm violations in societies that rely on diffuse punishment (Jordan et al. 2014; McAuliffe et al. 2015).

In light of this evidence, these various evolutionary models should be thought of as hypotheses about the kinds of institutions that cultural evolution may have generated to sustain cooperation, both in larger groups and among ephemeral interactants. Facing different ecological, economic and social circumstances, we should expect cultural evolution to have rigged up distinct combinations of these cooperation-sustaining mechanisms, variously deploying elements of punishment, reputation and signaling (among others) in different ways in different societies and in different behavioral domains (e.g., food sharing, warfare, house building). In some societies, reputational incentives variously favor tipping at restaurants, obeying parking regulations, circumcising daughters, giving blood, sharing meat with campmates, raiding other communities and being equitable in monetary exchanges with strangers or anonymous others. In WEIRD societies, individuals can signal their trustworthiness by punishing uncooperative strangers (Jordan et al. 2016) while in other societies this would be seen and responded to as an anti-social attack (Enke 2019; Henrich forthcoming; Herrmann et al. 2008). Thus, larger scale human cooperation likely relies on a mosaic of cultural evolutionary mechanisms that variously harness reputation, signaling and punishment, among others (see below), in a diversity of creative and unexpected configurations.

To illustrate this, consider how village-level cooperation is sustained in the South Pacific (Henrich & Henrich 2014). In a subsistence-oriented Fijian community, a system involving negative indirect reciprocity—tolerance of those who exploit those with a poor reputation—maintains a wide range of social norms including those related to helping in community projects, contributing to village feasts (food sharing) and constructing one’s house in a prescribed orientation. If someone violates one of these social norms, both they and their extended family fall into bad standing. If this reputation gets bad enough, after repeated violations, it’s as if their reputational shield falls and their fellow villagers can exploit them with impunity. For example, a family who violated community-wide norms by working on Sundays had some of their cooking pots and crops stolen (while they were away in another village) and one of their agricultural fields was torched at night. Normally, had these acts been performed against someone in good standing, villagers would have pulled together, shared information and tracked down the thief-arsonist. But, when victims are in bad standing, villagers just shrug and let it pass. In this institution, norm violators are sanctioned but the punishments are neither costly nor altruistic. To the contrary, punishers get both material (e.g. food and pots) and social benefits. Most people don’t punish and those who do are widely believed to be rivals of the punished, who hold long simmering jealousies or grudges. No one thinks these punishers are admirable, trustworthy, or great future partners. Instead, people are willing to tolerate such anti-social actions when the victim is in bad standing. It’s only ‘bad’ to do ‘bad’ things to ‘good’ people. Those who do bad things to bad people are tolerated. A cultural evolutionary model inspired by this field data reveals the effectiveness and relative simplicity of this mechanism for sustaining large-scale cooperation (Bhui et al. 2019).

This Fijian mechanism for costly norms contrasts with the use of diffuse punishment found in WEIRD societies. In these peculiar populations, experimental research indicates that people are willing to pay costs to punish strangers and anonymous others for norm violations (Fehr & Fischbacher 2003; Fehr & Gachter 2002). Evolutionary models in which diffuse punishment sustains cooperation were developed early, which isn’t surprising since they reflect WEIRD intuitions about punishment. To see this experimentally, let’s begin by focusing on the differences in how Fijian villagers and Americans punish in the Ultimatum and Third-Party Punishment Games (Box 1). In the Ultimatum Game, over 70% of non-student Americans reject offers of 10% of the stake, the lowest possible offers that could be punished with a cost. In Fiji, 85% of participants refused to punish this offer amount. In the Third-Party Punishment Game, over half of American university students (no data for non-students) were willing to punish the lowest possible offer while among Fijian villagers that fraction drops to one-third. Post-game interviews indicate that while participants in both places felt that people should give half of the stake, Fijians but not Americans felt that unilaterally rejecting or punishing would not be appropriate. In post-game interviews, Fijians don't even report a desire to punish (Henrich & Henrich 2014). Despite their unwillingness to punish low offers, Fijians make relatively high offers on both experiments. The lack of punishment in these experiments doesn't reflect a lack of sanctioning for norm violations in village life but rather a lack of fit between people's cultural psychology, which is adapted to their local institutions (underpinned by negative indirect reciprocity), and the experimental design.

Cultural evolutionary theory suggests that small communities like those in Fiji require different mechanisms to sustain cooperation than those necessary in large, anonymous societies. In tightly-knit communities, diffuse punishment of any kind risks the (1) threat of counter-punishment—revenge—against either the punisher or their family and (2) damaging a long-term relationship from which one cannot easily escape—Fijians are tied to their lands by customary rights. By contrast, in large anonymous societies with high levels of residential mobility and formal policing institutions for serious harms, these issues are mitigated and, as discussed, diffuse punishment can be sustained by a variety of mechanisms. Confirming these theoretical predictions in a global sample from 33 communities from 15 subsistence-oriented societies that include foragers, farmers and pastoralists, costly punishment by both second and third parties in one-shot anonymous interactions varies dramatically with the size of the community. To measure people's willingness to punish, their Minimum Acceptable Offer (MAO) was calculated for both the Ultimatum and Third-Party Punishment Games. MAO is the lowest offer amount that a person won't punish. As Figure 3 shows, populations with larger communities express a much greater willingness to engage in the costly punishment of those who violate fairness norms in both the UG and TPG (Henrich et al. 2010). Smaller communities mostly do not punish while in large communities a majority or plurality of people will punish anything but an equal offer. Unsurprisingly, communities with more third party punishment also make more equal offers to anonymous members of their community in Dictator Games (Henrich et al. 2006).

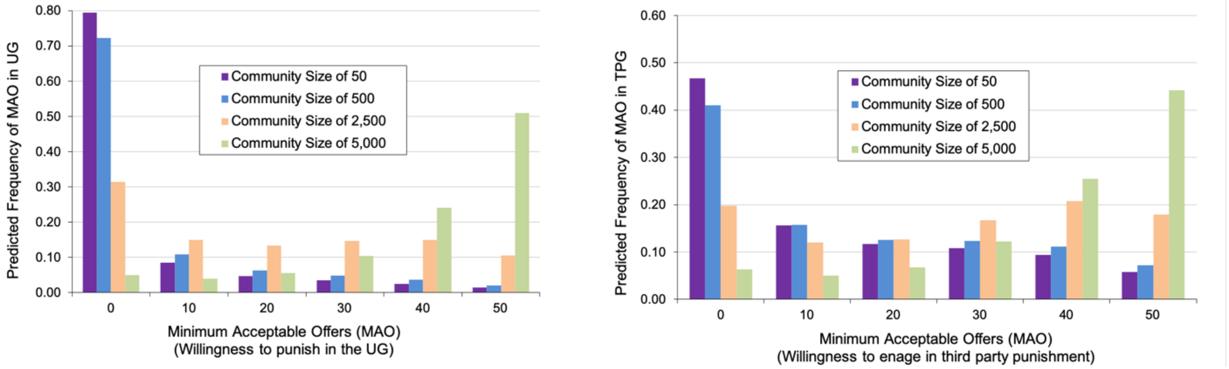

Figure 3. Predicted frequencies of MAOs across possible offer amounts for both the (A) Ultimatum Game and (B) Third Party Punishment Game. Predicted values are based on a fitted model that includes community size along with a host of control variables including demographics, schooling, income, wealth, household size and market integration. Adapted from Henrich et. al. (2010)

This line of theorizing, and now a substantial body of evidence including developmental and cross-cultural findings, suggests that when researcher study "human cooperation" in WEIRD societies using behavioral game experiments or similar methods, they are really studying the cultural psychology that has emerged in association with the spread of a particular constellation of institutions.

There is, however, an underappreciated issue with all models of large-scale cooperation discussed above: the problem of *equilibrium selection* (Box 1). As noted, these evolutionary models can sustain many different stable norms under identical conditions. A few of these norms are cooperative, in that they generate social benefits, but most are neutral or even socially costly (hurting others or the group as a whole). This raises a question: what kind of process can filter out the more cooperative norms from the multitude of other norms. Without some additional mechanism to 'select' the cooperative norms from all the other stable norms, cooperation would be quite rare. Theorists have proposed three kinds of equilibrium selection mechanisms to address the challenge. First, coalitions or powerful leaders might push social norms in ways that favor their own interests. The wealthy, for example, might use their political power over generations to push norms (or laws) to benefit themselves; for example, favoring low taxes or polygynous marriage (Singh et al. 2017). Second, some social norms are more stable than others to perturbations, so stochastic fluctuations and shocks—epidemics, floods, hurricanes, etc.—will tend to favor the most stable norms (Young 1998). Finally, competition among groups with different norms—different stable equilibria—will tend to favor the spread of group-beneficial norms (Boyd & Richerson 1990). These three processes can be integrated into models of multi-level cultural evolution.

