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# The Origins and Psychology of Human Cooperation

Joseph Henrich[1] and Michael Muthukrishna[2]

[1]Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA; email: henrich@fas.harvard.edu

[2]Department of Psychological and Behavioural Science, London School of Economics and Political Science, London WC2A 2AE, United Kingdom; email: m.muthukrishna@lse.ac.uk

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## Abstract

Humans are an ultrasocial species. This sociality, however, cannot be fully explained by the canonical approaches found in evolutionary biology, psychology, or economics. Understanding our unique social psychology requires accounting not only for the breadth and intensity of human cooperation but also for the variation found across societies, over history, and among behavioral domains. Here, we introduce an expanded evolutionary approach that considers how genetic and cultural evolution, and 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, reputation, signaling, and punishment; we discuss key culture–gene coevolutionary hypotheses, such as those surrounding self-domestication and norm psychology; and we consider the role of religions and marriage systems. Empirically, we synthesize experimental and observational evidence from studies of children and adults from diverse societies with research among nonhuman primates.

## Contents

## INTRODUCTION

The origins and nature of our species' cooperative psychology and prosocial behavior have 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 (see the sidebar titled An Evolutionary Approach to Cooperation).

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

### AN EVOLUTIONARY APPROACH TO COOPERATION

Substantial progress has been made on the problem of cooperation by integrating four converging lines of inquiry:

1. Phylogeny: 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?
4. Ontogeny: How, when, and why do these psychological mechanisms develop?

These questions, named eponymously after the ethologist Nikolaas Tinbergen (1963), have catalyzed efforts to understand human cooperation, driven much comparative research, and permitted our species to be seated within the natural world.

presents an immediate puzzle: Both the scale and the intensity of human cooperation are substantially greater than those 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 both at small scales, such as within hunter-gatherer 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 2011). Experimental studies incorporating cross-cultural, developmental, and comparative perspectives reveal that humans—usually by middle childhood—are substantially more inclined toward food sharing than nonhuman primates (Ensminger & Henrich 2014; House 2017; House et al. 2013a,b, 2020; Jaeggi et al. 2010; Jensen et al. 2007a; Silk et al. 2005; Silk & House 2016). Interestingly, while the cooperation observed in experiments with nonhuman 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 favored 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 2015, Lachmann & Bergstrom 2004, McNally & Jackson 2013, McNally et al. 2012). To the contrary, we argue that the door to the evolution of cooperative communication systems (e.g., spoken languages) was opened by the emergence of greater sociality in our lineage. Similarly, regarding our cognitive abilities, the question to focus on is how our social environments have become structured such that the smart move is often to cooperate and help rather than to 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 also provide little explanation 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 in which 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. Research using behavioral experiments, survey measures, and ecologically valid observational techniques over two decades has repeatedly documented this ample and important variation (Algan & Cahuc 2013; Balliet & Van Lange 2013; 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. Noncooperative 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. These same mechanisms sometimes even 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 puzzling patterns. 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 discuss below, the current evidence supports the view that our psychology coevolves culturally with our institutions, so that any account of human cooperative psychology requires a theory that integrates the cultural evolution of social norms and institutions.

We 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 review key results related to kinship, direct reciprocity, reputation, punishment, and signaling. For each of these mechanisms, we consider the potential role for both genetic and cultural evolutionary processes in light of research from diverse human populations as well as from other primates. After highlighting the limitations of these mechanisms for explaining human cooperation, we consider how intergroup competition in cultural evolution interacts with these within-group mechanisms. Next, having illustrated various ways that cultural evolution produces social norms, we 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. We conclude by presenting research that anchors the cultural evolution of psychology in history, and we discuss 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 profoundly ill-equipped for helping us to survive as hunter-gatherers (Henrich 2016). We do not innately know, and usually cannot 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—that is, to acquiring a substantial portion of our phenotype by tapping into a large body of nongenetic 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 to do with little to no cultural input (Dean et al. 2014, Henrich 2016). Without access to this nongenetic 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: (*a*) the genetic evolution of our species' capacities for culture, (*b*) cultural evolution and the emergence of institutions, and (*c*) the process of culture–gene coevolution.

