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Culture–gene coevolution, norm-psychology and the emergence of human prosociality

Maciej Chudek[1] and Joseph Henrich[1,2,3]

[1] Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver, BC, V6T 1Z4, Canada
[2] Department of Economics, University of British Columbia, 2136 West Mall, Vancouver, BC, V6T 1Z4, Canada
[3] Canadian Institute for Advanced Research, 180 Dundas Street West, Suite 1400, Toronto ON, M5G 1Z8, Canada

Diverse lines of theoretical and empirical research are converging on the notion that human evolution has been substantially influenced by the interaction of our cultural and genetic inheritance systems. The application of this culture–gene coevolutionary approach to understanding human social psychology has generated novel insights into the cognitive and affective foundations of large-scale cooperation, social norms and ethnicity. This approach hypothesizes a norm-psychology: a suite of psychological adaptations for inferring, encoding in memory, adhering to, enforcing and redressing violations of the shared behavioral standards of one's community. After reviewing the substantial body of formal theory underpinning these predictions, we outline how this account organizes diverse empirical findings in the cognitive sciences and related disciplines. Norm-psychology offers explanatory traction on the evolved psychological mechanisms that underlie cultural evolution, cross-cultural differences and the emergence of norms.

Culture–gene coevolved norm-psychology

Converging lines of theoretical and empirical research indicate that culture has shaped the human genome by driving the evolution of both our brains and bodies along trajectories not available to less cultural species [1,2]. Meanwhile, new evidence is pushing the earliest origins of complex cultural adaptations, such as tools, manufacturing techniques, cooking and fire control, deeper into our evolutionary past [3–6]. Consequently, evolutionary approaches to human psychology must increasingly consider culture–gene coevolutionary hypotheses alongside gene-only hypotheses [7]. Here, we review research on how the interaction between genes and culture might have shaped our species' social psychology, including elements that underpin large-scale cooperation. We conclude that understanding human cooperation requires understanding culturally transmitted cooperative norms and the evolved cognitive mechanisms that generate them (Box 1).

Culture–gene coevolutionary models of social behavior are converging with independent empirical results from psychology and economics to sketch a pivotal role in our evolutionary history for norms and norm-psychology [8–10]. By norms, we mean learned behavioral standards shared and enforced by a community. By norm-psychology, we mean a suite of cognitive mechanisms, motivations and dispositions for dealing with norms. Heuristically, we partition these mechanisms by the selective processes that favored them: (i) the accumulating corpus of adaptive cultural information and the increasingly plentiful coordination opportunities it entails and (ii) the emergence of norm-enforcing phenotypes – detailed below (Figure 1). In this review, we summarize theoretical research suggesting that a species which passes a crucial threshold of dependence on culturally transmitted information will probably evolve a norm-psychology. We argue that large-scale cooperation in our species is best understood as one product of culturally evolving social norms, supported by norm-psychology. Previous evolutionary approaches to understanding human cooperation have postulated universal cognitive adaptations. The norm-psychology account builds on these by describing evolved cognitive mechanisms that generate cross-cultural variation and cumulative cultural evolution. This insight connects the evolutionary dynamics of cultural learning, coordination and cooperation to explain our species' distinct patterns of prosociality, organizes evidence from otherwise disconnected empirical programs, and helps answer an outstanding question in cognitive science: how can natural selection produce dispositions for prosocial third-party condemnation [11].

The evolution of culture and culture–gene coevolution

The evolutionary emergence of a capacity for cumulative culture involves (and then amplifies) two types of selection pressures: those associated with the acquisition of adaptive non-social information by learning from others (e.g., which plants are toxic) and social behaviors or strategies that permit coordinating with conspecifics (e.g. seasonally aggregating at the same locations or using the same gesture when a viper is spotted).

Within the last two million years our ancestors surmounted the barrier between non-cumulative social learning (common in many species) and cumulative cultural evolution [12,13]. Adaptive cultural information began gradually accumulating over generations, eventually encoding a phenotypic repertoire more complex and fitness-enhancing than any single individual could discover by asocial

Corresponding author: Chudek, M. (Maciek@psych.ubc.ca).

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Glossary

Cooperation dilemma: a social interaction in which individuals can 'free ride' on the efforts or contributions of one or more members of their group, by reducing their personal costs while still getting a share of the available group benefits. In such dilemmas, the group maximizes its total payoff when no one free rides, whereas individuals can often increase and never decrease their immediate payoffs by free riding. One simple model is the Prisoner's dilemma. We refer to 'not free riding' as the prosocial or group-beneficial behavior.

Coordination dilemma: a situation where individuals can benefit by adopting the same behavior as their interaction partners, for instance by walking on the same side of a path, using the same display when a particular predator is spotted or waking up at a similar time.

Culture: information stored in people's brains, nervous systems or bodies that affects behavior and got there through some social learning process, broadly defined.

Cultural group selection: the global frequency of culturally transmitted aspects of individuals' phenotypes – learned practices, strategies and preferences – can depend in part on their effects on the relative survival and proliferation of cultural groups. For example, groups with more cooperative norms can displace those with fewer such norms via success in war, demographic competition or differential migration [98]. Consistent with much evolutionary modeling, when social behaviors give rise to multiple stable equilibria (which are effectively group-level properties) most variation in norms exists between groups, making group interactions a potent component of the overall evolutionary process [99]. A coevolving norm-psychology only galvanizes this process by further assorting phenotypes into groups.

Cumulative culture: cultural information too complex for a single individual to devise in a one generation. Dependence on fitness-enhancing cumulative culture is a key transition in our species' evolution history that set several new evolutionary dynamics in motion (Figure 1).

Large-scale cooperation: regular cooperation and exchange among ephemeral interactants (e.g. strangers), often involving many contributors or cooperators. Modern cities are rife with such behavior; for instance: voting, giving blood, food sharing, not extorting each other, policing and territorial defense. The available ethnographic data suggests that even foraging societies have solved some elements of large-scale cooperation.

Multiple stable equilibria: Some dynamic systems can stabilize arbitrary costly behaviors within a group - they may for instance sustain prescribed behaviors using reputation or punishment (see Box 2) – generating a population of groups at multiple, different stable equilibria. Other processes (e.g., cultural group selection) are needed to explain what happens in the longer run.