Multi-level cultural evolution and cooperation

Thinking about individuals as nested into overlapping hierarchies of social groups has provided a powerful way to think about the pyramid of conflicts of interest between individuals within smaller groups and among smaller groups within larger populations. Competition among groups at lower levels can favor cooperation at higher levels. Nuclear families that manage to expand into clans beat independent nuclear families. Clans that bind themselves into tribes, through either age-sets or segmentary lineages, tend to beat lone clans. But, at each level, the interests of lower level groups can be at odds with larger formations—patrilineal clans within tribes compete for grazing lands, access to water holes and wives. This means stronger cooperation and greater solidarity at lower levels can be detrimental to cooperation at higher levels (Maynard Smith & Szathmáry 1999; Muthukrishna 2017).

Within multi-level structures, it's intergroup competition that drives the cultural evolution of cooperative norms, which can operate directly (e.g., norms for bravery in warfare) or indirectly by shaping the social networks or organization of groups (Henrich forthcoming). Importantly, intergroup competition need not take the form of violent conflict, though this has certainly been a salient form over human history (Bowles 2006; Wrangham & Glowacki 2012). Researchers are studying (at least) four additional forms of intergroup competition (Henrich 2016; Richerson et al. 2016):

1) **Prestige-biased group transmission**: Individuals and communities preferentially attend to and learn from more successful or prestigious groups. This causes social norms and beliefs to diffuse from more successful groups, firms or other communities to less successful ones and can drive the spread of more competitive institutions. When countries preferentially

copy the U.S. Constitution in setting up new governments, that's prestige-biased group transmission (Rockmore et al. 2018).

2) **Differential reproduction**: Norms can influence the rate at which individuals have children. Since children tend to share the norms of their community, any norms that increase birth rates or slow death rates will tend to spread. Some world religions, for example, have spread more rapidly due to their pronatalist norms: the Mormon polygyny and large families in the 19th century facilitated the rapid expansion of this religion (Daynes 2001).
3) **Differential migration**: Whenever possible, people will migrate from less prosperous communities to more prosperous ones. Since migrants, and especially their descendants, typically adopt the local social norms, beliefs and customs (Mesoudi et al. 2016), differential migration propels the spread of norms and institutions that generate prosperity and security, as more successful communities grow at the expense of less successful ones.
4) **Differential group survival without conflict**: In hostile environments, only groups with institutions that promote extensive cooperation and sharing can survive. Groups without such either retreat to more plentiful environments or significantly decline during droughts, hurricanes, eruptions or other shocks. The right norms and institutions allow groups to thrive in ecological niches where other groups cannot. Some groups succeed and others fail without the groups ever meeting each other.

To test these ideas empirically, researchers have drawn on multi-level models of the evolution of cooperation (Richerson et al. 2016; Zefferman & Mathew 2015). These models predict that intergroup competition can sustain greater cooperation when interacting groups maintain stable differences in social norms. Specifically, cooperation can be sustained when $R \cdot b > c$, where R = $CF_{ST}/(1-CF_{ST})$ and CF_{ST} is the ratio of the cultural variation between groups to the total cultural variation (Muthukrishna et al. 2020a). CF_{ST} measures how much of the individual differences in cooperative norms are structured into groups (for genetic evolution, this is F_{ST}). Working among four rural Kenyan populations, Handley and Mathew (2020) collected data from 759 individuals in different patrilineal clans across four tribes (ethno-linguistic groups). To assess variation in social norms, individuals were interviewed about 49 different practices. To assess cooperative inclinations and their parochial boundaries, participants responded to 16 vignettes in which a main actor either helped or didn't exploit a target individual. Instead of the abstract structures of economic games, the vignettes involved common circumstances from daily life in East Africa—cattle raiding, sharing water, grazing, lying, etc. The social identity of the target in the vignettes varied from a fellow clan member to someone from one of the other three tribal populations. As predicted by formal theory, Figure 4 shows that cooperative inclinations (the percentage of cooperative responses to the vignettes) rise as CF_{ST} between groups declines. The data predict that most of the fiercest intergroup competition should occur between tribes. Consistent with this, detailed studies among one of these populations, the Turkana, suggest that the moral circle ends at the tribal border: its bad to raid other Turkana, even if they are physically and socially distant, but not to raid surrounding non-Turkana (Mathew & Boyd 2011b). Sometimes it's even perceived as 'good' to harm other tribes.

A wide range of other research supports an important role for intergroup competition. This work includes laboratory studies that illustrate how introducing intergroup competition drives up cooperation in public goods games (Bornstein & Benyossef 1994; Saaksvuori et al. 2011), longitudinal field studies among hunter-gatherers that suggest how competitive interactions among bands may sustain food sharing (Smith et al. 2018), and natural experiments that demonstrate how increasing inter-firm competition can drive up impersonal trust and cooperation among strangers (Francois et al. 2018).

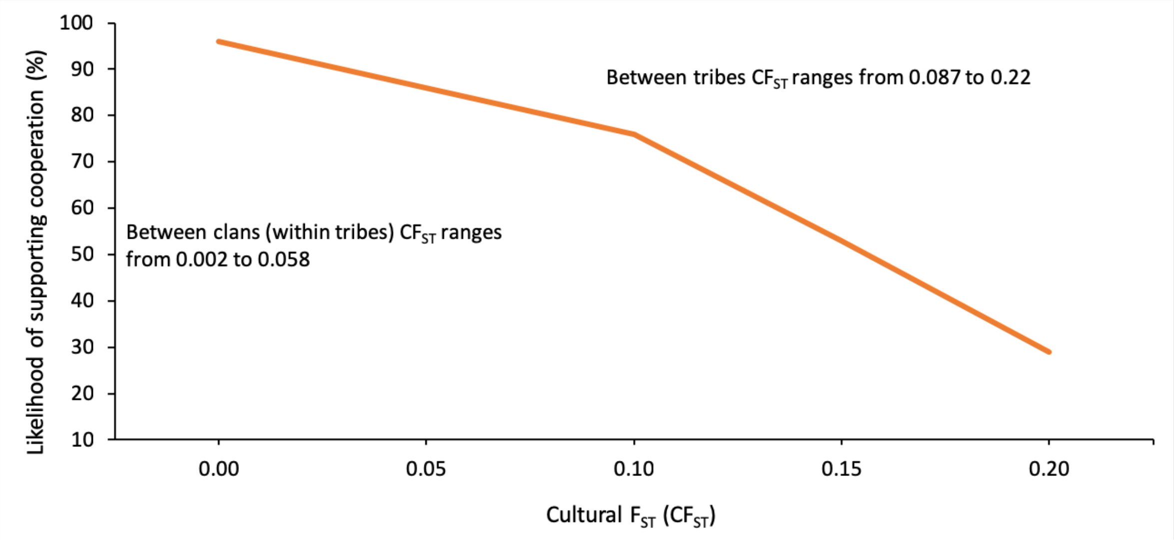

Figure 4. The structure of cultural variation creates conditions in which intergroup competition can favor greater parochial cooperation. The plot shows the relationship between CF_{ST} estimates based on 48 social norms with the extent of cooperation assessed using 16 vignettes with targets at different social distances. Adapted from Handley and Mathew (2020).

Some evolutionary psychologists have expressed concerns about any theory of cooperation that considers a role for intergroup competition or what is often termed "group selection" (Krasnow et al. 2016; Pinker 2012). This skepticism, unfortunately, largely arises from two related misunderstandings. First, such critiques often fail to appreciate that cultural evolutionary models involving intergroup competition usually solve the free-rider problem using purely within-group selective processes (not 'group selection'), such as those built on reputation, punishment and signaling (Boyd & Richerson 1990; Henrich 2004). Intergroup competition is only employed to tackle the equilibrium selection problem, not the free-rider problem (Box 1). So, it makes no sense to write as if explanations based on signaling, reputation and punishment are alternatives to those that include intergroup competition. Instead, those who put forth explanations rooted in these within-group mechanisms must explain how they address the equilibrium selection problem. Opposing equilibrium selection mechanisms like intergroup competition in favor of free-rider suppression mechanisms like signaling makes about as much sense as arguing for spark plugs over carburetors in explaining how combustion engines function.

A related, misunderstanding arises from importing theoretical insights about the operation of intergroup competition from models of genetic evolution. The well-established differences between cultural and genetic transmission mean that cultural evolution (see side bar) is more likely to create conditions favorable to intergroup competition. Cultural evolution is fast, noisy and non-vertical compared to genetic evolution (Boyd et al. 2011; Perreault 2012). Intergroup competition requires group differences; the impact of intergroup competition on genetic evolution is diminished when there is gene flow or migration between groups; these deplete the variation between groups and drives down F_{ST} values. If defectors migrate into groups of mostly cooperators, they can prosper and produce offspring who are also defectors. However, under cultural transmission, the children of immigrants are often culturally distinct from their parents (due to powerful non-vertical transmission) and culturally indistinguishable from the non-migrants around them. The children of immigrants, for example, will typically speak the local language without their parents accent, a cue of where they're acquiring their culture (Cohen 2012). If we, for example, compare the CF_{ST} values calculated by Mathew and Handley to the genetic equivalents for other African tribal populations, we find that Kenyan CF_{ST}'s are around 0.1-0.2 whereas genetic F_{ST}'s are around 0.002—a difference of two orders of magnitude in the potential role for intergroup competition. Qualitatively, this same pattern holds at the level of countries (Bell et al. 2009; Muthukrishna et al. 2020a; Richerson et al. 2016).