## Evolved Capacities for Culture

The development of this expanded evolutionary framework begins by asking, How has natural selection shaped our minds and brains to allow us to most effectively extract adaptive practices, know-how, strategies, preferences, and decision heuristics from the minds and behaviors of those around us? This leads us 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 (i.e., 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 weigh more heavily what they acquire from other people, even over their own direct observations, as situations become more uncertain and problems get more difficult (Morgan et al. 2012, Muthukrishna et al. 2016).

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 also 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 mechanisms that shape "what" we learn, human cultural learning abilities influence an incredibly wide range of behavioral domains that extend well beyond the recurrent fitness challenges faced by our evolutionary ancestors over the last 6 million years. 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 at a deeper level, 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 judgment 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. 2020), 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

**Third-party punishment:** sanctions administered to a norm violator or noncooperator by an individual not directly affected by the errant action (i.e., a third party)

& 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-rewarding (Bandura & Kupers 1964), and third-party punishment (Salali et al. 2015).

## 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 (see the sidebar titled Dual Inheritance Theory), theorists have constructed mathematical models rooted in what is 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, whereby 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. Therefore, 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 clarify and standardize the informal institutions generated by social norms, often by translating them into written rules.

In the next section, we consider 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 first consider the origins of social norms at a more abstract level: Once individuals possess sufficiently sophisticated cognitive abilities to reliably culturally learn both (*a*) how to behave in particular contexts and (*b*) the standards for judging others

### 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; Cavalli-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 are low, and natural selection is weak. By contrast, in cultural evolution, individuals often acquire and recombine their cultural traits from many models (termed 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 affect 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.

**Table 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 the receiver role. The proposer must allocate the money between the two participants, from zero to the full endowment. The receiver can either accept or reject the proposed division. If they accept, the money is divided as per the proposal. If the responder 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 nonzero amount. |
| Dictator game | This two-player experimental interaction parallels the ultimatum game, except that the receiver is passive and 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's profits. In the world of *Homo economicus*, player C will not pay to punish, so player A allocates nothing to B. |
| Public goods game | In this interaction, $n$ participants are each given a monetary endowment, and they can anonymously contribute any portion of it 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 contributes 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—for example, a player in the public goods game who contributes zero to the public good free-rides on the contributions of other players. |
| Second- 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 benefits from other players' willingness to punish free-riders but do not themselves pay the costs 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—for example, 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 the proliferation of equilibrium states that are rare or difficult to access. |

in these contexts, stable patterns of costly behavior emerge and can be sustained for long periods within a community. These patterns are social norms because anyone who deviates—who does not pay the cost—will be sanctioned or otherwise incentivized to conform in some way. Below, we 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). For now, however, let us begin by considering evidence indicating that social norms do indeed matter for individually costly behaviors and that this is associated with variation across societies.

House et al. (2020) deployed a simple dictator game (see description in **Table 1**) among both children ($n = 833$) and adults ($n = 255$) across eight populations (**Figure 1**), ranging from hunter-gatherers in Tanzania to urbanites in Berlin, to assess people's willingness to share equally with

