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The Decent of Man II

On the Origin of Cooperation

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You take a flight from New York to London. Thousands and perhaps millions of people—including ticket agents, baggage handlers, security personnel, air traffic controllers, pilots, and flight attendants, but behind the scenes also airline administrators, meteorologists, engineers, aircraft designers, and many others—cooperated to get you there safely. No one stole your luggage, no one ate your in-flight food, and no one tried to sit in your seat. In fact, the hundreds of people on the airplane, despite being mainly strangers, behaved in an entirely civilized and respectful manner throughout.

For most of us in the industrialized world, every aspect of our lives is utterly reliant on thousands of such cooperative interactions with millions of individuals from hundreds of countries, the vast majority of whom we never see, don't know, and indeed never knew existed. Just how exceptional in nature such intricate coordination is—with many unrelated individuals performing many different roles—remains hard to appreciate. Notwithstanding the familiar examples of ants, bees, and other species known for coordinating their behavior, largely with relatives, nothing remotely as complex as human cooperation is found in any of the other millions of species on the planet. And although modern marvels like air travel are very striking examples of large-scale cooperation, human societies have engaged in impressive feats of organized cooperation for many thousands of years. Carving terraces out of mountains, planting and harvesting crops, building granaries, and managing city-states all involved extraordinary levels of cooperation among community members. Hunter-gatherers also coordinated their actions in cooperative endeavors such as group hunting and foraging, as well as through sharing food, labor, and childcare, and when hostility or disputes with other societies arose. How is it that humans came to be the most cooperative species on earth? And how can understanding our evolutionary history help to explain human

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cultural, cooperative achievements, whether technological or artistic, linguistic or moral?

Evolutionary explanations for cooperation may at first seem paradoxical, since evolution is often conceived of in terms of competition between individuals and their struggle for survival and reproduction. The fittest, we might think, are those that care least about the success of others. But this impression is misleading. Cooperation is integral to the flourishing of many forms of life, and has long been a subject of study for evolutionary biologists. Indeed, virtually all of the major transitions in evolution, for instance the development of the first cells, of eukaryotes, or of multicellular organisms, required the establishment of new forms of cooperation between hitherto independent elements. The challenge in finding evolutionary explanations for cooperation is to identify behaviors that provide a benefit to another individual and that would likely have been favored by natural selection because of this positive effect on the recipient or the group.

One simple evolutionary explanation for cooperation is readily available. It is what biologists call "kin selection," which is the way individuals can help propagate their own genes by helping biologically related kin who share those genes. But while kin selection can account for some aspects of the cooperation in human societies—most obviously when people cooperate to raise their relatives' children—it does not explain the larger-scale projects created by unrelated or distantly related individuals that set humans apart from other animals. Our distant ancestors are thought to have aggregated into small bands that were often kin-based, but present-day hunter-gatherer societies are known to have extensive interactions with nonrelatives, even in societies numbering only a few hundred individuals. In these small societies, cooperative activities are regulated by systems of norms and institutions, which become even more important in larger agricultural societies, where cooperative arrangements have to be negotiated and maintained among thousands of often unrelated individuals. Kin selection alone cannot explain the vast scale of human cooperation.

In some instances certainly, cooperation with distantly related individuals was a result of coercion—powerful leaders and groups forcing the weak to do their hard labor. By 4000 B.C., the Sumerians were building cities of over ten thousand people by using the labor of slaves captured from the hill country, and the Old Testament book of Exodus reports that the Egyptians "put slave masters over [the Israelites] to oppress them with forced labor." But coercion cannot be the whole story behind large-scale human cooperation. In order to acquire slaves, societies would

need to engage in impressive acts of cooperation already, either to field an organized army capable of capturing and subduing those whom the society would enslave, or to suppress and control large numbers of its own people. Moreover, historical research has established that some of the major architectural projects of antiquity did not rely on slave labor. The pyramids, for instance, are now thought to have been built by paid laborers. The builders came from poor families from the north and south of Egypt and were respected for their work—indeed, those who died during construction were bestowed the honor of being buried in the tombs near the sacred pyramids of their pharaohs. Ancient societies, just like those of today, including contemporary hunter-gatherer societies, were built using complex forms of cooperation in which most individuals participated entirely voluntarily.