The above account suggests that individuals, and their genes, would have increasingly found themselves in groups governed by social norms, including many cooperative norms, maintained by mechanisms related to reputation, signaling and punishment. In light of this, researchers have argued that these cultural products—social norms and institutions—have long generated powerful social selection on our genes and thereby shaped our evolved psychology.

COEVOLUTIONARY PSYCHOLOGY

Cultural evolution and its products interact with genetic evolution to produce culture-gene coevolution. This process, considered to be largely theoretical speculation until only a few decades ago, has now emerged as central to understanding the selection pressures on hundreds of specific genes in our species (Laland et al. 2010). By generating increasingly complex tools (e.g. spear-throwers), food processing techniques (e.g., cooking), languages (e.g., larger vocabularies) and institutions (e.g., clans) over hundreds of thousands of years, cumulative cultural evolution has shaped the environments faced by our genes and thereby drove the genetic evolution of the uniquely human aspects of our bodies and minds. For example, our small stomachs, short colons and weak jaw muscles, compared to other primates, were only favored once fire and cooking had spread culturally in our species (Wrangham 2009). Our bodies rely on cooked food, yet we have no innate ability to cook or create fires. Thus, an increasing number of researchers argue that a proper evolutionary approach to human behavior and psychology requires considering the interaction of genes and culture over hundreds of thousands of years (Muthukrishna et al. 2018; Street et al. 2017).

The emergence of social norms, as a feature of our ancestral environments, may have created selection pressures on genes for various aspects of our species' psychology, which would have in turn strengthened the power of social norms (Henrich 2016).

SELF-DOMESTICATION AND NORM PSYCHOLOGY

Social norms can create powerful selection pressures on genes. As explained above, cultural evolution will often favor social norms that suppress aggression toward fellow group members and inhibit theft, rape, and other harms. Over evolutionary time, these processes would have also often assembled norms that supported food sharing, mutual aid, communal defense, and cooperative hunting. Norm violators would have initially been sanctioned in various ways, perhaps by losing skilled hunting partners, attractive mates, and valuable allies. When such sanctions fall short, modern hunter-gatherers readily escalate to ostracism, beatings, and even executions. Dominant individuals, or others unable to suppress aggressive reactions, would have been particularly likely to be executed in acts of coordinated punishment (Wrangham 2019). Such normative sanctions would have created genetic selection pressures favoring reduced reactive aggression, stronger self-control, and greater docility. These norms, by selecting for less reactive aggression, longer developmental windows for learning and greater self-control, may have favored a set of corresponding morphological changes including more juvenile faces and reduced brow ridges (Hare 2017).

To more effectively navigate a social world organized by norms, researchers have also proposed that our species has evolved a *norm psychology* that facilitates the rapid acquisition of, and adherence to, social norms (Chudek & Henrich 2010). Unlike other animals, we rapidly develop a norm ontology, approaching the social world as if its governed by rules even if we don't yet know those rules, and readily recognize that rule violations could (and should) have negative consequences. Testing this hypothesis, Rakoczy, Schmidt and colleagues have shown that young (German) children automatically assume that what they've seen others do in some novel situation is the 'correct way' of doing it (Rakoczy & Schmidt 2013; Schmidt & Tomasello 2012). Young children will try to precisely copy the protocol involved in some action; but, even if they themselves don't copy accurately, they'll often react negatively and seek to 'correct' those who use alternative methods. Children do this regardless of whether they have been told that there's a 'right way' to do something or whether they've seen anyone get corrected. This work, along with earlier research, suggests that children reliably develop an automatic tendency to infer the existence of social norms and correct norm-violators in a broad range of activities, from how to use toys to the proper size of charitable donations (Mischel & Liebert 1966).

As part of this norm psychology, evidence suggests that humans have evolved to—at least partially—internalize norms as context-specific motivations or frugal heuristics for navigating daily life (Henrich et al. 2005; Rand 2016). This internalization may have evolved for several reasons, including to minimize cognitive effort and/or to mitigate the decision-making challenges of considering reputational payoffs or penalties that only arrive in the future (and are thus discounted) compared to immediate payoffs from not complying with a costly norm now (Richerson & Henrich 2012). To empirically investigate norm internalization, researchers have integrated a range of experimental techniques, including decision-making under time pressure and brain imaging. When placed under time pressure, which limits the analysis of costs and benefits, people become more likely to behave in normative ways (Rand 2016; Yamagishi et al. 2017)—though a selection bias cannot be excluded (Bouwmeester et al. 2017). If the relevant norms are prosocial, people become more cooperative and fair-minded. Complementing this with the tools from neuroscience, research suggests that both complying with costly social norms and punishing norm violators (also at a personal cost) activates reward circuits, suggesting that complying and enforcing norms can become goals in themselves (Buckholtz et al. 2008; Buckholtz & Marois 2012).

Interdependent fitness and fusion

Because cultural evolution has created institutions that share costs, mitigate risks and diffuse benefits across groups, evolutionary theorists have hypothesized that culture may have strengthened genetic selection pressures for an *interdependence psychology* (Henrich forthcoming; Tomasello et al. 2012). To understand this, consider the food sharing norms that have developed among all known populations of mobile foragers. Imagine a small band of 5 fishers, their spouses and two children per couple (20 people in total). The fishing is challenging and luck plays a big role, so the fishers succeed on only 5% of all days. This means that each nuclear family will go without marine protein for a month during one out of every five months, on average. However, if they share their catch, the band will almost never go a month without fish (less than 0.05% of months). Interestingly, now that they are sharing, the survival of each individual is intertwined with everyone else. If Natalie the fisher dies, the chances that Stephanie and her family go a month without fish rises by a factor of four. Even worse, Natalie's absence increases the chances that one of the other fishers or their spouse will die in the coming years—poor nutrition leads to sickness, etc. If another fisher dies, or leaves the band because her spouse passes, each remaining person's chances of going a month without fish increases further as does the chances of someone else falling ill or dying. From an evolutionary point of view, social norms like those that create broad food sharing mean that an individual's fitness—their ability to survive and reproduce—is interwoven with the fitness of everyone else in the band. This entangles even band members who don't directly contribute to each other's welfare: if Stephanie's spouse nurses her back to health when she's ill, and Stephanie shares her catch with Natalie and her family, then Natalie needs to worry about Stephanie's spouse. Though food sharing norms represent one well-studied case of interdependence, the same point applies to other norms, such as those related to common defense. In fact, the threat posed by violent intergroup conflict may be the most important domain of interdependence and thus existential threats against one's group may represent a particularly important cue of interdependence (Navarrete & Fessler 2005)—giving rise to what has been called a coalitional psychology.

The upshot is that social norms can create communities in which every individual's health and survival depends on almost everyone else. Psychologically, this hypothesis proposes that natural selection has shaped people's minds to assess their degree of interdependence with others, and to use these assessments to motivate greater affiliation, personal concern, and support (Bowles et al. 2004). Cues of greater interdependence likely include eating together, sharing social ties, collaborating on joint projects, and co-experiencing traumatic events. And, though people continue to assess their degree of interdependence throughout their lives, many of these cues operate most powerfully on children, adolescents and young adults, when they are forming their life-long social networks (Bauer et al. 2014).

This interdependent psychology may create what psychologists have called identity fusion, a psychological package characterized by deep emotional bonds that create life-long, familial-like relationships (Swann & Buhrmester 2015). Shared trauma is a powerful cue of interdependence and thus interdependence psychology may explain the increase in prosociality observed among people who have been affected by war or violent attacks (Bauer et al. 2014, 2016; Buhrmester et al. 2015), and may even create the 'band of brothers' phenomena found in military units (Whitehouse et al. 2014). Interestingly, cultural evolution has figured out how to regularly evoke these psychological effects through terrifying rites of passage (Whitehouse & Lanman 2014) and potentially through ritualized forms of economic exchange that artificially create a greater sense of interdependence (Durkheim 1933).

CULTURAL EVOLUTIONARY PSYCHOLOGY

The approach we've presented here generates a range of psychological hypotheses, including predictions about both reliably developing aspects of human nature and patterns of variation among populations. Perhaps most important, this framework also provides a rich array of concepts and tools for generating additional hypotheses. Collections of social norms form institutions, which in turn create incentives that our minds adapt to, both during development (Figures 1 and 2) and over cultural evolutionary time as more successful motivations, strategies, heuristics, world views, socialization practices and decision-making biases proliferate. Better institutions, infused with custom-fit psychologies, can spread by the various processes discussed above to increase the scale and intensity of cooperation. This means that to understand contemporary psychological variation, we need to examine how societies have scaled up (and fallen apart) in different places and over millennia.