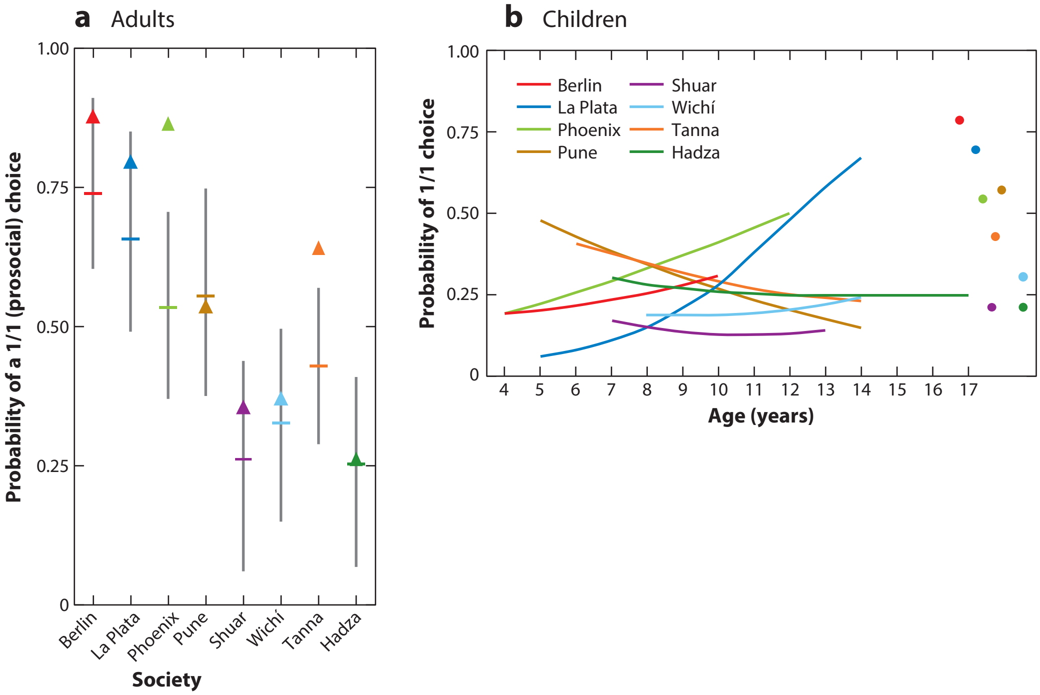

**Figure 1**

Binary dictator game results from eight diverse populations. (*a*) For adults, the panel 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 panel shows 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. The Shuar are Amazonian slash-and-burn horticulturalists in Ecuador; the Wichí are sedentarized hunter-gatherers in Argentina; the Hadza are Tanzanian hunter-gatherers; Tanna is an island in Vanuatu where a population of hunter-horticulturalists was sampled; Pune is a city in Maharashtra, India; and La Plata is a provincial capital in Argentina. Data from House et al. (2020).

an anonymous partner. Participants had to pick one of two possible allocations: two rewards for themselves and nothing for their partner (2/0), or 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 stated that (*a*) the 1/1 option was good and the 2/0 bad (fair condition), (*b*) the 2/0 was good and the 1/1 bad (selfish condition), or (*c*) both were ok (neutral condition). After making their choices, many participants were shown both the fair and the selfish condition videos and asked which statement was more correct—a normative assessment.

**Figure 1*a*** shows that, unsurprisingly, adults were more likely to make 1/1 choices in places where this was judged as more correct. The analysis reveals that adult's choices are influenced both by their own preferences regarding which choice is more correct and by the normative judgments of their communities. These findings indicate a role for normative concerns in adults' decisions.

Turning to the developmental data, **Figure 1*b*** models the age trajectories of the 1/1 choices. In all societies, as they got older, children moved toward both the behaviors and the normative judgments of the adults, leading to quite different trajectories across societies. This suggests that norms not only influence adult behavior but also 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, children from WEIRD (Western, educated, industrialized, rich, and democratic) societies 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 in human life history, evolved to support cultural learning and, specifically, the acquisition of social norms (Henrich 2016).

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, although 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.

## EVOLUTIONARY MECHANISMS OF COOPERATION

Sustaining individually costly behaviors, including those that deliver benefits to others, requires some form of nonrandom 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, for example, the simplest case of 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 nonrandom association or preferential delivery ($\beta$, that is, how much shared food is delivered to other sharers versus nonsharers). Cooperation is sustained when $\beta \times b > c$. More complex mechanisms for cooperation involve sanctioning those who do not pay the required costs, for example, through preferential exclusion, ostracism, exploitation, or punishment (Bhui et al. 2019). Here, we briefly review the theory and evidence for some of the most fundamental mechanisms underlying cooperation, 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). Here the nonrandom association is created by favoring relatives: $r \times b > c$. By directing help in accordance with $r$ (the coefficient of relatedness) 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. From a gene's eye view, this means that genes that, however indirectly, 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 nonhuman primates, there is good reason to believe that we humans have inherited a genetically evolved psychology for this kin-based altruism from our common ancestors. Ample evidence from both monkeys and nonhuman apes reveals the impact of genealogical relatedness on social patterning (i.e., 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 found across human societies, there is relatively little voluntary food sharing in nonhuman primates.