How was this possible? Conventional evolutionary explanations that focus only on genetic variation and inheritance—such as kin selection theory—cannot account for the most impressive forms of large-scale human cooperation. The answer is more multifaceted, and draws on some rarely appreciated connections between cooperation and social learning—and, more broadly, between our biological history and our cultural history.

Language, Teaching, and Norms

One of the most distinctive features of the human species is our capacity for language, and linguistic ability is one factor that helps to explain our ability to cooperate. The origin of language is a highly contentious topic in human evolution, and there are many theories that attempt to explain it. Perhaps the most plausible theory is that language developed in conjunction with the early culture made possible by our ancestors' ability to teach, imitate, and learn. Language may initially have evolved to enhance the efficiency and accuracy of teaching kin, and although teaching may not be the first thing that comes to mind when we think of cooperation, it is in fact a fundamental early form of cooperation.

Teaching is widespread in humans because cumulative cultural knowledge builds up over time, keeping difficult-to-learn but highly advantageous information (such as how to make a functional stone tool or to gather honey) available in the population as tutors impart it to their pupils. Evolutionary models have shown that the likelihood of teaching was at first highest when tutor and pupil were closely related. We can envisage the kind of widespread, generalized teaching observed in humans to have initially appeared among close relatives; for instance, parents teaching

foraging skills to offspring, or siblings helping each other learn tool-making. Yet, without some rudimentary form of language, the teaching of more distant relatives would rarely have been worth the investment of time and effort. But by making teaching easier and more accurate, the advent of language would have made it more feasible for would-be teachers to instruct distantly related pupils as well. Such language-mediated teaching may have sufficed to allow individuals in small groups to teach each other specific roles in coordinated tasks, such as hunting antelope or driving off predators, thereby broadening the scale of kin-based cooperation to include more distant relatives.

The ability of humans to transmit knowledge between generations, especially through language, can also help explain how human societies are able to sustain the kinds of norms and institutions necessary to enforce cooperation—laws, for instance, must be taught if they are to function properly. But how are these norms and institutions different from the patterns of learning we observe in nonhuman animals?

Many animals that are proficient at social learning (such as primates, whales, and dolphins) exhibit behavioral traditions, which are society-specific conventions for such behaviors as singing or ways of hunting prey. Our ancestors also had group-specific habits maintained as social conventions. Some traditional behaviors could be picked up through observational learning, while other, more challenging habits would have spread through teaching among relatives. But unlike much human teaching, most animal teaching merely creates enhanced opportunities for learning in the pupil, as when meerkats provide pups with disabled scorpions so the pups learn how to handle the dangerous prey. In rare cases, however, animals show hints of "coaching," in which the teacher responds in ways that encourage or discourage the pupil's behavior, such as the maternal display of a mother hen who pecks and scratches the ground intensively to distract her chicks from unpalatable food.

Such error correction is, of course, a feature of human teaching as well, and systematic error correction likely led to the transition from reliance on mere conventions toward governance through norms. Instead of illustrating only *a* way to behave, people began insisting on *the* way to behave. Eventually, each society was characterized by a particular set of norms that dictated how individuals *should* act—for example, how they should build fires, how they should catch turtles, how they should till the soil—each of which was propagated through verbal instruction. Norms specify rules of social interaction too, including how people should respond to violations of norms. With the advent of norms, the social life

of our ancestors transformed from simply living in groups to identifying with the group, abiding by its rules, and privileging in-group members. Norms facilitated group coordination and thereby substantially enhanced social cooperation. To resolve conflicts or prevent social problems from arising in the future, institutionalizing the norm as a rule of law that all members of the society must abide by, and agreeing on sanctions for violators, would sometimes have been necessary.

The ability to teach cultural norms using language also laid the foundation for the emergence of rule-governed social institutions. The rules that different human societies live by are often not at all intuitive, and young members of a community must be taught both the nature of the norms and the need to conform to them. There are many examples of complex rule-governed behavior in modern societies that must be taught: how to write a check; when, how, and why citizens should pay their taxes; or the rules of driving. All human societies possess such norms that require active instruction of the young, sometimes simply by parents and family members, but also in socially organized learning environments, such as schools.