Kin-based Institutions

The most primordial of human institutions are those surrounding kinship, and in most societies over our species' history, these institutions have dominated social, political, and economic life (Murdock 1949). Formed by constellations of norms, kin-based institutions regulate and influence (1) the treatment of a large extended network of relatives, including distant cousins and affines (e.g. obligations to in-laws), (2) who marries whom (e.g. preferences for cousin marriage), (3) the inheritance of social identity (e.g. what's my clan?), (5) post-marital residence (where should newly married couples live?) and (4) economic interdependence (e.g. corporately-owned clan lands). Such norms are particularly powerful and highly stable because they anchor on, harness and extend, aspects of our evolved psychology, including those related to kin altruism, incest aversion, reciprocity and pair-bonding (Henrich 2016; McNamara & Henrich 2017), and thereby effectively shape the social networks within which people operate. After the origins of agriculture, fierce intergroup competition to control territory favored increasingly intensive forms of kinship that tied people together in tight interdependent webs that supported high-levels of parochial cooperation and solidarity toward one's kin group—toward one's clan, kindred or tribe (Henrich forthcoming; Zeng et al. 2018). With the rise of states, kin-based institutions were weakened, but kinship nevertheless remained the most important institution in people's lives.

While galvanizing cooperation at lower levels, powerful kin-based institutions inhibit the formation of voluntary associations, modern firms, and effective secular governing institutions. That is, they impede cooperation at higher levels and among strangers. This suggests that people from populations that have been dominated by intensive kin-based institutions will behave less cooperatively towards strangers, anonymous others, and impersonal organizations (e.g. the government). Two papers have recently tested these ideas using both global and regional datasets (Enke 2019; Schulz et al. 2019). Globally, using national-level data, Schulz et. al. show that populations with less intensive kin-based institutions contribute more to strangers in public goods games, engage less in anti-social (revenge based) punishment, and make more voluntary blood donations to anonymous strangers. Using first- and second-generation immigrants from different places both Enke and Schulz et. al confirm these same patterns using various survey-based measures of trust and fairness towards strangers. These analyses compare individuals living in the same country, but with different cultural origins.

If intensive kin-based institutions do indeed have substantial impacts on trust, fairness and cooperation toward strangers and anonymous others then this psychological question is transformed into a historical question: how can we account for the variation in the intensity of kin-based institutions around the world?

Ritual and Religion

Social scientists have long proposed a link between cooperation and religion (Wilson 2002; Wright 2009). Even in the smallest scale societies, ethnographers have argued that participation in communal rituals strengthens group solidarity and improved social harmony (Whitehouse & Lanman 2014). Recently, experimentalists have begun to put these ethnographic speculations to the test through both systematic field studies and laboratory experiments (Fischer & Xygalatas 2014). Laboratory studies, for example, have shown that synchronous movements, like dancing or marching, foster greater solidarity and more cooperation (Lang et al. 2017; Launay et al. 2016). Consistent with the multi-level account above, both ethnographic and historical studies reveal how intergroup competition has driven the diffusion of effective rituals and devotions (McNeill 1995; Sosis & Bressler 2003). This suggests that deep in our evolutionary history, intergroup competition was favoring social norms and rituals that increased cooperation.

However, because they evolved to bond face-to-face communities, group-bonding rituals would not have helped, and may have even hindered, the scaling up of cooperation to larger 'imagined communities' in which thousands of individuals interact, exchange and cooperate. To facilitate this degree of scaling up, researchers have argued that cultural evolution, by anchoring on our species' innate capacities to entertain the existence of supernatural agents, favored the emergence of increasingly powerful and morally concerned deities (or supernatural forces) who monitor and punish non-cooperative or anti-social actions, such as murder, theft or adultery (Norenzayan et al. 2016). Over time, beliefs about these beings evolved to increase their effectiveness: gods expanded their range of moral concerns (e.g., honesty towards strangers), ability to monitor norm-violators (e.g. mind-reading abilities, omniscience), and power to punish (e.g. controlling the afterlife). Here, consistent with models of social norms based on costly sanctioning, gods are turned into super-punishers who can confer costs in this life and the next.

A key psychological test of this hypothesis is whether people who believe in more powerful, moralizing gods are indeed more inclined to cooperate with co-religionists. Establishing this correlation, researchers have shown that individuals from diverse religious traditions who report stronger beliefs in more powerful moralizing gods are more fair-minded in experiments with anonymous (and distant) co-religionists (Lang et al. 2019) and more supportive of public goods (Atkinson & Bourrat 2011). To examine whether supernatural agents can indeed *cause* people to behave more cooperatively, many studies have shown that when primed with thoughts of god (Shariff et al. 2016; White et al. 2019), and specifically thoughts of supernatural punishment (Yilmaz & Bahçekapili 2016), believers become more fair-minded, cooperative and honest with strangers. Together with historical and cross-cultural data supporting the claim that gods became increasingly morally-concerned, powerful and punishing over historical time (Botero et al. 2014), this psychological evidence suggests that religions may have evolved culturally in ways that alter people's psychology and thereby permit the scaling up of societies.

Keeping in mind, as noted above, that cooperation at lower levels can undermine higher-level cooperation, it's worth considering how religions have shaped families. Beginning a few thousand years ago, some religions began to tinker with kin-based institutions. During late antiquity, for example, the branch of Christianity that evolved into the Roman Catholic Church developed a set of prohibitions and prescriptions about marriage and family that dissolved the intensive kin-based institutions of Europe, leaving primarily monogamous nuclear families by the end of the Middle

Ages. Thus, the relatively weak European kin-based institutions that can explain a large swath of the global variation in cooperation with strangers may be a consequence of the medieval Church's relentless and centuries long attack on traditional families (on cousin marriage, polygamy, clans, etc.). Strikingly, the duration that populations around the globe have spent under the Medieval Catholic Church predicts 24 different psychological measures, including individualism, conformity, analytic thinking, universal moral principles, impersonal honesty, and cooperation with strangers. The psychological impacts of these religiously-motivated changes in the family may have opened the door to the proliferation of impersonal markets, voluntary communities (charter towns), residential mobility and representative governments (Schulz et al. 2019).

CONCLUSION

We began by introducing five key features of human cooperation that challenge standard evolutionary and economic accounts of cooperation. To address these, we presented an extended evolutionary synthesis, which considers both genetic and cultural evolution as well as their interaction, and evaluated leading hypotheses in light of the available evidence. Now, let's return to our opening challenges.

(1) **Ultrasociality**: Genetic evolutionary mechanisms, such as kin-based altruism and direct reciprocity, may be adequate to explain cooperation in other animals; but, tackling human ultrasociality requires understanding our second system of inheritance—culture—and the ways that it has altered our psychology, suppressed our reactive aggression, enhanced our capacity for internalizing norms and driven our genetic evolution in several ways. Culture is what has domesticated our species.

(2) **Differences in the domains of cooperation**: The domains of cooperation vary across societies because, at least in part, social norms vary (e.g., norms for raiding, food sharing, etc.). If a population has no social norms prescribing recycling, tithing, or tipping, people don't generally engage in such costly behaviors.

(3) **Differences in the scale and intensity of cooperation across populations:** The scale and intensity of human cooperation varies dramatically across societies because it has been heavily influenced by cultural evolution, driven by the effect of intergroup competition on institutions. The intensity of intergroup competition has varied dramatically across populations for a variety of ecological, climatic, geographic and historical reasons (Turchin 2015). This competition has selected for more prosocial norms and institutions and in some cases, such as the Catholic Church's weakening of kin-bonds (Schulz et al. 2019), operated by undermining the effectiveness of lower-scale mechanisms.

(4) Rapid rise in the scale of cooperation: Beginning about 12,000 years ago, the origins of intensive food production and the stabilization of global climates dramatically increased the intensity of intergroup competition and began driving cultural evolution to scale up cooperation (Turchin 2015). This process continues to this day.

(5) Non-cooperative and maladaptive behaviors sustained by the same mechanisms as cooperation: Because cultural evolutionary mechanisms related to punishment, signaling and reputation can stabilize any costly norm, even norms that are costly for both the individual and group (e.g., female genital cutting), non-cooperative and maladaptive behavior can persist for long periods. Intergroup competition provides a process that filters out group-damaging norms, but it can be slow and incomplete, especially when many such norms are tightly intertwined with other important cooperative norms.

Understanding the origins and psychology of human cooperation is an exciting and rapidly developing enterprise. Those interested in engaging with this grand question should consider three elements of this endeavor: (1) theoretical frameworks, (2) diverse methods, and (3) history. To the first, the extended evolutionary framework we described comes with a rich body of theories and hypotheses as well as tools for developing new theories, about both human nature and cultural psychology. A relatively small amount of training in formal modeling is required to engage with the primary literature (McElreath & Boyd 2007). Second, the nature of human cooperation demands cross-cultural, comparative and developmental approaches that integrate experiments, observation, and ethnography. Haphazard cross-country cyber sampling is less efficient than systematic tests with populations based on theoretical predictions. Finally, the evidence makes it clear that as norms evolve over time, so does our psychology; historical differences can tell us a lot about contemporary psychological patterns. This means that researchers need to think about psychology from a historical perspective and begin to devise ways to bring history and psychology together (Muthukrishna et al. 2020b).