As 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 history (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 many more (see the sidebar titled Kin Recognition).

In principle, the logic of kin-based altruism can apply to both cultural and genetic inheritance. In genetic models, genealogical relatedness provides the probability that two individuals share altruism genes by recent common descent—that is, if one has the altruism gene there is a 50% chance (roughly and on average) that their 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 is little reason to suspect much of a role for cultural relatedness on cooperation—that is, to infer that individuals will 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, one analysis found that cultural relatedness based on common descent (i.e., learning from the same models) was 0.053 or less (Boyd et al. 2011). This value implies that the costs of helpful actions $c$ would have to generate benefits $b$ that are 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.

Nevertheless, theorists have identified one set of conditions in which cultural kinship can favor cooperation: In groups dominated by a single highly prestigious leader, where individuals look to this person for cues of how to behave, cooperative actions can spread 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

## KIN RECOGNITION

Paralleling their 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).

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 nonrandomness 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 (i.e., you scratch my back, I'll scratch yours) can operate through mechanisms based on partner choice, 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 nonhuman apes suggest 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 experimentalists 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 plausible real-world conditions remains largely elusive (Warneken 2018). Taken together, the mixed results regarding reciprocity in other primates suggest that humans have probably inherited some capacity for reciprocity based on partner choice from our shared ancestors but have likely inherited only some of the rudiments of partner fidelity (see the sidebar titled Partner Choice is WEIRD).

In contrast to kinship, our dual inheritance system complicates matters because cultural transmission is particularly well suited to produce, or enhance, both 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

### PARTNER CHOICE IS WEIRD

In contrast to most societies across human history, where people experience 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, in which short-term tit-for-tat accounting is eschewed in favor of aggregated emotional indices, and numerous shorter-term acquaintances, in which tit-for-tat-style accounting is relevant (Silk 2003). In other societies, including some forager societies, conditions are less favorable to partner choice and this mechanism is less important (Smith et al. 2018).

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 preprogram one successful strategy or even an ensemble of them. Cultural learning can tackle this dilemma by allowing individuals to rapidly adapt their behavior to the local distribution of strategies by copying the most successful strategies currently in use 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 of the rudiments of partner choice (Kuhlmeier et al. 2014, Olson & Spelke 2008), the development of actual reciprocity-based cooperation and contingent helping does not 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 (i.e., you scratch my back, I'll scratch yours) contrasts with negative reciprocity (i.e., 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, children who had been given a sticker only gradually developed the inclination to reciprocate a sticker to this partner (see **Figure 2*a***). This rising inclination toward contingent reciprocity is matched by a parallel rise in

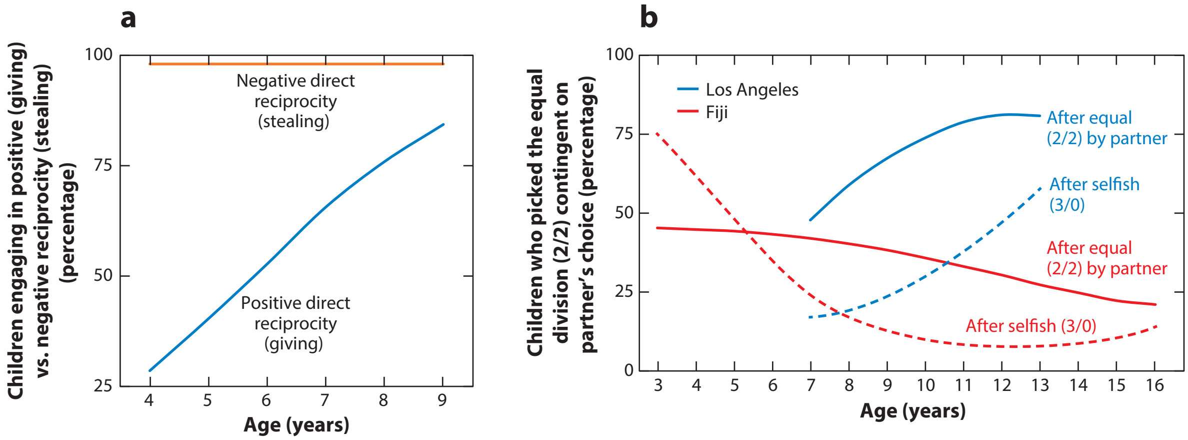

**Figure 2**

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 2/2 or 3/0 split, in Fiji and Los Angeles. Data for panel *a* from Chernyak et al. (2019); data for panel *b* from House (2017).