Neuroeconomics: an interdisciplinary field that combines tools principally from neuroscience and behavioral economics (as well as other fields, e.g. cognitive psychology) to study decision-making, particularly involving choices among alternatives. In prototypical studies, subjects make social or individual choices that influence their take-home payoffs while being monitored by functional magnetic resonance imaging, positron emission tomography or other neuroimaging tools.

Non-cumulative social learning: social learning abilities that do not generate the accumulation of adaptive information over generations. Many animal species display such social learning, including primates, corvids, cetaceans, mongooses and fish [100].

Norm: behavioral standards shared and enforced by a community.

Phenotypic assortment: phenotypic assortment is a population statistic that measures the phenotypic similarity on relevant traits, relative to chance, between partners in social interactions. Mechanisms that generate greater phenotypic assortment (i.e. make cooperators likely to interact with other cooperators) facilitate cooperation (Box 2). Both cultural learning and norm-psychology can create phenotypic assortment, as can mechanisms related to kinship and reciprocity.

learning alone. This expanding early cultural corpus might have included know-how about tool-making, fire use and food preparation [3,6,14]. Brains better at acquiring, storing and organizing this growing corpus of adaptive information had a selective advantage over their less cultural brethren. By mathematically coupling evidence-based assumptions about ancestral environments to the constraints imposed by natural selection, culture–gene coevolutionary models explore the causes and consequences of this evolutionary transition [12,15]. These processes are 'coevolutionary' because by shaping human behavior, this expanding cultural corpus shaped the selection pressures acting on our genome; our evolving genome, in turn, sculpted the brains that acquire and transmit the information in the cultural corpus, shaping, constraining and allowing it to expand further. These processes favored the evolution of cognitive biases for extracting 'better quality' (more fitness enhancing) information from the minds and behavior of others. Much modeling work shows when and how these adaptive cognitive biases or strategies improve cultural learning [16] by discriminating content, making certain types of information easier to acquire/infer [17], or by exploiting cues of skill, success, prestige, age, sex, health, ethnicity, confidence [18–21] and trait frequency (e.g. conformist transmission, the disposition to disproportionately imitate the most common trait/behavior [22]).

In social groups these cultural learning biases, particularly prestige and conformity biases, create phenotypic assortment [23]: they make it more probable that regularly interacting individuals resemble one another. This generates many new fitness-enhancing social interactions that require greater coordination. As coordination with community members came to represent an ever larger proportion of lifetime fitness, early cultural learners faced an additional selection pressure to adopt the majority practices of their community. Ever more synchronized communities, in strategies related to movements (home bases), defense, gestural communication, exchange, courting and pair-bonding (marriage) made miscoordinating ever more costly. Of course, adopting complementary phenotypes is sometimes better than coordinating. To address this, human populations, even foragers, self-organize into marked subgroups, such as those based on sex, age, ethnicity and caste [24]. Sorting into subgroups transforms complementarity back into coordination. For example, a forager household might need experts on both hunting and gathering. If males hunt and females gather, well-complimented households can form by individuals learning from those within their sex-based subgroups. Such processes could be responsible for our same-sex cultural learning biases. Coordinating can generate a coevolutionary selection for an 'ethnic psychology': a tendency for social group members to adopt arbitrary ethnic markers (e.g. dialect) and preferentially interact with and learn from people who share those markers [25], further reinforcing the degree of and pressure for coordination.

In this first stage, the increasing fitness-relevance of coordination creates genetic selection pressures for skill at recognizing and representing the most common behaviors, beliefs or strategies in one's community and for dispositions to adopt or even internalize them as proximate