The scale of human cooperation is unprecedented in large part because it is uniquely built upon socially learned and transmitted norms. Other animals do exhibit cooperative foraging, hunting, and defense—lions hunting, for instance, or the circular defensive maneuvers of musk oxen against wolves—but in such societies individuals rarely take up a variety of distinct and coherently integrated roles. However, through our language, teaching, and the construction of learning environments for others, humans can solve the problem of how to coordinate many separate tasks; we can assign distinct roles to individuals, and ensure each is trained. And because cultural norms can be taught and learned using language, they would have been critical for expanding cooperation beyond kin groups.

Training through apprenticeship may also have played a vital role in organizing the coordination of groups. In early agricultural societies the pressure to generate enough food to feed the mushrooming population demanded division of labor and occupational specializations. For society to function efficiently, relevant skills and expertise would need to be passed on to unrelated individuals, but these skills would frequently be far too complex to pick up simply through imitation and would require systematic, long-term instruction. Much of the complex knowledge required for manufacturing tools or goods, for instance, or the extensive knowledge associated with many professions or trades can reliably be passed on only through long apprenticeship. Unlike earlier forms of teaching

where parents and other relatives instructed their kin, masters instructed apprentices in exchange for resources such as food, clothing, or protection. Various classes of professional teachers emerged: teachers of farming methods, of military combat, of dance, and of the skills and knowledge that the children of the wealthy needed for their future roles.

Money, Gossip, and Armies

The importance of the uniquely human capacity for social learning, teaching, and language—and thus for large-scale cooperation—becomes even clearer when we consider how this capacity supports three distinct cooperative processes: mutually beneficial exchanges, indirect reciprocity, and group selection.

Many animals engage in mutually beneficial exchanges on a small scale, such as when a bird called the oxpecker takes a ride on the back of rhinoceroses, zebra, or cattle, and eats the ticks and other parasites that live on their skin. The evolution of this type of exchange is fairly straightforward—the "trade" of parasites from the rhinoceros to the oxpecker is beneficial for both parties: the birds find food and the mammals receive effective pest control.

But more challenging to understand is the evolution of the kind of trade or barter commonly observed in humans, like swapping a tool for food. In bartering, both parties value both of the commodities, but, as the items are different, the exchange currency requires negotiation. This form of mutually beneficial exchange appears to be rare or absent among animals. Some primatologists have reported the apparent trading of meat for sex among some chimpanzees that hunt red colobus monkeys, and a group of Balinese long-tailed macaques have devised a learned tradition of stealing objects from tourists, such as cell phones and sunglasses, and then trading them back in exchange for food. But such rare examples aside, trade may be largely unique to humans, which is not surprising, as it typically requires some capacity to agree on a rate of exchange, something that would be difficult without at least the rudiments of language. With language, trade becomes easier; with trade comes the complex linguistic activity of negotiation—and so the development of trade would have given rise to increasingly advanced linguistic ability.

Trade exploits a division of labor in which valuable goods or services, available to some individuals or societies but not to others, are exchanged. The emergence of large-scale, stratified societies, and the associated development of distinct professions, would immediately have

created extensive opportunities for trade; indeed, such division of labor almost certainly could not have arisen without trade. The more division of labor exists within and between societies, the more opportunities for trade arise. Eventually, a threshold is passed after which it becomes convenient to facilitate trade with a common currency, and the institution of money arises. As early as eleven thousand years ago, both grain and cattle were used as money or as barter. The Hebrew shekel is thought to have originated as a weight of barley, corresponding to about 180 grains. Through trade—and the norms, institutions, and laws that served to stabilize it—cooperative interactions between nonrelatives became possible on huge scales, while language helped to ensure that rules or agreements were specified in detail and widely known.

Language, teaching, and norms are also fundamental to another of the most important developments in large-scale human cooperation, namely indirect reciprocity—the tendency of individuals not only to help those who help them personally, but also to help those who are known to help others. Theoretical models have demonstrated that indirect reciprocity can lead to cooperation, and explain why it might benefit individuals to develop a reputation for this. However, language is also important for explaining indirect reciprocity, as evolutionary biologist Martin Nowak and science journalist Roger Highfield write in their book on the evolution of human cooperation: "Language is intimately linked with cooperation. For the mechanism of indirect reciprocity to work efficiently it needs gossip, from names to deeds and times and places, too." Verbally taught social norms also allow humans to institutionalize the punishment of non-cooperative individuals—for instance, through policing or socially sanctioned retaliation, which are more effective means of preserving cooperation than individual-level retaliation. But norms don't rule out the possibility of cheating. Subtle cheats can tweak messages and verbal agreements—remaining cooperative but maximizing their benefits or those of their group. Such cheating might again have contributed to the development of more competent, skillful communicators. And as language became more complex and the repertoire of local symbols expanded, it would have become increasingly difficult to understand the symbols of other societies without effort, which further reinforced the benefits of biasing learning toward the local population. With time, local variants of early linguistic symbols would start to resemble dialects, which may have begun to define and signify distinct communities.