REFERENCES

Algan Y, Cahuc P. 2013. Trust and growth. *Annual Review of Economics*. 5(1):521–49

Allison P. 1997. Cultural Relatedness Under Oblique and Horizontal Transmission Rules. *Ethology and Sociobiology*. 13:153–69

Alvard M. 2009. Kinship and Cooperation: The Axe Fight Revisited. *Human Nature*. 20(4):394–416

Aoki K, Feldman MW. 2014. Evolution of learning strategies in temporally and spatially variable environments: A review of theory. *Theor Popul Biol Theor Popul Biol*. 91:3–19

Atkinson QD, Bourrat P. 2011. Beliefs about God, the afterlife and morality support the role of supernatural policing in human cooperation. *Evolution and Human Behavior*. 32(1):41–49

Axelrod R, Hamilton WD. 1981. The evolution of cooperation. *Science*. 211(1):390–96

Balliet D, Van Lange P. 2012. Trust, punishment and cooperation across 18 societies: A meta-analysis. *Perspectives on Psychological Science*

Bandura A. 1977. *Social Learning Theory*. Englewood Cliffs, N.J: Prentice Hall

Bandura A, Kupers CJ. 1964. Transmission of patterns of self-reinforcement through modeling. *Journal of Abnormal & Social Psychology*. 69(1):1–9

Barclay P. 2011. Competitive helping increases with the size of biological markets and invades defection. *Journal of Theoretical Biology*. 281(1):47–55

Barrett HC, Broesch J. 2012. Prepared social learning about dangerous animals in children. *Evolution and Human Behavior*. 33(5):499–508

Barrett L, Dunbar R, Lycett J. 2002. *Human Evolutionary Psychology*. Princeton: Princeton University Press

Bauer M, Blattman C, Chytilová J, Henrich J, Miguel E, Mitts T. 2016. Can war foster cooperation? *Journal of Economic Perspectives*. 30(3):249–74

Bauer M, Cassar A, Chytilová J, Henrich J. 2014. War's enduring effects on the development of egalitarian motivations and in-group biases. *Psychological Science*. 25(1):47–57

Bell AV, Richerson PJ, McElreath R. 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *P Natl Acad Sci USA*. 106(42):17671–74

Belot M, Crawford VP, Heyes C. 2013. Players of Matching Pennies automatically imitate opponents' gestures against strong incentives. *Proceedings of the National Academy of Sciences of the United States of America*. 110(8):2763–68

Berns GS, Capra CM, Moore S, Noussair C. 2010. Neural mechanisms of the influence of popularity on adolescent ratings of music. *NeuroImage*. 49(3):2687–96

Bhui R, Chudek M, Henrich J. 2019. How exploitation launched human cooperation. *Behavioral Ecology and Sociobiology*. 73(6):

Birch LL. 1987. Children's food preferences: Developmental patterns and environmental influences. *Annals of Child Development*. 4:171–208

Blake PR, Corbit J, Callaghan TC, Warneken F. 2016. Give as I give: Adult influence on children's giving in two cultures. *Journal of Experimental Child Psychology*. 152:149–60

Blake PR, McAuliffe K, Corbit J, Callaghan TC, Barry O, et al. 2015a. The ontogeny of fairness in seven societies. *Nature*. 528(7581):258–61

Blake PR, Rand DG, Tingley D, Warneken F. 2015b. The shadow of the future promotes cooperation in a repeated prisoner's dilemma for children. *Sci Rep*. 5(1):14559

Bornstein G, Benyossef M. 1994. Cooperation in Intergroup and Single-Group Social Dilemmas. *J Exp Soc Psychol*. 30(1):52–67

Botero CA, Gardner B, Kirby KR, Bulbulia J, Gavin MC, Gray RD. 2014. The ecology of religious beliefs. *Proceedings of the National Academy of Sciences*. 111(47):16784–89

Bouwmeester S, Verkoeijen PPJL, Aczel B, Barbosa F, Bègue L, et al. 2017. Registered Replication Report: Rand, Greene, and Nowak (2012). *Perspectives on Psychological Science*. 12(3):527–42

Bowles S. 2006. Group competition, reproductive leveling, and the evolution of human altruism. *Science (New York, N.Y.)*. 314(5805):1569–72

Bowles S, Choi J-K, Hopfensitz A. 2004. The coeveolution of individual behaviors and group level instituitons. *Journal of Theoretical Biology*. 223(2):135–47

Boyd R, Gintis H, Bowles S. 2010. Coordinated Punishment of Defectors Sustains Cooperation and Can Proliferate When Rare. *Science*. 328(5978):617–20

Boyd R, Mathew S. 2014. The evolution of language may require third-party monitoring and sanctions. . 1–17

Boyd R, Richerson P. 1976. A simple dual inheritance model of the conflict between social and biological evolution. . 11(3):

Boyd R, Richerson PJ. 1985. *Culture and the Evolutionary Process*. Chicago, IL: University of Chicago Press

Boyd R, Richerson P. 1988. The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology*. 132:337–56

Boyd R, Richerson PJ. 1990. Group Selection Among Alternative Evolutionarily Stable Strategies. *Journal of Theoretical Biology*. 145:331–42

Boyd R, Richerson P. 1992. Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups. *Ethology & Sociobiology*. 13(3):171–95

Boyd R, Richerson PJ, Henrich J. 2011. Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behavioral Ecology and Sociobiology*. 65(3):431–44

Brosnan SF, Silk JB, Henrich J, Mareno MC, Lambeth SP, Schapiro SJ. 2009. Chimpanzees (Pan troglodytes) do not develop contingent reciprocity in an experimental task. *Anim Cogn Anim Cogn*. 12(4):587–97

Buckholtz JW, Asplund CL, Dux PE, Zald DH, Gore JC, et al. 2008. The neural correlates of third-party punishment. *Neuron*. 60(5):930–40

Buckholtz JW, Marois R. 2012. The roots of modern justice: cognitive and neural foundations of social norms and their enforcement. *Nature neuroscience*. 15(5):655–61

Buhrmester MD, Fraser WT, Lanman JA, Whitehouse H, Swann WB. 2015. When terror hits home: Identity fused Americans who saw Boston bombing victims as "family" provided aid. *Self and Identity*. 14(3):253–70

Camerer C. 2003. *Behavior Game Theory: Experiments in Strategic Interaction*. Princeton: Princeton University Press

Campbell DT. 1983. *The Two Distinct Routes beyond Kin Selection to Ultrasociality: Implications for the Humanities and Social Sciences*. New York: Academic Press

Casler K, Terziyan T, Greene K. 2009. Toddlers view artifact function normatively. *Cognitive Development*. 24(3):240–47

Cavailli-Sforza LL, Feldman M. 1981. *Cultural Transmission and Evolution*. Princeton: Princeton University Press

Cheng JT, Anderson C, Tenney ER, Brion S, Moore DA, Logg JM. 2017. The social contagion of overconfidence

Chernyak N, Leimgruber KL, Dunham YC, Hu J, Blake PR. 2019. Paying Back People Who Harmed Us but Not People Who Helped Us: Direct Negative Reciprocity Precedes Direct Positive Reciprocity in Early Development. *Psychol Sci*. 30(9):1273–86

Chudek M, Brosseau P, Birch S, Henrich J. 2013. Culture-gene coevolutionary theory and children's selective social learning. In *The Development of Social Cognition*, eds. M Banaji, S Gelman. New York: Oxford

Chudek M, Henrich J. 2010. Culture-Gene Coevolution, Norm-Psychology, and the Emergence of Human Prosociality. *Trends in Cognitive Sciences*. 15(5):218–26

Cohen E. 2012. The Evolution of Tag-Based Cooperation in Humans: The Case for Accent. *Current Anthropology*. 53(5):588–616

Creanza N, Kolodny O, Feldman MW. 2017. Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. *Journal of the Royal Society Interface*. 14(130):1–11

Curry OS, Mullins DA, Whitehouse H. 2019. Is It Good to Cooperate? Testing the Theory of Morality-as-Cooperation in 60 Societies. *Current Anthropology*. 60(1):47–69

Daynes KM. 2001. *More Wives than One : Transformation of the Mormon Marriage System, 1840-1910*. Urbana: University of Illinois Press

de Waal FBM, Leimgruber K, Greenberg AR. 2008. Giving is self-rewarding for monkeys. *Proceedings of the National Academy of Sciences*. 105(36):13685–89

Dean LG, Vale GL, Laland KN, Flynn E, Kendal RL. 2014. Human cumulative culture: A comparative perspective. *Biological Reviews*. 89(2):284–301

Diamond JM. 1997. *Guns, Germs, and Steel: The Fates of Human Societies*. New York: W.W. Norton & Co.