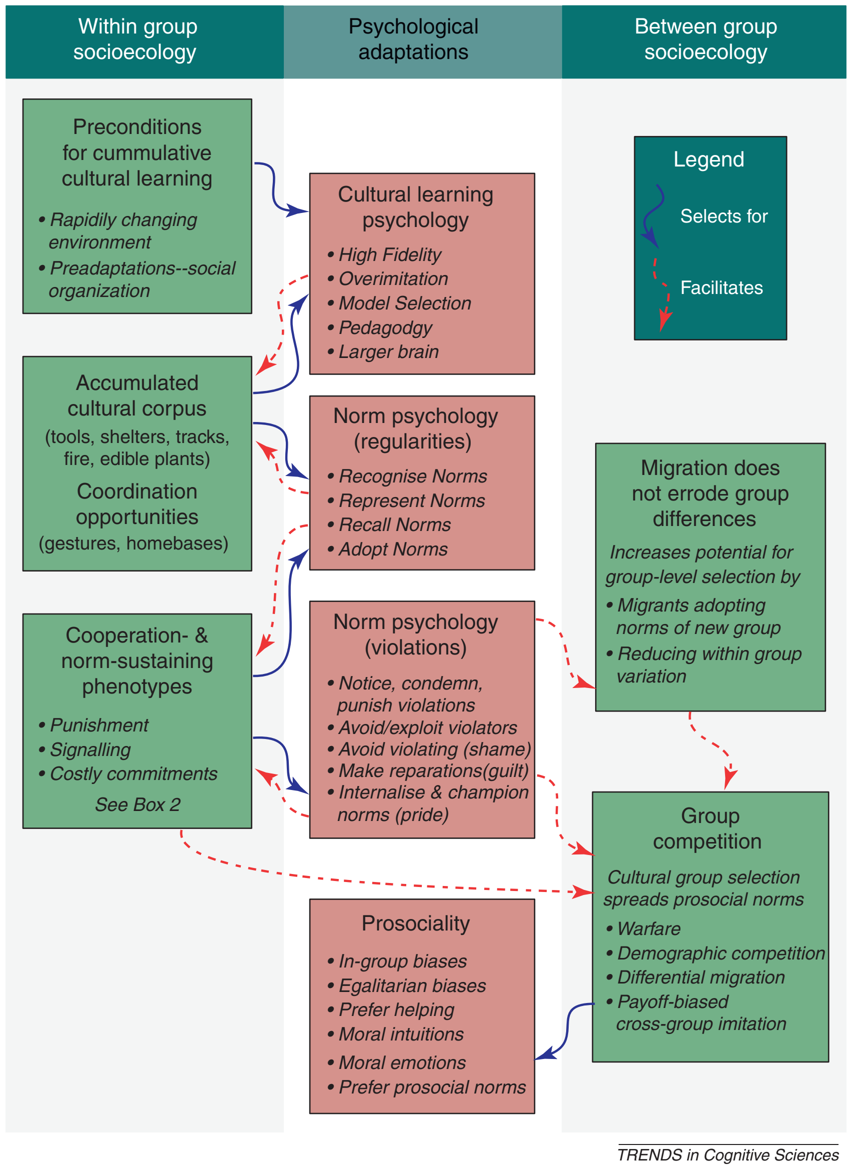

Figure 1. Key relationships in the coevolutionary path from cumulative cultural learning to norm psychology and eventually to prosocial dispositions and biases. In this visual guide to the evolutionary psychological dynamics, the central column contains cognitive and affective adaptations, whereas the left and right columns highlight, respectively, individual- and group-level socioecological features that select for, or are generated by, these adaptations. Solid, blue arrows indicate that the socioecological features select for a set of cognitive adaptations, whereas dashed, red arrows indicate which aspects of cognition and which socioecological features facilitate the emergence of which others.

motivations or heuristics. As this coevolving psychology emerges, it re-enforces these selection pressures; first, by increasing the quality and quantity of information in the cultural corpus, and thus pressure for bigger brains better at accessing, organizing and storing it; and second, by increasing phenotypic similarity within groups, and thus pressure and opportunities for coordination. Jointly, all these forces increase our species' sociality and, motivations to interact with and avoid exploiting conspecifics [26] (which increases group size), because other individuals become both easier to coordinate with and sources of adaptive information.

This coevolutionary account of culture, coordination and cognition also impacts cooperation. Cumulative cultural evolution is entangled with the evolution of cooperation for three reasons. First, the tension between the benefits of honestly sharing information and the temptation to manipulate others' culture-dependent phenotypes to one's own advantage itself represents a cooperative dilemma [17,27] (see Glossary). Second, the advent of language makes it far easier to both transmit complex, abstract information and to lie, greatly exacerbating the dilemma [28]. Finally, culturally transmitted social strategies involving reputation, punishment and signaling (Box 2) substantially increase phenotypic assortment and facilitate the spread of self-reinforcing cooperative norms, creating genetic selection for a prosocial psychology.

Many roads to norms for large-scale cooperation

Many agree that large-scale cooperation in human societies is puzzling because it occurs among distant- or non-relatives in large groups, even in foraging societies [29]. In addition to explaining how exploitative strategies might be held at bay at these larger scales, theories of human

Box 1. The five challenges of large-scale human cooperation

Theories that aim to explain large-scale human cooperation need to account for some peculiar features:

1) **Scale variation**: some societies lack collective action or cooperation beyond the extended family (little or no large-scale cooperation), whereas others routinely cooperate on the order of thousands or even millions of individuals. The norm-psychology approach proposes that social norms, which effectively harness and extend elements of our evolved social psychology (e.g. kinship), have emerged culturally over thousands of years, driven by a process involving competition among societies, organizations and institutions [8,38].
2) **Domain variation**: much ethnography and recently some experiments [91,92,101] indicate that the behavioral domains in which people cooperate vary dramatically from society to society. Although some groups cooperate only in warfare and fishing, others in the same ecology and with the same technology cooperate only in house-building and rituals [8]. The norm-psychology approach predicts that different groups will have different context-specific, self-re-enforcing social norms, which might or might not be cooperative.
3) **Rapid intensification and expansion**: not only does the scale of cooperation vary dramatically across societies, but in some societies (and not others) the scale and intensity of cooperation has expanded rapidly over the past 12 000 years. The norm-psychology approach proposes that the stabilization of global climates, which permitted the emergence of agriculture [102], led to enduring periods of intense inter-group competition [103] that has favored the social norms that foster success in such competitions [38].
4) **Species difference**: evolutionary accounts of human cooperation either need to also apply to other species (such as kin recognition) or be specific about why they do not apply to non-humans. Many standard evolutionary accounts aimed at human cooperation also predict large-scale cooperation in other primates, such as chimpanzees [29,97]. However, such large-scale cooperation has not been observed in other primates [8]. The norm-psychology account hinges on the emergence of cumulative cultural evolution, a phenomenon not observed in other species.
5) **Non-cooperative behavior**: ethnographic evidence indicates that the same incentive mechanisms (e.g. reputation) that support cooperation in humans also enforce behaviors unrelated to cooperation, such as ritual practices, food taboos and clothing choice [29]. In the norm-psychology account, theoretical research repeatedly shows that a variety of different mechanisms, including reputation, will maintain culturally transmitted behaviors independent of any benefits delivered to others (Box 2).

cooperation also face five species-specific challenges (Box 1). These challenges are crucial, although standard evolutionary approaches have not addressed them.

It is well established that stable cooperation depends on the positive assortment of cooperative phenotypes [30]: that is, some mechanism must ensure cooperators help cooperators more than non-cooperators. Several formal models using a variety of mechanisms suggest that cultural evolution – with its unique properties, rates and patterns of transmission – has many different ways to stabilize high levels of cooperation in large groups. Mechanisms that create mutually re-enforcing and stable cooperative groups include those based on reputation [31], punishment [32,33], signaling [34], aspects of cultural transmission [17] and combinations of these [35–37] (Box 2). Evidence from diverse populations suggests that different societies might have followed different cultural evolutionary roads to cooperation [29,38]. The genetically evolved cultural learning psychology described above strengthens phenotypic assortment, amplifying and re-enforcing this process.