The coexistence of populations that are culturally diverse would mean that members from each group would recognize and prefer to learn

from other members of the same group who have useful local knowledge, rather than from outsiders who come from other groups. Theoretical analyses suggest that conforming to local traditions is favored in such circumstances, with several important consequences, including the evolution of "ethnic markers" that symbolized group membership, increased cooperation within groups, and the potential for greater conflict between groups. Languages or dialects can function effectively as ethnic markers and promote local learning and other parochial tendencies. In turn, imitation, teaching, languages, and local conventions all act to ensure that local differences in behavior among groups are maintained even when individuals disperse. This allows an unusually stable form of group selection to arise, known as "cultural group selection," which has shaped human history dramatically.

Anthropologists Rob Boyd and Peter Richerson, in their 1985 book *Culture and the Evolutionary Process*, first brought to prominence the hypothesis that group selection works at the cultural level through the selection of cultural traits. Groups that possessed more efficient traditions, norms, or institutions fared better in competition with other groups. Societies with an organized army are more likely to win conflicts than those without; city-states with division of labor and occupational specializations tend to outcompete those without these innovations; agricultural communities that have devised irrigation systems flourish more readily than others, and societies with religious doctrines that stabilize cooperative activities within the group thrive at the expense of those with no gods to help ensure compliance. The net result is the spread of military technology, division of labor, irrigation, religious doctrines, and many other cooperative endeavors.

The idea of natural selection operating on groups, as opposed to individuals or genes, has been controversial in recent evolutionary biology. Some might explain the evolution of cultural practices like agriculture by focusing only on individual selection. The argument would go like this: If individuals in agricultural societies end up having more offspring than those in non-agricultural societies, then agriculture will increase in frequency (provided offspring tend to adopt the means of subsistence of their parents). But what is missing from this line of reasoning is the recognition that most of the fitness benefits associated with agriculture derive from group-level activities. Consider that a lone farmer scratching out a living solely through his own efforts would not typically produce any more food or raise any more offspring than a hunter-gatherer. Agriculture does not become highly productive until groups of people engage in shared

enterprises to produce resources that benefit the group. It typically takes several hundred people to construct a decent irrigation system, or to build a corral suitable for catching antelope or horses. Some fish weirs—traps built of stone, nets, or wooden fencing for catching fish—are several hundred meters long and would have required a large group of individuals to manufacture. Burning land, sowing seeds, and harvesting crops have all traditionally been activities in which entire communities engaged. Such activities are infeasible for an individual farmer, but a group of agriculturalists working together could yield substantial dividends, and those who cooperate in this manner generally outcompete those who do not. The end result is the propagation of cooperative practices.

Agricultural communities are of course not the only ones to engage in group-level cooperative enterprises. The Nuer and the Dinka are African cattle-herding societies that live in Sudan. The two groups have a long history of conflict, with the Nuer dramatically expanding their territory at the expense of the Dinka throughout the nineteenth century. The Nuer were successful in warfare because their social structure allowed them to call on larger war parties than the Dinka. As a consequence, the Nuer's beliefs and practices spread. More generally, many small-scale societies engage in cooperative hunting and foraging, and form war parties when conflicts arise; group selection likely operated on these societies to propagate their cultural traditions.

Boyd and Richerson emphasize the importance of accurate social learning, a "when in Rome, do as the Romans do" conformity in which individuals adopt the behavior of the majority, as well as the norms and institutions that regulate social behavior. Conformist transmission minimizes behavioral differences within groups, while maintaining differences between groups. However, even subpopulations in identical environments may end up with quite different forms of behavior, because any behavior that occurs frequently in a given local area may become part of the culture of a small group. In other words, cultural processes generate plenty of variation among human groups for natural selection to act upon, much as processes like recombination and mutation generate genetic variation.