Dunbar RIM, Clark A, Hurst NL. 1995. Conflict and cooperation among the Vikings: Contingent behavioral decisions. *Ethology and Sociobiology*. 16(3):233–46

Durham WH. 1991. *Coevolution : Genes, Culture, and Human Diversity*. Stanford, Calif: Stanford University Press

Durkheim E. 1933. *The Division of Labor in Society*. New York: Free Press

Eisenberg N, Mussen PH. 1989. *The Roots of Prosocial Behavior in Children*. Cambridge ; New York: Cambridge University Press

Engelmann JM, Herrmann E. 2016. Chimpanzees Trust Their Friends. *Current Biology*. 26(2):252–56

Engelmann JM, Herrmann E, Tomasello M. 2012. Five-Year Olds, but Not Chimpanzees, Attempt to Manage Their Reputations. *Plos One*. 7(10):

Engelmann JM, Herrmann E, Tomasello M. 2015. Chimpanzees trust conspecifics to engage in low-cost reciprocity. *Proceedings of the Royal Society B: Biological Sciences*. 282:20142803

Enke B. 2019. Kinship, Cooperation, and the Evolution of Moral Systems*. *The Quarterly Journal of Economics*. 134(2):953–1019

Ensminger J, Henrich J, eds. 2014. *Experimenting with Social Norms: Fairness and Punishment in Cross-Cultural Perspective*. New York: Russell Sage Press

Fehr E, Fischbacher U. 2003. Third Party Sanction and Social Norms. *Evolution and Human Behavior*. 25(2004):63–87

Fehr E, Gachter S. 2002. Altruistic punishment in humans. *Nature*. 415(6868):137–40

Feldman MW, Cavalli-Sforza LL. 1976. Cultural and biological evolutionary processes, selection for a trait under complex transmission. *Theoretical Population Biology*. 9(2):238–59

Fischer R, Xygalatas D. 2014. Extreme Rituals as Social Technologies. *Journal of Cognition and Culture*. 14:345–55

Fiske A. 1991. *Structures of Social Life*. New York: Free Press

Fowler JH, Christakis NA. 2010. Cooperative behavior cascades in human social networks. *Proceedings of the National Academy of Sciences of the United States of America*. 107(12):5334–38

Francois P, Fujiwara T, van Ypersele T. 2018. The Origins of Human Pro-Sociality: A Test of Cultural Group Selection on Economic Data and in the Laboratory. *Scientific Advances*. (September):1–10

Frank S. 1998. *Foundations of Social Evolution*. Princeton: Princeton University Press

Gächter S, Nosenzo D, Renner E, Sefton M. 2012. Who makes a good leader? Cooperativeness, optimism, and leading-by-example. *Economic Inquiry*. 50(4):953–67

Gächter S, Renner E. 2018. Leaders as role models and 'belief managers' in social dilemmas. *Journal of Economic Behavior & Organization*. 154:321–34

Garvert MM, Moutoussis M, Kurth-Nelson Z, Behrens TEJ, Dolan RJ. 2015. Learning-Induced Plasticity in Medial Prefrontal Cortex Predicts Preference Malleability. *Neuron*. 85(2):418–28

Gintis H, Smith EA, Bowles S. 2001. Costly signaling and cooperation. *J Theor Biol J Theor Biol*. 213(1):103–19

Gomes CM, Mundry R, Boesch C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*. 276(1657):699–706

Gowdy J, Krall L. 2016. The economic origins of ultrasociality. *Behavioral and Brain Sciences*. 39:

Greif ML, Nelson DGK, Keil FC, Gutierrez F. 2006. What do children want to know about animals and artifacts? Domain-specific requests for information. *Psychological Science*. 17(6):455–59

Gurven M, Stieglitz J, Hooper PL, Gomes C, Kaplan H. 2012. From the womb to the tomb: The role of transfers in shaping the evolved human life history. *Experimental Gerontology*. 47(10):807–13

Hamilton WD. 1964. The genetical evolution of social behavior I. *Journal of Theoretical Biology*. 7:1–16

Handley C, Mathew S. 2020. Human large-scale cooperation as a product of competition between cultural groups. *Nature Communications*. 11(1):702

Hare B. 2017. Survival of the Friendliest: *Homo sapiens* Evolved via Selection for Prosociality. *Annual Review of Psychology*. 68(1):155–86

Harris PL. 2012. *Trusting What You're Told : How Children Learn from Others*. Cambridge, Mass.: Belknap Press of Harvard University Press

Harris PL, Corriveau KH. 2011. Young children's selective trust in informants. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 366(1567):1179

Hauser OP, Hendriks A, Rand DG, Nowak MA. 2016. Preserving the global commons. *Nature Publishing Group*. 1–44

Henrich J. forthcoming. *The WEIRDest People in the World: How the West Became Psychologically Peculiar and Particularly Prosperous*. New York: Farrar, Straus and Giroux

Henrich J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior & Organization*. 53:3–35

Henrich J. 2009. The evolution of costly displays, cooperation and religion. Credibility enhancing displays and their implications for cultural evolution. *Evolution and Human Behavior*. 30(4):244–60

Henrich J. 2016. *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter*. Princeton: Princeton University Press

Henrich J, Boyd R. 2001. Why People Punish Defectors: Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology*. 208(1):79–89

Henrich J, Boyd R. 2002. On Modeling Cultural Evolution: Why replicators are not necessary for cultural evolution. *Journal of Cognition and Culture*. 2(2):87–112

Henrich J, Boyd R. 2008. Division of labor, economic specialization, and the evolution of social stratification. *Current Anthropology*. 49(4):715–24

Henrich J, Boyd R, Bowles S, Camerer C, Fehr E, et al. 2005. "Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*. 28(6):795–815; discussion 815-55

Henrich J, Boyd R, Bowles S, Gintis H, Camerer C, et al. 2001. In search of Homo economicus: Experiments in 15 Small-Scale Societies. *American Economic Review*. 91:73–78

Henrich J, Boyd R, Richerson PJ. 2008. Five misunderstandings about cultural evolution. *Human Nature-an Interdisciplinary Biosocial Perspective*. 19(2):119–37

Henrich J, Chudek M, Boyd R. 2015. The big man mechanism: How prestige fosters cooperation and creates Prosocial leaders. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 370(1683):

Henrich J, Ensminger J, McElreath R, Barr A, Barrett C, et al. 2010. Market, religion, community size and the evolution of fairness and punishment. *Science*. 327:1480–84

Henrich J, Henrich N. 2010. The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society B: Biological Sciences*. 277(1701):3715–24

Henrich J, Henrich N. 2014. Fairness without punishment: behavioral experiments in the Yasawa Island, Fiji. In *Experimenting with Social Norms: Fairness and Punishment in Cross-Cultural Perspective*, eds. J Ensminger, J Henrich. New York: Russell Sage Press

Henrich J, McElreath R, Barr A, Ensminger J, Barrett C, et al. 2006. Costly punishment across human societies. *Science*. 312(5781):1767–70

Henrich J, Tennie C. 2017. Cultural Evolution in Chimpanzees and Humans. In *Chimpanzees and Human Evolution*, eds. M Muller, R Wrangham, D Pilbream. Cambridge: Harvard University Press

Henrich N, Henrich J. 2007. *Why Humans Cooperate: A Cultural and Evolutionary Explanation*. Oxford: Oxford University Press

Herrmann B, Thöni C, Gächter S. 2008. Antisocial punishment across societies. *Science*. 319(5868):1362–67

Hill KR, Walker RS, Božičević M, Eder J, Headland T, et al. 2011. Co-Residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure. *Science*. 331(6022):1286–89

House BR. 2017. Diverse ontogenies of reciprocal and prosocial behavior: cooperative development in Fiji and the United States. *Dev Sci*. 20(6):e12466

House BR, Henrich J, Brosnan SF, Silk JB. 2012. The ontogeny of human prosociality: behavioral experiments with children aged 3 to 8. *Evolution and Human Behavior*. 33(4):291–308

House BR, Henrich J, Sarnecka B, Silk JB. 2013a. The development of contingent reciprocity in children. *Evolution and Human Behavior*. 34(2):86–93

House BR, Kanngiesser P, Barrett HC, Broesch T, Cebioglu S, et al. 2019. Universal norm psychology leads to societal diversity in prosocial behaviour and development. *Nature Human Behaviour*

House BR, Silk JB, Henrich J, Barrett HC, Scelza BA, et al. 2013b. Ontogeny of prosocial behavior across diverse societies. *Proceedings of the National Academy of Sciences*. 110:14586–91

Hruschka D, Henrich J. 2006. Friendship, Cliquishness, and the Emergence of Cooperation. *Journal of Theoretical Biology*. 239(1):1–15

Hruschka DJ, Efferson C, Jiang T, Falletta-Cowden A, Sigurdsson S, et al. 2014. Impartial institutions, pathogen stress and the expanding social network. *Human Nature*. 25(4):567–79

Jaeggi AV, Burkart JM, Van Schaik CP. 2010. On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 365(1553):2723–35

Jaeggi AV, Gurven M. 2013. Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*. 280(1768):20131615–20131615

Jensen K, Call J, Tomasello M. 2007a. Chimpanzees are rational maximizers in an ultimatum game. *Science*. 318(5847):107–9

Jensen K, Call J, Tomasello M. 2007b. Chimpanzees are vengeful but not spiteful. *Proceedings of the National Academy of Sciences of the United States of America*. 104(32):13046–50