normative endorsements of reciprocity regarding what one should do in this context. By contrast, revenge or negative direct reciprocity appears already fully developed in 4-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 find neither positive reciprocity based on partner fidelity (Melis et al. 2016) nor third-party punishment (Riedl et al. 2012).

Importantly, Chernyak et al. (2019) 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 on, 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 do not 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 those shown in **Figure 2*a*** reliably emerge in WEIRD populations (House 2017, House et al. 2012), **Figure 2*b*** 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: 2 rewards for the actor and 2 for their partner or 3 rewards for the actor and 0 for the other person. Children in both populations developed contingent responding, which indicates that reciprocity reliably develops in diverse social contexts. Yet, these populations showed rather divergent trajectories: In Fiji, the older kids increasingly selected the 3/0 option, so playing tit-for-tat drove cooperation down, not up.

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 (*a*) our ultrasociality (relatedness is not sufficiently higher than in other primates), (*b*) domain differences in cooperation (except based on the ratio of cooperative benefits delivered to helping costs, or $b/c$), (*c*) rapid expansion (genetic relatedness $r$ declines dramatically as groups expand), and (*d*) noncooperative or maladaptive behavior (kin-based altruism requires $b > 0$). When kin-based altruism does appear to play a broader role, it is usually supported by cooperative norms, such as those that prescribe prosociality toward 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, such as among clans or ethnic groups (Schulz et al. 2019). What we call corruption, cronyism, or nepotism is really just cooperation on a smaller scale, often among relatives, friends, and reciprocal partners, at the expense of cooperation on a larger, impersonal scale (Muthukrishna 2018, 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 decline, 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—for example, by not 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 is called the second-order free-rider problem (**Table 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 is 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 noncooperators (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 a sufficient number of group members 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 guarantees that punishers will tend to end up in cooperative groups, and when they do not, they can still avoid the costs of punishment.

Large-scale cooperation can also be sustained by reputational systems, often termed indirect reciprocity, that tie 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 interaction 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., paying 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 the donor (without getting themselves 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 noncontributors 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 the ability to track and verify the accuracy of reputations and may be undermined by reputations in different domains and at different scales.

Collectively, these and 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 sizes, error rates, etc.—there are stable states for the populations in which no costly norms exist (e.g., all members defect) 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 (*a*) shared behavioral standards (what counts as cooperation or qualifies as good standing), (*b*) recognized social roles (who is a donor) and institutions for punishment, and (*c*) the ability to disseminate reputational information (Bhui et al. 2019, Leimar & Hammerstein 2001). Empirically, reputations are formed and shared primarily via cultural transmission, because most people do not directly observe most social interactions—therefore, most reputation-based models presuppose sophisticated cultural learning abilities. The interpretation of these models as cultural evolutionary processes is encouraged by the fact that none of them has been successfully applied to explain cooperation in nonhumans. Consistent with this, experimental work indicates that nonhuman 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 1*b***), and willing to engage in the 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 might 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 antisocial attack (Enke 2019, Henrich 2020, 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 other mechanisms, 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—that is, 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 is as if their reputational shield fell, 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 do not 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 antisocial actions when the victim is in bad standing. It is 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 these field data reveals the effectiveness and relative simplicity of this mechanism for sustaining large-scale cooperation (Bhui et al. 2019).