Cultural inheritance is much more important than genetic inheritance for explaining the evolution of human cooperation through group selection, for a number of reasons. First, in cultural inheritance, unlike genetic inheritance, descendants can learn from individuals other than their biological parents, allowing them to be sensitive to the most frequent cultural traits in their society and to conform to the dominant local behavior. This helps preserve cultural differences. Second, the symbolic

systems that serve to mark a group—such as languages, rituals, dances, songs, dress, and flags—make it relatively easy for cultures to maintain their identities, and to resist imported cultural traits from immigrants, or for immigrants to resist the cultural traits of the dominant culture. In contrast, gene flow between groups—where members of one group mate with members of another—will often introduce genes that were once unique to one group into the other, reducing the amount of genetic variation between the groups. While migration will lead to gene flow between groups, reducing genetic variation, symbolic systems will often maintain cultural differences. Third, institutionalized punishment (such as by a police force) or socially sanctioned retaliation (such as the penalizing of deserters during warfare) can stabilize cooperative norms within the society, whereas there is no comparable stabilizing force for genetic selection at the level of groups.

So the kind of group selection that is most important for the evolution of cooperation is selection for the group's culture.

Genes and Culture

Genetic inheritance, however, still plays a significant part in the evolution of cooperation, specifically through a process known as "gene–culture coevolution"—a dynamic in which cultural processes, including cultural group selection, generate a feedback effect on genetic evolution, and vice versa. Through this interaction, natural psychological predispositions for cultural life and cooperation may have been favored by natural selection.

In a 2011 paper, anthropologists Maciej Chudek and Joseph Henrich described what they called "norm psychology," by which they meant "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." Once a species becomes heavily reliant on social learning and culture, as humans have, then a specialized norm psychology is likely to follow. As a result, humans are particularly adept at recognizing, representing, and adopting the local norms of their society, as well as noticing, condemning, and punishing violations of those norms.

Consider, for instance, how social norms and a psychological preference for cooperation could have evolved together, with one providing the conditions for the other, and vice versa in feedback fashion. Individuals who are naturally more inclined to conform to norms would find it easier to live in larger norm-bound societies and to abide by the rules than

individuals lacking such conformist tendencies. These more "docile" individuals would be at an advantage, because they would be better placed to benefit from living in society and less vulnerable to exclusion or punishment, and so they would also be more likely to pass on their genes to a larger number of offspring. Conversely, unlike in most nonhuman societies, non-cooperative individuals would face serious sanctions. In turn, a population of more docile individuals could then encourage the cultural evolution of more sophisticated and effective norms, and allow groups to maintain more reliable cooperation. A similar dynamic could have favored a tendency of individuals to feel shame or guilt when they violate a social norm. While such arguments are speculative, the general idea that docile tendencies in humans were favored throughout recent evolutionary history is entirely credible. The fact that we would struggle to imagine that other, less docile primates could live in such a norm-governed cooperative manner as humans suggests that our cooperative tendencies require an evolved disposition toward docility. (And of course we know that *artificial* selection in many domesticated animals has favored docility.)

In addition, our long history of coordinated group behavior and collective problem-solving through social learning, teaching, and language have seemingly also fed back to shape human psychology in ways that leave us uniquely able to understand and share the goals and intentions of others. We humans appear unusually inclined and able to share experiences with others; humans have evolved not just advanced levels of individual cognition but also extensive skills and motivations for shared cognition, where knowledge is constructed through dialogue between individuals. The typical pattern of social foraging among other primates is strong competition for food, low tolerance for food sharing, and almost no food offering at all. Our ancestors somehow broke away from this pattern to become cooperative foragers. And so one consequence of our cultural evolution through teaching and learning has perhaps been the development of a more socially tolerant temperament.

Or consider how genetic and cultural evolution together could be involved in the development of the enhanced human capacity for imitation, as well as the social bonding that imitation generates, and the activities of caretakers that elicit childhood imitation. There are several reasons why it may be appealing or advantageous for an adult to be imitated by a child. First, being imitated as an adult may be flattering because it means that I, my values, or my choices have been noticed or chosen. Second, I may wish to encourage the child in learning important life skills, either because I want the child to develop and mature, or because I want to be relieved of

my child-caring responsibilities as soon as possible. Third, children who imitate may be less disruptive, or even more helpful, than children who do not imitate (consider children helping our ancestors with foraging activities, or helping us clean up the living room). These advantages of imitation might explain why parents and helpers commonly encourage imitation in the children they look after, often showering them with praise and giving rewards and sometimes even imitating the child's own actions and sounds. Theoretical analyses have shown that such responses could strengthen the child's imitative competence and elicit further imitation.