Importantly, these models/mechanisms (e.g. reputation, signaling and punishment, among others) can stabilize any

Box 2. Mechanisms for sustaining cooperation and other norms

Generally, formal evolutionary models act as mental prostheses that help build intuitions about how complex evolutionary dynamics operate. For cooperation, theoretical models strive to explain the persistence of individually costly cooperation by describing strategies which, when sufficiently common, allow cooperators to outcompete non- cooperators while ‘paying’ for themselves [17,31,34,35]. These mechanisms share two important features. First, cooperative strategies cannot spread when rare, but are stable once common. The initial emergence of costly norms requires other mechanisms, such as stochastic fluctuations, non-random group fragmentations or other shocks. Cultural learning psychology and norm-psychology help fill this role: prestige- and success-biases allow influential leaders to seed new behavioral norms in small founder groups, which can then grow large; conformist-learning and norm-psychology ensure that new migrants to those groups conform to these norms (generating phenotypic assortment); cultural group selection spreads the more cooperative norms. Second, these models specify strategies that, once common, stabilize either cooperation or any other arbitrary norm. Because, in a public goods game (e.g. community defense or well-digging), the costs of cooperation create fitness differences among strategies but the benefits do not (i.e. they are shared equally), any mechanism that sustains this form of cooperation can sustain any equivalently costly behavior. Although these mechanisms are all conceptually rather different, they all yield higher fitness for individuals who behave according to arbitrary, individually costly local norms.

Here we summarize four types of mechanisms.

Reputation: ‘indirect reciprocity’ proposes that choices in one type of interaction have consequences in future interactions with other individuals in different contexts. In such models, defection in large-scale cooperative interactions (or any norm violation) can be sanctioned by others in dyadic interactions with violators [31], for example by not helping them. Norm violators accrue bad reputations, which allow others to exploit them without reputational damage.

Costly punishment: punishment-enforced, large-scale cooperation can be undermined by the proliferation of second order free riders, who cooperate but do not punish non-cooperators. One way to address this is to realize that learners use conformist transmission when payoff differences among alternative strategies become small [35,36]. Although conformist transmission might be too weak to maintain cooperation or punishing non-cooperators, it can (for example) maintain the punishment of non-punishers, which then stabilizes punishment and then cooperation. Alternatively, another way to resolve this is by establishing a ‘punishment pool’ [33], such as a police force, which can become self-sustaining by punishing those who do not contribute resources to it and can then sustain other costly behaviors.

Signaling intentions: the second order free rider problem can also be resolved if cooperators send an honest, costly signal of their intention to punish [37]. Fitness benefits accrue to those who adopt two different community-enforced norms: performing the costly signal and the costly behavior it stabilizes. Individuals effectively make a costly, norm-specified commitment to punish norm violators.

Signaling quality: if the quality of potential social partners is difficult to observe, and high quality individuals can signal their quality by punishing norm violators, then costly norms can be sustained by punishment. Here, having honestly communicated their higher quality to others, signaler-punishers obtain the benefits of preferred matings/alliances [34].

similarly costly behavior, strategy or practice, independent of whether it delivers benefits to anyone; the costs of the action matter but the benefits are irrelevant for stability (Box 2). These mechanisms generate multiple stable equilibria. Even behaviors with a net cost for the group can be sustained. Thus, these models concern more than cooperation *per se*: they are about what we call social norms. Social norms are emergent phenomena and fundamentally group-level properties.

Multiple stable equilibria pose a problem for explanations of large-scale cooperation, especially in purely genetic models. Most possible norms are not cooperative and these models alone provide no way to sort the cooperative equilibria from the non-cooperative or plainly maladaptive ones. Although a few groups might happen to develop cooperative norms, without some mechanism selecting between them, most would enforce non-cooperative behaviors. In one sense this is an important feature of this approach, since the ethnographic record shows that societies do possess many non-cooperative, and even group-damaging, social norms (e.g. disease spreading endocannibalism, infantile skull deformation, female infibulations, subincision) [39,40]. However, these within-group mechanisms alone do not explain the prevalence of large-scale cooperation. From Box 1, they address Challenges 2 and 5, but not 3.

Fortunately, cultural evolution provides at least three different processes to select among these different stable equilibria: (i) rational, forward-looking, calculation by individuals; (ii) high levels of stochasticity (random fluctuations) such that stable equilibria with larger basins of attraction will emerge more frequently; and (iii) cultural group selection. For brevity, we skip the first two, which we feel have been less important over the course of human history [29].

The emergence of multiple stable equilibria creates the conditions for inter-group competition to influence the prevalence of different types of social norms, a process labeled cultural group selection. Genetic group selection is typically rather weak compared with within-group selection in genetically well-mixed species, such as humans. By contrast, cultural learning biases and norm-psychology maintain culturally transmitted phenotypic similarity within groups and differences between groups even in the face of migration, making cultural group selection a potentially potent force in shaping norms. Empirical evidence for cultural group selection is plentiful (see reviews in [7,29]), and recent studies indicate that cultural differences are much greater than genetic differences among groups [41]. When groups compete cultural group selection favors whichever internally stable norms best facilitate their success and longevity [23,29,42]. Competition among groups can take the form of warfare (with assimilation or extinction, [43]), demographic production, or more subtle forms. For instance, individuals might imitate the (on average) more successful members of groups at more prosocial equilibria, leading to a differential flow of decisions, strategies and even preferences from higher to lower payoff groups [44] or differential migration from lower payoff groups to higher payoff groups [45]. Over centuries, this process sustains and aggregates group-beneficial norms (into institutions) that foster success in competition with other societies – addressing Challenge 3 in Box 1.

Through these ongoing processes, cultural evolution has shaped the selective social environment for genes. Genes that cause their bearers to rapidly identify local norms and adhere to them will avoid negative consequences and gain any social benefits of norm-compliance. Proximate mechanisms evolved to these ends include emotional and motivational systems such as shame/guilt (to motivate avoiding or repairing reputational damage), pride in attaining social ideals, and norm internalization, which can counteract temptations to short-term defection and avoids costly errors from miscalculations of costs and benefits.

Much of the psychological machinery for identifying both norms and deviations from them is already in place at this point in our account, described above. The additional psychological machinery that motivates disliking and sanctioning norm violators is favored in several models of cooperation for different reasons (Box 2), including avoiding being punished for not punishing and to gainfully exploit norm violators.