This mechanism for sustaining costly norms in Fijian villages 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 2004, Fehr & Gachter 2002). Evolutionary models in which diffuse punishment sustains cooperation were developed early, which is not surprising given that they reflect WEIRD intuitions about punishment. To see this experimentally, let us begin by focusing on the differences in how Fijian villagers and WEIRD people punish in the ultimatum and third-party punishment games (**Table 1**). In the ultimatum game, over 70% of nonstudent Americans rejected offers of 10% of the stake, the lowest possible offer 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 one-half of American university students (no data for nonstudents) were willing to punish the lowest possible offer, while among Fijian villagers that fraction dropped to one-third. Postgame interviews indicate that although 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 postgame interviews, Fijians did not even report a desire to punish (Henrich & Henrich 2014). Despite their unwillingness to punish low offers, Fijians made relatively high offers in both experiments. The lack of punishment in these experiments does not 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 from those necessary in large anonymous societies. In tight-knit communities, diffuse punishment of any kind risks (*a*) the threat of counter-punishment—revenge—against either the punisher or their family and (*b*) the damaging of a long-term relationship from which one cannot easily escape (as 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 diffuse punishment can be sustained by a variety of mechanisms. Confirming these theoretical predictions, a comparative project using a global sample from 33 communities from 15 subsistence-oriented societies including foragers, farmers, and pastoralists found that costly punishment by second and third parties in one-shot anonymous interactions varies dramatically with the size of the community (Henrich et al. 2010). To measure people's willingness to punish, their minimum acceptable offer (MAO) was calculated for both the ultimatum and third-party punishment games.[1] MAO is the lowest offer amount that a person will not 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 ultimatum and third-party punishment games. Smaller communities mostly do not punish, whereas 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 communities in dictator games (Henrich et al. 2006).

This line of theorizing, and now a substantial body of evidence including developmental and cross-cultural findings, suggests that when researchers 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.

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[1] In a simpler version of the third-party punishment game used here (see **Table 1**), player C could only choose between paying $10 (20% of their stake) to take $30 away from player A or do nothing (pay zero).

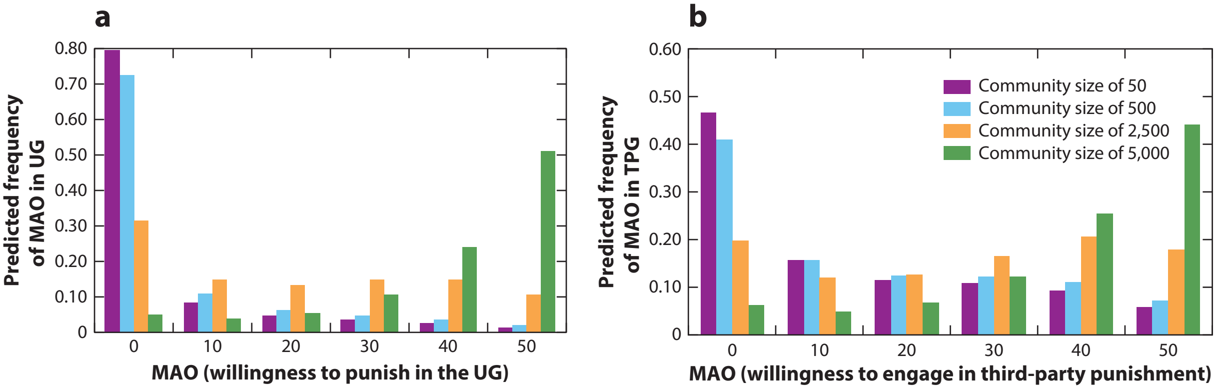

**Figure 3**

Predicted frequencies of minimal acceptable offers (MAOs) across possible offer amounts for (*a*) the ultimatum game (UG) and (*b*) the third-party punishment game (TPG). 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. Data from Henrich et al. (2010).

There is, however, an underappreciated issue with all of the models of large-scale cooperation discussed above: the problem of equilibrium selection (see **Table 1**). As noted above, 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 (i.e., hurting others or the group as a whole). This raises the 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. First, through some form of intra-population bargaining process, 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) that benefit them—for example, favoring low taxes or polygynous marriage (Singh et al. 2017). Second, some social norms are more stable to perturbations than others, 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—that is, 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 multilevel cultural evolution.

## MULTILEVEL 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 that stronger cooperation and greater solidarity at lower levels can be detrimental to cooperation at higher levels (Maynard Smith & Szathmáry 1999, Muthukrishna 2018).