Johnson A. 2003. *Families of the Forest: Matsigenka Indians of the Peruvian Amazon*. Berkeley: University of California

Jordan JJ, Hoffman M, Bloom P, Rand DG. 2016. Third-party punishment as a costly signal of trustworthiness. *Nature*. 530(7591):473–76

Jordan JJ, McAuliffe K, Warneken F. 2014. Development of in-group favoritism in children's third-party punishment of selfishness. *Proceedings of the National Academy of Sciences*. 111(35):12710–15

Kramer KL. 2010. Cooperative Breeding and its Significance to the Demographic Success of Humans. *Annu Rev Anthropol*. 39:417–36

Krasnow MM, Delton AW, Cosmides L, Tooby J. 2016. Looking Under the Hood of Third-Party Punishment Reveals Design for Personal Benefit. *Psychological Science*

Kuhlmeier VA, Dunfield KA, Oâ€™Neill AC. 2014. Selectivity in early prosocial behavior. *Front. Psychol.* 5:

Lachmann M, Bergstrom CT. 2004. The disadvantage of combinatorial communication. *Proceedings of the Royal Society of London Series B-Biological Sciences*. 271(1555):2337–43

Laland KN, Odling-Smee J, Myles S. 2010. How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics*. 11(2):137–48

Lang M, Bahna V, Shaver JH, Reddish P, Xygalatas D. 2017. Sync to link: Endorphin-mediated synchrony effects on cooperation. *Biological Psychology*. 127(March):191–97

Lang M, Purzycki BG, Apicella CL, Atkinson QD, Bolyanatz A, et al. 2019. Moralizing gods, impartiality and religious parochialism across 15 societies. *Proceedings of the Royal Society B: Biological Sciences*. 286(1898):20190202

Langergraber KE. 2012. Cooperation among Kin. In *The Evolution of Primate Societies*, eds. JC Mitani, J Call, PM Kappeler, RA Palombit, JB Silk. Chicago: The University of Chicago Press

Launay J, Tarr B, Dunbar RIM. 2016. Synchrony as an adaptive mechanism for large-scale human social bonding. *Ethology*. 122(10):779–89

Legare CH, Souza AL. 2014. Searching for control: Priming randomness increases the evaluation of ritual efficacy. *Cognitive Science*. 38(1):152–61

Leimar O, Hammerstein P. 2001. Evolution of cooperation through indirect reciprocity. *Proceedings: Biological Sciences*. 268(1468):745–53

Lorberbaum JP, Bohning DE, Shastri A, Sine LE. 2002. Are there really no evolutionary stable strategies in the iterated prisoner's dilemma? *Journal of Theoretical Biology*. 214:155–69

Mackie G. 1996. Ending Footbinding and Infibulation: A Convention Account. *American Sociological Review*. 61(6):999–1017

Mathew S, Boyd R. 2011a. Punishment sustains large-scale cooperation in prestate warfare. *Proceedings of the National Academy of Sciences of the United States of America*. 108(28):11375–80

Mathew S, Boyd R. 2011b. Punishment sustains large-scale cooperation in prestate warfare. *Proceedings of the National Academy of Sciences of the United States of America*. 108(28):11375–80

Mathew S, Boyd R, van Veelen M. 2013. Human cooperation among kin and close associates may require enforcement of norms by third parties. In *Cultural Evolution*, eds. PJ Richerson, MH Christainsen. Cambridge, MA: MIT Press

Maynard Smith J, Szathmáry E. 1999. *The Origins of Life : From the Birth of Life to the Origin of Language*. Oxford ; New York: Oxford University Press

McAuliffe K, Jordan JJ, Warneken F. 2015. Costly third-party punishment in young children. *Cognition*. 134:1–10

McElreath R. 2003. Reputation and the Evolution of Conflict. *Journal of Theoretical Biology*. 220:345–57

McElreath R, Boyd R. 2007. *Mathematical Models of Social Evolution: A Guide for the Perplexed*. Chicago ; London: University of Chicago Press

McElreath R, Boyd R, Richerson PJ. 2003. Shared norms and the evolution of ethnic markers. *Current Anthropology*. 44(1):122–29

McNally L, Brown SP, Jackson AL. 2012. Cooperation and the evolution of intelligence. *P Roy Soc B-Biol Sci P Roy Soc B-Biol Sci*. 279(1740):3027–34

McNally L, Jackson AL. 2013. Cooperation creates selection for tactical deception. *Proceedings of the Royal Society B-Biological Sciences*. 280(1762):

McNamara RA, Henrich J. 2017. Kin and kinship psychology both influence cooperative coordination in Yasawa, Fiji. *Evolution and Human Behavior*. 38(2):197–207

McNeill WH. 1995. *Keeping Together in Time: Dance and Drill in Human History*. Cambridge, Mass.: Harvard University Press

Melis AP, Grocke P, Kalbitz J, Tomasello M, San Martín R, et al. 2016. One for You, One for Me: Humans Unique Turn-Taking Skills. *Psychological Science*. (January):nsw026

Melis AP, Hare B, Tomasello M. 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour*. 76(3):951–62

Mesoudi A, Magid K, Hussain D. 2016. How do people become W.E.I.R.D.? Migration reveals the cultural transmission mechanisms underlying variation in psychological processes. *PLoS ONE*. 11(1):1–17

Mesoudi A, Whiten A, Laland KN. 2006. A science of culture: Clarifications and extensions. *Behavioral and Brain Sciences*. 29(4):366–83

Mischel W, Liebert RM. 1966. Effects of discrepancies between observed and imposed reward criteria on their acquisition and transmission. *Journal of Personality and Social Psychology*. 3:45–53

Morgan TJH, Rendell LE, Ehn M, Hoppitt W, Laland KN. 2012. The evolutionary basis of human social learning. *Proceedings of the Royal Society B-Biological Sciences*. 279(1729):653–62

Murdock GP. 1949. *Social Structure*. New York: Macmillan

Muthukrishna M. 2017. Corruption, Cooperation, and the Evolution of Prosocial Institutions. *SSRN Journal*

Muthukrishna M, Bell AV, Henrich J, Curtin CM, Gedranovich A, et al. 2020a. Beyond Western, Educated, Industrial, Rich, and Democratic (WEIRD) Psychology: Measuring and Mapping Scales of Cultural and Psychological Distance. *Psychol Sci*. 095679762091678

Muthukrishna M, Doebeli M, Chudek M, Henrich J. 2018. The Cultural Brain Hypothesis: How culture drives brain expansion, sociality, and life history. *PLOS Computational Biology*. 14(11):e1006504

Muthukrishna M, Francois P, Pourahmadi S, Henrich J. 2017. Corrupting cooperation and how anti-corruption strategies may backfire. *Nature Human Behaviour*. 1(7):0138

Muthukrishna M, Henrich J. 2019. A problem in theory. *Nature Human Behaviour*. 9

Muthukrishna M, Henrich J, Slingerland E. 2020b. Psychology as a Historical Science. *Annual Review of Psychology*

Muthukrishna M, Morgan TJH, Henrich J. 2016. The when and who of social learning and conformist transmission. *Evolution and Human Behavior*. 37(1):10–20

Naber M, Pashkam MV, Nakayama K. 2013. Unintended imitation affects success in a competitive game. *Proceedings of the National Academy of Sciences of the United States of America*. 110(50):20046–50

Navarrete CD, Fessler DMT. 2005. Normative Bias and Adaptive Challenges: A Relational Approach to Coalitional Psychology and a Critique of Terror Management Theory. *Evolutionary Psychology*. 3(1):147470490500300

Norenzayan A, Shariff AF, Gervais WM, Willard AK, McNamara RA, et al. 2016. The cultural evolution of prosocial religions. *Behavioral and Brain Sciences*. 39:1–86

O'Gorman R, Henrich J, Van Vugt M. 2009. Constraining free riding in public goods games: designated solitary punishers can sustain human cooperation. *P R Soc B*. 276(1655):323–29

Olson KR, Spelke ES. 2008. Foundations of cooperation in young children. *Cognition*. 108(1):222–31

Panchanathan K, Boyd R. 2004. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature*. 432:499–502

Perreault C. 2012. The Pace of Cultural Evolution. *PLoS ONE*. 7(9):e45150

Pinker S. 2012. *The False Allure of Group Selection*. http://edge.org

Purzycki BG, Apicella CL, Atkinson QD, Cohen E, McNamara RA, et al. 2016. Moralistic gods, supernatural punishment and the expansion of human sociality. *Nature*. 530(7590):327–30

Rakoczy H, Schmidt MFH. 2013. The Early Ontogeny of Social Norms. *Child Development Perspectives*. 7(1):17–21

Rand DG. 2016. Cooperation, Fast and Slow: Meta-Analytic Evidence for a Theory of Social Heuristics and Self-Interested Deliberation. *Psychological Science*. 27(9):1192–1206

Rendell L, Fogarty L, Hoppitt WJE, Morgan TJH, Webster MM, Laland KN. 2011. Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*. 15(2):68–76