The interaction between culture and genes is continuous. The more genes respond by building and honing the above-described norm-psychology, the more they power up the cultural processes that generate and sustain local phenotypic assortment, sanction deviations within groups and select for more cooperative norms. This creates a culture–gene coevolutionary ratchet for both the importance of social norms and the intensity of prosociality [23]. As cultural group selection increasingly guarantees that learners find themselves in social groups organized by norms that incentivize prosocial or cooperative behavior [8,23], within-group (and between-group) genetic selection processes will favor genes that build prosocial, norm-adhering phenotypes. This evolutionary trajectory – from cultural learning, to norm-psychology, to cultural group selection for prosocial norms to psychological adaptation to a world dominated by prosocial norms – may help explain some of the puzzling prosocial experimental results that have been dubbed 'strong reciprocity'.

A major take-home point from this review is that cultural evolution, increasingly reinforced by norm-psychology, can solve the problem of large-scale cooperation in a variety of ways. Over time cultural evolution has honed and recombined the above mechanisms, often by harnessing our more ancient instincts for dominance, reciprocity and kinship, and in the process cobbled together elegant informal institutions that we have just begun to glimpse. Empirically, this implies that studying sociality among Westerners can only teach us about the inner-workings of one system of social norms [46], and tells us little about how human cooperation works in general.

Culture-free evolutionary approaches to large-scale cooperation

Building on models developed for non-cultural species, existing evolutionary approaches to understanding human psychology and behavior have generated many important insights into our species' sociality and cooperation. Key areas of research include kin-based cooperation [47], direct reciprocity [48] and signaling approaches [49]. The norm-psychology account is not inconsistent with these theoretical lines. In fact, it postulates adaptations triggered by the emergence of cumulative culture that necessarily built on top of earlier cognitive adaptations to selection pressures faced by our less cultural primate ancestors ('ancient social instincts' [50]). It expands the scope of these explanations by considering how cultural evolution – driven by competition among social groups, institutions and organizations – might have harnessed, extended or suppressed these elements of our evolved psychology. For instance, in addition to predicting that all humans preferentially cooperate with close kin, it offers purchase on the origins of the complex kinship systems found in many small-scale societies, where evolved kin-intuitions interact with local norms to extend cooperation to some sets of distant kin but not others [51], and how this influences interactions between them. However, focusing exclusively on how our kin-based or reciprocity-based social psychology plays out within these different institutions misses the forest for the trees.

Some accounts argue that these culture-free standard models (e.g. kinship and reciprocity) alone suffice to explain the breadth of human cooperation [52,53]. These 'mismatch' arguments postulate that humans evolved cognitive dispositions for cooperating in ancestral societies that contained mostly kin in stable groups with few (if any) ephemeral interactants. These small-scale dispositions and heuristics maladaptively persist – as do our tastes for French fries and pornography – in today's anonymous environments.

We can only summarize the theoretical and empirical problems with this mismatch approach here, but have detailed them elsewhere [29,54]. Empirically, mismatch accounts cannot meet the five challenges in Box 1. Theoretically, mismatch hypotheses fail for two reasons. First, an examination of the formal models on which these hypotheses are grounded indicate they cannot even explain the cooperative patterns observed among small-scale societies [55], such as food sharing or territorial defense, which is a prerequisite for a maladaptive extension to modern societies. Small-scale societies are also governed by norms. Second, even if we assume these theoretical problems can be solved, the common assumptions that ancestral societies lacked a substantial fraction of non-relatives or fitness-relevant ephemeral interactions does not hold up empirically for either ethnographically and historically known foragers [56] or in studies of non-human primates.

Evidence

The above account of how – following the advent of cumulative culture – norm-psychology is shaped by the challenges of cultural learning, coordination and cooperation was constructed by applying the logic of natural selection with the aid of mathematics under the constraints imposed by ancestral conditions. The predictions it generates about human psychology are finding support in diverse research programs.

Evincing our cultural learning psychology, adults, young children and sometimes even infants readily demonstrate the learning biases predicted for a species reliant on social learning. Human learners, both adults and children, preferentially attend to and learn from individuals with

- greater skill or success [57–60];
- cues of confidence [61];
- more experience, including using age as an indirect cue [62,63];
- prestige (greater attention or deference from others, [18]);
- ethnic markers (e.g. dialect and language), matching their own or their parents [64–67]; and
- more common variants [68–70].

Although some of these predictions apply to any socially learning species, where they have also been recently demonstrated [71,72], the culture–gene coevolutionary account predicts that abilities for cultural learning will be the distinguishing cognitive specialization of our species (confirmed in [73]). Cumulative cultural evolution creates sufficiently complex artifacts and phenotypes (e.g. stone tools and shamans) that learners often need to faithfully copy elements that lack any obvious function (sometimes overriding their own intuitions). In support of this view, children from diverse societies accurately imitate adults' seemingly unnecessary behaviors (they 'overimitate') even though they are capable of disregarding them [74,75]. This is not true for chimpanzees in the same scenarios, who drop the unnecessary steps when copying [76], focusing on the goal not the process [13]. Moreover, research on natural pedagogy suggests that humans are programmed to attend to non-verbal cues (e.g. eye contact) that initiate a special 'cultural learning mode', which increases expectations of generalizable knowledge (including social rules), transmission fidelity and overimmitative errors [77].

In the norm-psychology account, norms create selection pressures for learners to act as though they live in a world governed by social rules that they need to acquire, many of which are prosocial. Young children show motivations to conform in front of peers [78], spontaneously infer the existence of social rules by observing them just once, react negatively to deviations by others to a rule they learned from just one observation, spontaneously sanction norm violators [79] and selectively learn norms (that they later enforce) from older [63] and more reliable [59] informants. Children also acquire context-specific prosocial norms by observing others perform actions consistent with such norms and spontaneously (without modeling) enforce these norms on other children. Such norm acquisition endures in retests weeks or months later (reviewed in [8]). As expected, such cognitive mechanisms for norm-psychology are on-line early, as even young infants can evaluate actions as helpful or hurtful (using the prosocial inferential biases) and use this information to decide with whom to interact [80,81] and learn from.

The norm-psychology account explains how prosocial dispositions can evolve in the niche created by the internally enforced cooperative norms spread by cultural group selection. Consistent with this possibility, prosocial dispositions are being observed in ever younger children [82], including actively intervening to prevent and ameliorate harm to others [83] and discriminating against norm violators [84]. Meanwhile, convergent evidence from cross-cultural, social and moral psychology is describing a robust adult disposition to condemn to others' norm violations, even when this incurs immediate costs (for a recent review, see [11]).