Natural selection can act on this dynamic, favoring a tendency to respond positively to and encourage imitation by a child, and a corresponding tendency for infants to imitate adult caregivers spontaneously and respond to encouragement with further imitation. The positive emotions experienced by both caregiver and child following imitation, and the enhanced social relationship that results, may be nature's way of encouraging imitation to the benefit of both parties. One special case of this more general process may be infant-directed speech, or baby talk. Natural selection may have favored the tendency for adults to use baby talk with infants, and for infants to respond to it, because it accelerates language learning. Even smiling and frowning may have become part of our norm psychology; as cheap-to-produce but nonetheless highly effective signals of approval or disapproval, they can be easily used to teach others what they should or shouldn't do.

Imitation, in turn, connects in a curious way back to cooperation. Like other animals, humans (often inadvertently) copy each other's postures, mannerisms, and facial expressions. This form of social learning is known variously as "response facilitation," "mimicry," or the "chameleon effect." While experiments have established that such copying allows animals to acquire valuable life skills, in humans it also appears to enhance social interaction. Experimental investigations have shown that simple imitation is causally related to the emergence of cooperative attitudes, and that the relationship between imitation and cooperation goes both ways: being imitated makes individuals more cooperative, while being cooperative makes one more likely to imitate others. The experiments show that if people are imitated, they begin to like their imitators more, find them more persuasive, and describe their time together as more enjoyable than if they are not imitated. Children as young as eighteen months will rush to help adults (for instance, by picking up items that the adult has dropped) more readily when the adult has imitated the child, compared to when no such imitation has taken place. Adults too are more willing to help others with

simple tasks, and even donate more money to charity, after being imitated. People imitate those they like more than those they don't like, and show a preference for imitating members of their own group over members of an out-group, a finding that has held for both religious and ethnic groups.

Oxford psychologist Cecilia Heyes has argued that the two-way causal relationship between imitation and cooperation may function to maintain cooperation, collective action, and information-sharing among members of a social group through a "virtuous circle" of subconscious imitation and prosocial attitudes. Because this virtuous circle helps to maintain group boundaries, we can imagine again that imitation and cooperation have evolved through a process of cultural group selection. Like dialects, local mannerisms can spread through imitation to act as ethnic markers that, often subconsciously, symbolize group membership. A tendency to be well disposed toward individuals who behave like you and exhibit your mannerisms may have been favored as an aspect of our evolved psychology, because it helps promote cooperation among the group's members. Conversely, in variable environments it often pays to copy locals, since they are more likely to know best how to deal with their environment.

Numerous social practices that have persisted through human history may foster the development of enhanced imitative capabilities. Many societies possess traditions of dancing in synchrony, and train their military through extensive synchronous marching and fighting drills. Such groups may have been more successful than others in part because this synchronous activity trained individuals' neural circuitry for imitative proficiency, enabling them to connect the perception of others performing the action to their own performance, thereby promoting group bonding. Synchronous action that triggers endorphin release (such as a group of individuals that exercise together) may lead to individuals associating the simultaneous activity with positive reward, resulting in synchrony itself becoming rewarding. Or, if rewards are received at the end of synchronous action, such as hunting together, again a learned association may arise. If synchrony is rewarding, then social behavior that promotes synchronous action will be more likely to occur. The extensive use of rhythm, for example in drumming—and music more generally—as a means of helping to coordinate the actions of large numbers of individuals and to promote social bonding could be favored because of positive group effects. Groups of soldiers that sing or chant when running are often thought to run further and faster, with less pain, and to bond with each other in the process.

Selection for more accurate and efficient forms of social learning might have in turn generated selection for enhanced imitative capabilities,

as well as other aspects of cognition. For instance, brain structures that would have been favored by selection include those that allow us, with relevant experience, to solve what is known as "the correspondence problem"—the challenge of imitating when the perception of oneself and of another individual performing the same action can be quite different. (Consider mirror neurons, which fire both when an individual performs an action and when the individual observes someone else performing the same action.) Perhaps our potent capacity for imitation is itself an adaptation to cultural life.