Within multilevel structures, it is 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 2020). 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), listed below.

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. For example, as a consequence of the United States' rise to global prominence over the last two centuries, other countries have engaged in prestige-biased group transmission when they have preferentially copied the US Constitution in creating their own institutional foundations (Rockmore et al. 2018).
2. Differential reproduction: Norms can influence the rate at which individuals have children. Because children tend to share the norms of their community, any norms that increase birth rates or slow down death rates will tend to spread. Some world religions, for example, have spread more rapidly due to their pronatalist norms: The large, polygynous families adopted by Mormons in the nineteenth-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. Because migrants, and especially their descendants, typically adopt the local social norms, beliefs, and customs of their communities (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 institutions 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 multilevel 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 $R \times b > c$, where $R = CF_{ST}/(1 - CF_{ST})$, and $CF_{ST}$ is the ratio of cultural variation between groups to total cultural variation (Muthukrishna et al. 2020a). In genetics, the fixation index ($F_{ST}$) measures the extent to which the total genetic variation is structured into groups within the overall population; here, $CF_{ST}$, or cultural fixation index, can measure the extent to which the individual differences in cooperative norms are structured into groups. Working among four rural Kenyan populations, Handley & Mathew (2020) collected data from 759 individuals in different patrilineal clans across four tribes (ethnolinguistic 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 did not exploit

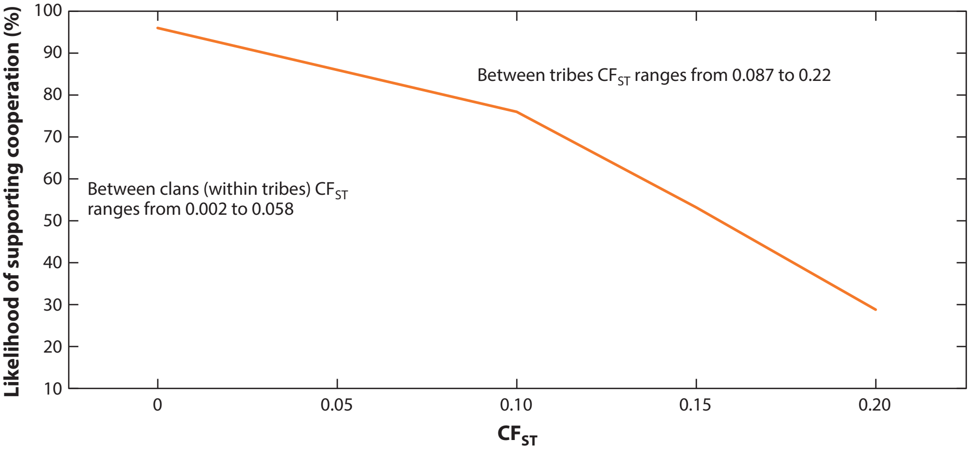

**Figure 4**

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. Abbreviation: $CF_{ST}$, cultural fixation index. Data from Handley & Mathew (2020).

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 the formal theory, the researchers found that cooperative inclinations (the percentage of cooperative responses to the vignettes) rose as $CF_{ST}$ between groups declined (see **Figure 4**). The data predict that 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: It was bad to raid other Turkana, even if they were physically and socially distant, but not to raid surrounding non-Turkana (Mathew & Boyd 2011). Sometimes even harming other tribes was perceived as "good." Overall, this work strongly supports a role for intergroup competition in favoring the norms that support larger-scale human cooperation.

A wide range of further studies 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 interfirm competition can drive up impersonal trust and cooperation among strangers (Francois et al. 2018).

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 (and 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 (see **Table 1**). So, it makes no sense to argue that 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 (i.e., "by showing that spark plugs are important, we've clearly shown that carburetors are irrelevant!").