The selection pressures created by reputational damage and punishment can also favor norm-internalization. Neuroeconomic studies suggest that social norms are internalized as intrinsic motivations in people's brains. Both cooperating and punishing in locally normative ways activates the brain's rewards or reward anticipation circuits in the same manner as does obtaining a direct cash payment [85–87]. Moreover, violating norms (i.e. breaking promises or inflicting harm) requires overriding automatic responses by brain regions responsible for cognitive control [88]. After acquiring norms, we have to 'think' in order to break them, not to adhere to them.

A broad range of findings from behavioral economics can be explained by recognizing that experimental games tap culture-specific norms, often involving monetary transactions with strangers. First, measures of fairness and willingness to punish from standard bargaining experiments vary dramatically across societies in a manner that covaries with market integration and community size, respectively [29,38]. Second, framing the games to cue local norms can alter behavior in predictable ways [89,90], including findings showing that the same frames have different effects in different populations [91–94]. Third, game behaviors can be experimentally influenced by observational learning [95], and prosocial game behavior emerges gradually over development (unlike reciprocity), not plateauing until people reach their mid-twenties [96]. Finally, despite living in small-scale foraging groups, nonhuman primates fail to reveal the prosocial preferences towards strangers so puzzling in the largest-scale human societies [97].

Concluding remarks

The account presented in this article complements other evolutionary approaches to human sociality, including those focused on kinship, reciprocity and social status, which are important components of our evolved psychology [8,18]. By taking seriously our long history as a cultural species, a coevolutionary approach offers explanatory traction on not just why humans cooperate on large-scales with strangers, but also why the forms of this cooperation vary so dramatically between societies and across time. More generally, norm-psychology connects ethnographic, archaeological, historical, genomic and climatological evidence about ancestral conditions in a formal framework to derive specific predictions about individual level cognitive adaptations that influence learning, and thereby generate and sustain cross-cultural variability and the group-level dynamics that result. As such, it can help integrate disparate empirical and theoretical programs under a broadened evolutionary umbrella (Box 3).

The central theoretical insight stemming from the norm-psychology account is that once individuals can culturally learn social behavior with sufficient fidelity, self-enforcing stable states will spontaneously emerge in social groups. The self-re-enforcing nature of norms will lead to competition among groups with different norms (varying in prosociality) and to selection pressures within groups to avoid deviations. An important consequence of this is that the most selection-relevant features of social environments are norms, not just opportunities for cooperation. This suggests that if we want to carve nature at its joints, the functionally relevant aspects of our psychology will concern social norms, not cooperation *per se*. This conceptual shift illuminates several otherwise puzzling aspects of large-scale human cooperation (Box 2).

Box 3. Questions for future research

- How are norms actually sustained in human societies, institutions and organizations, particularly in small-scale societies? Although anthropologists have supplied general accounts of diverse norms, we need research by theoretically informed fieldworkers using methods that can distinguish how norms in different societies and contexts are sustained.
- When in human evolutionary history did our lineage cross the threshold into the regime of cumulative cultural evolution, the point from which cultural and genetic evolution began interacting in substantial ways? Whereas earlier paleoanthropological research suggests that this reliance might have been relatively recent, current research suggests that a substantial reliance on culture could go back hundreds of thousands of years, or more.
- What pathways has culture–gene coevolution taken within the past ten millennia? Much research in evolutionary psychology has assumed that genetic change is relatively slow, leaving modern humans little differentiated genetically from our Paleolithic ancestors. However, recent research from genetics suggests that (i) genetic change across many species occurs more rapidly than previously thought; (ii) rates of human genetic evolution have, if anything, only accelerated recently; and (iii) culturally constructed environments create powerful – and often autocatalytic – selection pressures on genes, and appear to have had a substantial impact on the patterns of genetic variation in the modern human genome [1].

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References

1 Laland, K.N. *et al.* (2010) How culture shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* 11, 137–148
2 Richerson, P.J. *et al.* (2010) Gene–culture coevolution in the age of genomics. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8985–8992
3 Alperson-Afil, N. *et al.* (2009) Spatial organization of hominin activities at Gesher Benot Ya'aqov, Israel. *Science* 326, 1677–1680
4 Brown, K. *et al.* (2009) Fire as an engineering tool of early modern humans. *Science* 325, 859
5 Thieme, H. (1997) Lower Palaeolithic hunting spears from Germany. *Nature* 385, 807–810
6 Wrangham, R. (2009) *Catching Fire: How Cooking Made us Human*, Basic Books
7 Richerson, P. and Boyd, R. (2005) *Not by Genes Alone: How Culture Transformed Human Evolution*, University of Chicago Press
8 Henrich, N. and Henrich, J. (2007) *Why Humans Cooperate: A Cultural and Evolutionary Explanation*, Oxford University Press
9 Fessler, D.M.T. (2007) From appeasement to conformity: evolutionary and cultural perspective on shame, competition and cooperation. In *The Self-Conscious Emotion: Theory and Research* (Tracy, J. *et al.*, eds), pp. 174–193, The Guilford Press
10 Sripada, C. and Stich, S. (2006) A framework for the psychology of norms. In *The Innate Mind: Culture and Cognition* (Carruthers, P. *et al.*, eds), pp. 280–301, Oxford University Press
11 DeScioli, P. and Kurzban, R. (2009) Mysteries of morality. *Cognition* 112, 281–299