This issue remains contentious, however. Heyes, for instance, has argued that the human capacity for imitation is not an adaptation but instead relies on an ancient learning capability—the kind of associative learning that we essentially share with other animals—and that both the extent of our reliance on imitation and our imitative proficiency are socially constructed. According to this argument, our use of mirrors and engagement in synchronous activities such as dance and sports have helped to produce vast opportunities for developing imitative competences through experience, and the relative lack of these experiences in nonhuman animals explains why they are less capable of imitating than we are.

Although it is true that our use of artifacts like mirrors and activities like dance and sports have encouraged our imitative tendencies, the human mind is unique in its ability to imitate in complex ways. There has been extensive natural selection acting on the human brain in the period since humans and chimpanzees shared a common ancestor, leading to our vastly superior natural ability to learn. The selection pressure for greater and greater learning abilities in our ancestors was generated by the social learning that was so important for our ancestors to flourish, meaning that cultural evolution interacted with genetic evolution to make us the best imitators, the best learners, and the most cooperative species on earth.

Cultural by Nature

What precisely are human social-learning adaptations? This remains one of the great unresolved questions in the field of cultural evolution. Showing that *any* given trait is an adaptation can be very difficult, so demonstrating that certain human cognitive traits are adaptations to promote social learning is no trivial task. Still, although definitive answers are elusive, we have discussed a number of human behaviors and features that may one day be shown to be cognitive adaptations for social learning, as that is currently the most plausible explanation for their presence in humans.

Our capacity for teaching, as well as the motivation to teach and be taught, our ability to comprehend the state of knowledge of the pupil, and various means of facilitating learning in others are possible social-learning adaptations. And if the original function of language is indeed to promote teaching, then language is another adaptation (or set of adaptations) for social learning. The tendency to produce, and to attend to, infant-directed speech may have evolved to promote social transmission. The extraordinary social motivation to imitate, which anyone with children will recognize as powerful and pervasive, and the social bonding between individuals that this generates, is another strong example of a possible evolved adaptation for social learning and cooperation, as is the tendency of young children to attend to the gaze of others, and the motivation to share experiences with others through joint attention. Even the whites of our eyes may have evolved to make it easier for us to follow another individual's gaze in a conversation. Or consider again the extraordinary human tendency to conform to the majority. Gene–culture coevolution is better suited than models of associative learning to explain such experimental findings as the fact that humans are more likely to copy an action that is performed by three individuals one time each than an action performed by one individual three times. Our capacities for having a theory of mind and for taking a perspective other than our own, and abilities to read the intentions of others, are surely also part of this story.

There is both neural and genetic evidence that humans possess elevated levels of developmental plasticity that allows them to form neural connections between sensory inputs and motor outputs that may make imitation easier, by linking the observation of a given behavior with its performance. Humans have evolved to possess an extended period of juvenile dependency—from infancy to late adolescence—that promotes the transfer of knowledge across generations, and so the period of synaptic plasticity characteristic of early brain development is longer in humans compared to other species. Even our basic and ancient learning capabilities, including our ability to see connections between events to discern the consequences of our actions and to adjust our behavior flexibly, are superior to other animals' learning abilities, probably due to selection for enhanced social learning. This enhancement in general learning and neural plasticity likely plays a critical role in human cognitive development.

The large-scale cooperation that exists solely in human societies arises because of our uniquely potent abilities for social learning, imitation, and teaching, combined with the coevolutionary feedbacks of these capabilities on the human mind. Culture took human populations down evolutionary

pathways not available to noncultural species, either by creating conditions that promoted established cooperative mechanisms, such as indirect reciprocity and mutually beneficial exchanges, or by generating novel cooperative mechanisms not seen in other animal populations, such as cultural group selection. In the process, gene–culture coevolution seems to have generated an evolved psychology comprising an enhanced ability and motivation to learn, teach, communicate through language, imitate, and emulate, as well as predispositions to docility, social tolerance, and the sharing of goals, intentions, and attention. This evolved psychology is entirely different from that observed in any other animal, or that could have evolved through genes alone.

The world's people exhibit an extraordinary diversity of appearance, fashion, language, diet, method of subsistence, and custom, and while there are genetic differences between human populations, the genetic variation among humans is tiny compared with that found in other primates. What separates all human societies has less to do with our genes than with a few thousand years of cultural evolution. However, it would be a mistake to assume that our biology is irrelevant to understanding contemporary human adaptation and diversity. Through our culture we have built our world, but that is only possible because we have been naturally fashioned for culture.