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 the sidebar titled Dual Inheritance Theory) is more likely to create conditions favorable to intergroup competition. Cultural evolution is fast, noisy, and nonvertical 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, as these deplete the variation between groups and drive 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 nonvertical transmission) and culturally indistinguishable from the nonmigrants around them. The children of immigrants, for example, typically speak the local language without their parents' accent, which is a cue about where they are acquiring their culture (Cohen 2012). If we, for example, compare the $CF_{ST}$ values calculated by Handley & Mathew (2020) to the genetic equivalents for other African tribal populations, we find that Kenyan $CF_{ST}$'s are ∼0.1–0.2, whereas genetic $F_{ST}$'s are ∼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, 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—over time have 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., spearthrowers), 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 has thereby driven 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 those of other primates, were only favored once cooking and other food-processing techniques 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 have argued 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 it is governed by rules even if we do not yet know those rules, and we 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 have 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 copy precisely the protocol involved in some action; and even if they themselves do not copy accurately, they will often react negatively and seek to correct those who use alternative methods. Children do this regardless of whether they have been told that there is a right way to do something or whether they have seen anyone being corrected. This work, along with earlier research, suggests that children reliably develop an automatic tendency to infer the existence of social norms and to correct norm violators in a broad range of contexts, 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 the 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 tools from neuroscience, research suggests that both complying with costly social norms and punishing norm violators (also at a personal cost) activate reward circuits, suggesting that complying and enforcing norms can become goals in themselves (Buckholtz & Marois 2012, Buckholtz et al. 2008).

## 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 2020, 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 2 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 one month 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's. If Natalie the fisher dies, the chances that Stephanie and her family will 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 spouses will die in the coming years, as poor nutrition leads to sickness, etc. If another fisher dies, or leaves the band because their spouse passes, each remaining person's chances of going a month without fish increases further, as do 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 do not directly contribute to each other's welfare: If Stephanie's spouse nurses her back to health when she is 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 depend 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. Although 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 lifelong 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 lifelong, 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 have presented so far 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, worldviews, 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 (*a*) the treatment of a large extended network of relatives, including distant cousins and affines (e.g., obligations to in-laws); (*b*) the preferences and taboos regarding who can marry whom (e.g., people should marry their cousins); (*c*) the inheritance of social identity (e.g., clan affiliation); (*d*) cultural prescriptions on postmarital residence (e.g., newly married couples must live with the husband's family); and (*e*) 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 they 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 supporting high-levels of parochial cooperation and solidarity toward one's kin group—toward one's clan, kindred, or tribe (Henrich 2020, 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 toward strangers, anonymous others, and impersonal organizations (e.g., the government). Two papers have recently tested these ideas using both global and regional data sets (Enke 2019, Schulz et al. 2019). Globally, using national-level data, Schulz et al. (2019) show that populations with less intensive kin-based institutions contribute more to strangers in public goods games, engage less in antisocial (revenge-based) punishment, and make more voluntary blood donations to anonymous strangers. Using first- and second-generation immigrants from different places, Enke (2019) and Schulz et al. (2019) confirm these patterns using various survey-based measures of trust and fairness toward strangers. These analyses compare individuals living in the same country but coming from 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 improves 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 multilevel 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 did not help, 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 noncooperative or antisocial 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 toward 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 impose 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 coreligionists. 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) coreligionists (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 have altered people's psychology and thereby permitted the scaling up of societies.

Keeping in mind, as noted above, that cooperation at lower levels can undermine cooperation at higher levels, it is 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 century-long attack on traditional families (on cousin marriage, polygamy, clans, etc.). Strikingly, the duration that populations around the globe have spent under the dominion of 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 (e.g., charter towns), residential mobility, and representative governments (Schulz et al. 2019).

## CONCLUSION

We began this review 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 us 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 do not generally engage in such costly behaviors.
3. Differences in the scale and intensity of cooperation across populations: The scale and intensity of human cooperation vary dramatically across societies because they have been heavily influenced by cultural evolution, driven by the effect of intergroup competition on institutions. The intensity of intergroup competition has varied substantially 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), has operated by undermining the effectiveness of lower-scale mechanisms.
4. Rapid rise in the scale of cooperation: Beginning about 12,000 years ago, the introduction 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. Mechanisms that sustain cooperation also sustain noncooperative and even maladaptive behaviors: 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 the group (e.g., female genital cutting), noncooperative 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: theoretical frameworks, diverse methods, and history. As 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).

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