12 Boyd, R. and Richerson, P.J. (1996) Why culture is common but cultural evolution is rare. *Proc. Br. Acad.* 88, 73–93
13 Tennie, C. *et al.* (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos. Trans. R. Soc. B* 364, 2405–2415
14 Toth, N. and Schick, K. (2009) The Oldowan: the tool making of early hominins and chimpanzees compared. *Annu. Rev. Anthrop.* 38, 289–305
15 Enquist, M. and Ghirlanda, S. (2007) Evolution of social learning does not explain the origin of human cumulative culture. *J. Theor. Biol.* 246, 129–135
16 Tomasello, M. (1999) *The Cultural Origins of Human Cognition*, Harvard University Press
17 Henrich, J. (2009) The evolution of costly displays, cooperation, and religion: credibility enhancing displays and their implications for cultural evolution. *Evol. Hum. Behav.* 30, 244–260
18 Henrich, J. and Gil-White, F. (2001) The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* 22, 165–196
19 Rendell, L. *et al.* (2011) Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends. Cogn. Sci.* 15, 68–76
20 Boyd, R. and Richerson, P.J. (1985) *Culture and the Evolutionary Process*, University of Chicago Press
21 McElreath, R. *et al.* (2003) Shared norms and the evolution of ethnic markers. *Curr. Anthrop.* 44, 122–129
22 Kendal, J. *et al.* (2009) The evolution of social learning rules: payoff-biased and frequency-dependent biased transmission. *J. Theor. Biol.* 260, 210–219
23 Henrich, J. (2004) Cultural group selection, coevolutionary processes and large-scale cooperation. *J. Econ. Behav. Organ.* 53, 3–35
24 Henrich, J. and Boyd, R. (2008) Division of labor, economic specialization, and the evolution of social stratification. *Curr. Anthrop.* 49, 715–724
25 McElreath, R. *et al.* (2003) Shared norms and the evolution of ethnic markers. *Curr. Anthrop.* 44, 122–130
26 Warneken, F. and Tomasello, M. (2009) Varieties of altruism in children and chimpanzees. *Trends Cogn. Sci.* 13, 397–402
27 Lachmann, M. and Bergstrom, C.T. (2004) The disadvantage of combinatorial communication. *Proc. R. Soc. Lond. B* 271, 2337–2343
28 Sperber, D. *et al.* (2010) Epistemic vigilance. *Mind Lang.* 25, 359–393
29 Chudek, M. *et al*. (forthcoming) Culture–gene coevolution, large-scale cooperation and the shaping of human social psychology. In: Joyce, R. *et al.*, (eds), *Signaling, Commitment, and Emotion,* MIT Press
30 Fletcher, J. and Doebeli, M. (2009) A simple and general explanation for the evolution of altruism. *Proc. R. Soc. Lond. B: Biol. Sci.* 276, 13–19
31 Panchanathan, K. and Boyd, R. (2004) Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature* 432, 499–502
32 Boyd, R. and Richerson, P. (1992) Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* 13, 171–195
33 Sigmund, K. *et al.* (2010) Social learning promotes institutions for governing the commons. *Nature* 466, 861–863
34 Gintis, H. *et al.* (2001) Costly signaling and cooperation. *J. Theor. Biol.* 213, 103–119
35 Henrich, J. and Boyd, R. (2001) Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *J. Theor. Biol.* 208, 79–89
36 Guzman, R.A. *et al.* (2007) When in Rome, do as the Romans do: the coevolution of altruistic punishment, conformist learning, and cooperation. *Evol. Hum. Behav.* 28, 112–117
37 Boyd, R. *et al.* (2010) Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science* 328, 617–620
38 Henrich, J. *et al.* (2010) Markets, religion, community size and the evolution of fairness and punishment. *Science* 327, 1480–1484
39 Durham, W. (1991) *Coevolution: Genes Culture and Human Diversity*, Stanford University Press
40 Edgerton, R.B. (1992) *Sick Societies: Challenging the Myth of Primitive Harmony*, Free Press
41 Bell, A.V. *et al.* (2009) Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proc. Natl. Acad. Sci. U.S.A.* 106, 17671–17674
42 Boyd, R. and Richerson, P.J. (1990) Group selection among alternative evolutionarily stable strategies. *J. Theor. Biol.* 145, 331–342
43 Choi, J-K. and Bowles, S. (2007) The coevolution of parochial altruism and war. *Science* 318, 636–640
44 Boyd, R. and Richerson, P. (2002) Group beneficial norms can spread rapidly in a structured population. *J. Theor. Biol.* 215, 287–296
45 Boyd, R. and Richerson, P.J. (2009) Voting with your feet: payoff biased migration and the evolution of group beneficial behavior. *J. Theor. Biol.* 257, 331–339
46 Henrich, J. *et al.* (2010) The weirdest people in the world? *Behav. Brain Sci.* 33, 1–23
47 Chagnon, N. and Irons, W. (1979) *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, Duxbury Press
48 Gurven, M. (2004) To give and to give not: the behavioral ecology of human food transfers. *Behav. Brain Sci.* 27, 543–583
49 Smith, E.A. and Bliege Bird, R.L. (2000) Turtle hunting and tombstone opening: public generosity as costly signaling. *Evol. Hum. Behav.* 21, 245–261
50 Richerson, P. and Boyd, R. (1998) The evolution of ultrasociality. In *Indoctrinability, Ideology and Warfare* (Eibl-Eibesfeldt, I. and Salter, F.K., eds), pp. 71–96, Berghahn Books
51 Alvard, M.S. (2003) Kinship, lineage, and an evolutionary perspective on cooperative hunting groups in Indonesia. *Hum. Nat.* 14, 129–163
52 Hagen, E.H. and Hammerstein, P. (2006) Game theory and human evolution: a critique of some recent interpretations of experimental games. *Theor. Popul. Biol.* 69, 339–348
53 Burnham, T.C. and Johnson, D.D. (2005) The biological and evolutionary logic of human cooperation. *Analyse Kritik* 27, 113–135
54 Fehr, E. and Henrich, J. (2003) Is strong reciprocity a maladaption? In *Genetic and Cultural Evolution of Cooperation* (Hammerstein, P., ed.), pp. 55–82, MIT Press
55 Alvard, M. (2009) Kinship and cooperation. *Hum. Nat.* 20, 394–416
56 Hill, K.R. *et al.* (2011) Co-Residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure. *Science* 331, 1286–1289
57 Birch, S.A.J. *et al.* (2008) Three- and four-year-olds spontaneously use others' past performance to guide their learning. *Cogn. Int. J. Cogn. Sci.* 107, 1018–1034
58 Corriveau, K. and Harris, P. (2009) Preschoolers continue to trust a more accurate informant 1 week after exposure to accuracy information. *Dev. Sci.* 12, 188–193
59 Rakoczy, H. *et al.* (2009) Young children's selective learning of rule games from reliable and unreliable models. *Cogn. Dev.* 24, 61–69
60 Brosseau-Liard, P.E. and Birch, S.A.J. (2010) I bet you know more and are nicer too!': what children infer from others' accuracy. *Dev. Sci.* 13, 772–778
61 Birch, S. *et al.* (2010) Two-year-olds are vigilant of others non-verbal cues to credibility. *Dev. Sci.* 13, 363–369
62 Jaswal, V. and Neely, L. (2006) Adults don't always know best. *Psychol. Sci.* 17, 757
63 Rakoczy, H. *et al.* (2010) Bigger knows better – young children selectively learn rule games from adults rather than from peers. *Br. J. Dev. Psychol.* 28, 785–798
64 Shutts, K. *et al.* (2009) Social information guides infants' selection of foods. *J. Cogn. Dev.* 10, 1–17
65 Efferson, C. *et al.* (2008) The coevolution of cultural groups and ingroup favoritism. *Science* 321, 1844–1849
66 Kinzler, K.D. *et al.* (2007) The native language of social cognition. *Proc. Natl. Acad. Sci. U.S.A.* 104, 12577
67 Kinzler, K.D. *et al.* (2009) Accent trumps race in guiding children's social preferences. *Soc. Cogn.* 27, 623–634
68 McElreath, R. *et al.* (2008) Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philos. Trans. R. Soc. B* 363, 3515–3528
69 Corriveau, K.H. *et al.* (2009) Going with the flow: preschoolers prefer nondissenters as informants. *Psychol. Sci.* 20, 372–377
70 Fusaro, M. and Harris, P.L. (2008) Children assess informant reliability using bystanders' non verbal cues. *Dev. Sci.* 11, 771–777
71 Laland, K.N. *et al.* (2011) From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philos. Trans. R. Soc. B: Biol. Sci.* 366, 958–968
72 Galef, B.G. and Whiskin, E.E. (2008) Conformity in Norway rats? *Anim. Behav.* 75, 2035–2039