Richerson P, Boyd R. 1998. The Evolution of Ultrasociality. In *Indoctrinability, Ideology and Warfare*, eds. I Eibl-Eibesfeldt, FK Salter, pp. 71–96. New York: Berghahn Books

Richerson PJ, Baldini R, Bell A, Demps K, Frost K, et al. 2016. Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence. *Behavioral and Brain Sciences*. 39:1–46

Richerson PJ, Henrich J. 2012. Tribal Social Instincts and the Cultural Evolution of Institutions to Solve Collective Action Problems. *Cliodynamics*. 3(1):38–80

Riedl K, Jensen K, Call J, Tomasello M. 2012. No third-party punishment in chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*. 109(37):14824–29

Rochat P, Dias MDG, Guo Liping, Broesch T, Passos-Ferreira C, et al. 2009. Fairness in Distributive Justice by 3- and 5-Year-Olds Across Seven Cultures. *Journal of Cross-Cultural Psychology*. 40(3):416–42

Rockmore DN, Fang C, Foti NJ, Ginsburg T, Krakauer DC. 2018. The cultural evolution of national constitutions. *Journal of the Association for Information Science and Technology*. 69(3):483–94

Rosenthal TL, Zimmerman BJ. 1978. Social learning and cognition. New York: Academic Press

Rushton JP. 1975. Generosity in children: Immediate and long term effects of modeling, preaching, and moral judgement. *Journal of Personality and Social Psychology*. 31:459–66

Rushton JP, Campbell AC. 1977. Modeling, vicarious reinforcement and extraversion on blood donating in adults. Immediate and long-term effects. *European Journal of Social Psychology*

Saaksvuori L, Mappes T, Puurtinen M. 2011. Costly punishment prevails in intergroup conflict. *P Roy Soc B-Biol Sci P Roy Soc B-Biol Sci*. 278(1723):3428–36

Salali GD, Juda M, Henrich J. 2015. Transmission and development of costly punishment in children. *Evolution and Human Behavior*. 36(2):86–94

Samuni L, Preis A, Mundry R, Deschner T, Crockford C, Wittig RM. 2017. Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proceedings of the National Academy of Sciences*. 114(2):268–73

Sandel AA, Mitani JC, Langergraber KE. 2019. Paternal kin discrimination by sons in male chimpanzees transitioning to adulthood. *bioRxiv*

Schino G, Aureli F. 2010. The relative roles of kinship and reciprocity in explaining primate altruism. *Ecology Letters*. 13(1):45–50

Schino G, Aureli F. 2017. Reciprocity in group-living animals: partner control *versus* partner choice: Reciprocity in group-living animals. *Biol Rev*. 92(2):665–72

Schmelz M, Grueneisen S, Kabalak A, Jost J, Tomasello M. 2017. Chimpanzees return favors at a personal cost. *Proceedings of the National Academy of Sciences*. 114(28):201700351

Schmidt MFH, Tomasello M. 2012. Young children enforce social norms. *Current Directions in Psychological Science*. 21(4):232–36

Schulz JF, Bahrami-Rad D, Beauchamp JP, Henrich J. 2019. The Church, intensive kinship, and global psychological variation. *Science*. 366(6466):eaau5141

Schweinfurth MK, Call J. 2019. Revisiting the possibility of reciprocal help in non-human primates. *Neuroscience & Biobehavioral Reviews*. 104:73–86

Shariff AF, Willard AK, Andersen T, Norenzayan A. 2016. Religious priming: A meta-analysis with a focus on prosociality. *Personality and Social Psychology Review*. 20(1):27–48

Silk JB. 1987. Adoption among the Inuit. *Ethos*. 15(3):320–30

Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, et al. 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*. 437(7063):1357–59

Silk JB, House BR. 2016. The evolution of altruistic social preferences in human groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 371(1687):

Singh M, Wrangham R, Glowacki L. 2017. Self-Interest and the Design of Rules. *Human Nature*. 28(4):457–80

Smith CE, Blake PR, Harris PL. 2013. I Should but I Won't: Why Young Children Endorse Norms of Fair Sharing but Do Not Follow Them. *PLoS ONE*. 8(3):e59510

Smith KM, Larroucau T, Mabulla IA, Apicella CL. 2018. Hunter-Gatherers Maintain Assortativity in Cooperation despite High Levels of Residential Change and Mixing. *Current Biology*. 28(19):3152-3157.e4

Sosis R, Bressler ER. 2003. Cooperation and commune longevity: A test of the costly signaling theory of religion. *Cross-Cult Res Cross-Cult Res*. 37(2):211–39

Sperber D. 1996. *Explaining Culture : A Naturalistic Approach*. Oxford, UK. Cambridge, Mass: Blackwell

St Clair JJH, Klump BC, Sugasawa S, Higgott CG, Colegrave N, Rutz C. 2018. Hook innovation boosts foraging efficiency in tool-using crows. *Nature Ecology and Evolution*. 2(3):441–44

Street SE, Navarrete AF, Reader SM, Laland KN. 2017. Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of the National Academy of Sciences*. 114(30):7908–14

Surbeck M, Mundry R, Hohmann G. 2011. Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B: Biological Sciences*. 278(1705):590–98

Swann WB, Buhrmester MD. 2015. Identity Fusion. *Current Directions in Psychological Science*. 24(1):52–57

Tomasello M, Melis AP, Tennie C, Wyman E, Herrmann E. 2012. Two Key Steps in the Evolution of Human Cooperation The Interdependence Hypothesis. *Current Anthropology*. 53(6):673–92

Trivers RL. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*. 46:35–57

Turchin P. 2013. The puzzle of human ultrasociality: How did large-scale complex societies evolve? In *Cultural Evolution: Society, Technology, Language, and Religion*, eds. PJ Richerson, MH Christiansen, pp. 61–73. Cambridge: MIT Press

Turchin P. 2015. *Ultrasociety: How 10,000 Years of War Made Humans the Greatest Cooperators on Earth*. Connecticut: Beresta Books

Van Cleve J, Akcay E. 2014. Pathways to Social Evolution: Reciprocity, Relatedness, and Synergy. *Evolution*. 68(8):2245–58

van Veelen M, García J, Rand DG, Nowak M a. 2012. Direct reciprocity in structured populations. *Proceedings of the National Academy of Sciences of the United States of America*. 109(33):9929–34

Vogt S, Efferson C, Fehr E. 2017. The risk of female genital cutting in Europe: Comparing immigrant attitudes toward uncut girls with attitudes in a practicing country. *SSM - Population Health*. 3:283–93

Warneken F. 2018. How Children Solve the Two Challenges of Cooperation. *Annu. Rev. Psychol.* 69(1):205–29

White CJM, Kelly JM, Shariff AF, Norenzayan A. 2019. Supernatural norm enforcement: Thinking about karma and God reduces selfishness among believers. *Journal of Experimental Social Psychology*. 84:103797

Whitehouse H, Lanman JA. 2014. The ties that bind us: Ritual, fusion, and identification. *Current Anthropology*. 55(6):674–95

Whitehouse H, McQuinn B, Buhrmester M, Swann WB. 2014. Brothers in arms: Libyan revolutionaries bond like family. *Proceedings of the National Academy of Sciences*. 111(50):17783–85

Wilson DS. 2002. *Darwin's Cathedral: Evolution, Religion, and the Nature of Society*. Chicago: University of Chicago

Wood LA, Kendal RL, Flynn EG. 2013. Whom do children copy? Model-based biases in social learning. *Developmental Review*. 33(4):341–56

Wrangham R. 2019. *The Goodness Paradox: How Evolution Made Us Both More and Less Violent*. Profile

Wrangham RW. 2009. *Catching Fire : How Cooking Made Us Human*. New York: Basic Books

Wrangham RW, Glowacki L. 2012. Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: evaluating the chimpanzee model. *Human nature (Hawthorne, N.Y.)*. 23(1):5–29

Wright R. 2009. *The Evolution of God*. Boston: Little, Brown and Company

Yamagishi T, Matsumoto Y, Kiyonari T, Takagishi H, Li Y, et al. 2017. Response time in economic games reflects different types of decision conflict for prosocial and proself individuals. *Proceedings of the National Academy of Sciences of the United States of America*. 114(24):6394–99

Yilmaz O, Bahçekapili HG. 2016. Supernatural and secular monitors promote human cooperation only if they remind of punishment. *Evolution and Human Behavior*. 37(1):79–84

Young HP. 1998. *Individual Strategy and Social Structure : An Evolutionary Theory of Institutions*. Princeton, N.J: Princeton University Press

Zaki J, Schirmer J, Mitchell JP. 2011. Social Influence Modulates the Neural Computation of Value. *Psychological Science*. 22(7):894–900

Zefferman MR, Mathew S. 2015. An Evolutionary Theory of Large-Scale Human Warfare : Group-Structured Cultural Selection. . 61:50–61

Zeng TC, Aw AJ, Feldman MW. 2018. Cultural hitchhiking and competition between patrilineal kin groups explain the post-Neolithic Y-chromosome bottleneck. *Nature Communications*. 9(1):1–12