73 Herrmann, E. *et al.* (2007) Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* 317, 1360–1366
74 Nielsen, M. and Tomaselli, K. (2010) Overimitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychol. Sci.* 21, 729–736
75 Lyons, D.E. *et al.* (2007) The hidden structure of overimitation. *Proc. Natl. Acad. Sci. U.S.A.* 104, 19751–19756
76 Whiten, A. *et al.* (2009) Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philos. Trans. R. Soc. B* 364, 2417–2428
77 Topal, J. *et al.* (2008) Infants perseverative search errors are induced by pragmatic misinterpretation. *Science* 321, 1831
78 Haun, D. and Tomasello, M. Conformity to peer-pressure in preschool children. *Child Dev.* (in press)
79 Rakoczy, H. *et al.* (2008) The sources of normativity: young children's awareness of the normative structure of games. *Dev. Psychol.* 44, 875–881
80 Hamlin, J.K. *et al.* (2007) Social evaluation by preverbal infants. *Nature* 450, 557–559
81 Hamlin, J.K. *et al.* (2010) Three-month-olds show a negativity bias in their social evaluations. *Dev. Sci.* 13, 923–929
82 Dunfield, K. *et al* Examining the diversity of prosocial behavior: helping, sharing, and comforting in infancy. *Infancy.* (in press)
83 Vaish, A. *et al.* (2011) Three year old children intervene in third party moral transgressions. *Br. J. Dev. Psychol.* 29, 124–130
84 Vaish, A. *et al.* (2010) Young children selectively avoid helping people with harmful intentions. *Child Dev.* 81, 1661–1669
85 Fehr, E. and Camerer, C.F. (2007) Social neuroeconomics: the neural circuitry of social preferences. *Trends Cogn. Sci.* 11, 419–427
86 Tabibnia, G. *et al.* (2008) The sunny side of fairness – preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). *Psychol. Sci.* 19, 339–347
87 de Quervain, D.J. *et al.* (2004) The neural basis of altruistic punishment. *Science* 305, 1254–1258
88 Baumgartner, T. *et al.* (2009) The neural circuitry of a broken promise. *Neuron* 64, 756–770
89 Henrich, J. *et al.* (2005) "Economic man" in cross-cultural perspective: behavioral experiments in 15 small-scale societies. *Behav. Brain Sci.* 28, 795–855
90 Herrmann, B. *et al.* (2008) Antisocial punishment across societies. *Science* 319, 1362–1367
91 Poppe, M. (2005) The specificity of social dilemma situations. *J. Econ. Psychol.* 26, 431–441
92 Goerg, S.J. and Walkowitz, G. (2010) On the prevalence of framing effects across subject-pools in a two-person cooperation game. *J. Econ. Psychol.* 31, 849–859
93 Pillutla, M.M. and Chen, X.P. (1999) Social norms and cooperation in social dilemmas: the effects of context and feedback. *Organ. Behav. Hum. Decis. Process* 78, 81–103
94 Ross, L. and Ward, A. (1996) Naive realism: implications for social conflict and misunderstanding. In *Values and Knowledge* (Brown, T. *et al.*, eds), pp. 103–135, Lawrence Erlbaum Associates
95 Cason, T.N. and Mui, V.L. (1998) Social influence in the sequential dictator game. *J. Math. Psychol.* 42, 248–265
96 Sutter, M. and Kocher, M. (2007) Age and the development of trust and reciprocity. *Games Econ. Behav.* 59, 364–382
97 Silk, J.B. (2008) Social preferences in primates. In *Neuroeconomics* (Glimcher, P.W. *et al.*, eds), pp. 269–284, Academic Press
98 Henrich, N.S. and Henrich, J. (2007) *Why Humans Cooperate: A Cultural and Evolutionary Explanation*, Oxford University Press
99 Boyd, R. *et al.* (2011) Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behav. Ecol. Sociobiol.* 65, 431–444
100 Laland, K.N. and Galef, B.G. (2009) *The Question of Animal Culture*, Harvard University Press
101 Cronk, L. (2007) The influence of cultural framing on play in the trust game: a Maasai example. *Evol. Hum. Behav.* 28, 352–358
102 Richerson, P.J. *et al.* (2001) Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *Am. Antiquity* 66, 387–411
103 Diamond, J.M. (1997) *Guns, Germs and Steel: The Fates of Human Societies*, W.W. Norton