CHAPTER 30

Cultural Evolution

MACIEJ CHUDEK, MICHAEL MUTHUKRISHNA, and JOE HENRICH

You and I are very unusual beasts. Our ancestors, mere African primates, spread across the globe long before the origins of agriculture, the first cities, or industrial technologies. More ecologically successful than any mammal, human foragers colonized most terrestrial ecosystems, from the frozen tundra of the Arctic to the arid deserts of Australia. Yet, despite our massive ecological success, we are physically weak, slow, and relatively bad at climbing trees; any adult chimp can kick our butts and any big cat can easily chase us down. We can't distinguish edible from poisonous plants, and our gut can't detoxify poisons. We can't survive without cooked food, but we aren't innately able to make fire (or cook). Our babies are born dangerously premature, with skulls that haven't yet fused. Our females stop reproduction long before they die (menopause), yet remain sexually receptive throughout their cycle. Perhaps most surprisingly, our kind are not very bright, and our success as a species is not due to our intelligence (Henrich, forthcoming).

Skeptical? Imagine we took you and 19 friends and pitted you against a troop of 20 capuchin monkeys from Costa Rica, without equipment. We parachute both teams into the Ituri Forest in central Africa. After 6 months, we return and count survivors. Who would you bet on? Well, do you know how to make arrows, nets, and shelters? Do you know which plants are toxic (many are)? You can start a fire without matches, right?

Chances are your team would lose, despite your oversized crania and vaulted intelligence. But, if not for figuring out how to survive as foragers—which our ancestors managed to do across a staggering variety of environments—what's that big brain *for*, anyway?

In fact, the human half of this experiment has played out many times. Hapless European explorers accidentally stranded in unfamiliar environments have typically floundered, and often died. History provides cases from the Arctic, tropical forests in South America and Africa, Australian deserts, and along the coasts of North America (Henrich, forthcoming). Forced to live as hunter-gatherers, these Europeans couldn't find food or distinguish poisonous from edible plants. They couldn't successfully hunt, locate water, avoid danger, make fire, or fashion tools, shelter, or watercraft. Meanwhile, foraging populations had inhabited these same environments for centuries, routinely overcoming such "challenges" (what they call "daily life").

Examples of such ill-fated ventures in the 19th century include the Franklin Expedition (Boyd, Richerson, & Henrich, 2011), where every member of the best-equipped expedition in the history of British polar exploration perished in a land in which local foragers had thrived for almost a millennium, or Burke and Wills's foray into the Australian outback (Henrich & McElreath, 2003), in which, despite their extensive preparations and equipment, they died because they did not know the local aboriginal techniques for detoxifying plants. You might also consider watching the film *Van Diemen's Land* (2009), which vividly depicts the travails of Alexander Pearce and seven other Europeans. In 1822, these men escaped a prison camp on the Australian island of Tasmania. Unlike the hostile conditions faced by Franklin, whose ship froze in the Arctic, or Burke and Wills, lost in the desolate deserts of central Australia, these men spent a mere three months in a verdant forest, equipped with a steel axe. Yet they found only two ways to feed themselves: stealing from local Aboriginal foragers, who had inhabited this ecology for at least 35,000 years (Cosgrove et al., 2010), and eating each other.

How does all this floundering by educated, technologically sophisticated explorers square with the massive ecological success of our species? How is it that we are so frail as individuals, so helpless when dropped into a novel ecology, and yet our ancestors, wielding merely stone tools, swept across almost the entire planet?

The reason we are such unusual animals is that we are an *evolved cultural species*. Unlike all other species, we are addicted to culture. You and I rely on a body of cultural know-how that is transmitted from one person to another, and accumulates over generations. Stripped of this nongenetic information, we are rather pathetic compared to other species (Boyd et al., 2011; Henrich, forthcoming).

We need an evolutionary explanation for the existence and behavior of a cultural species. Over the past three decades, the scientific enterprise of developing this explanation has advanced rapidly. In this chapter, we will try to bring you up to speed on our emerging understanding of the field of cultural evolution: how a species evolves to be cultural, how culture itself evolves, and how cultural evolution interacts with, and sometimes drives, genetic evolution.

A cultural species is one that has evolved to socially transmit complex behavior-shaping information between generations. A key threshold for defining a cultural species is *cumulative cultural evolution*: the point at which these transmitted behaviors accumulate enough that they are more complex, sophisticated, and well adapted than anything a single asocial or noncultural individual could devise alone in his or her lifetime, regardless of how individually intelligent that person is (Boyd & Richerson, 1996). No individual today, no matter how smart, could recreate the world we live in. Socially accumulated cultural adaptations have been so central to our species that they have driven subsequent genetic adaptations (Laland, Odling-Smee, & Myles, 2010; Richerson, Boyd, & Henrich, 2010).

As evolutionary researchers, if we want to understand a species that has crossed the threshold into cumulative cultural evolution, we need—in addition to ecology, evolution, and psychology—a theory of how cultural information itself changes over time (evolves). We need theoretically sound and empirically verified answers to questions such as:

1. Can culture evolve? Does the notion of evolution even apply to something so very different from genes?
2. How did a cultural species evolve? How could a species similar to extant, nonhuman apes come to possess such highly adaptive, but nongenetic, behavioral repertoires, and why haven't other species done the same?
3. What kind of psychological adaptations does a cultural species need? How do they influence cultural evolution?
4. How does culture itself evolve? How do these cultural repertoires adapt and accumulate over generations?
5. How do genes adapt to cultural evolution? Have culturally evolved products like tools, fire, languages, and knowledge about plants and animals shaped our genetic evolution and our evolved psychological adaptations?

Let's dive right in to the answers.

CAN CULTURE EVOLVE? DOESN'T EVOLUTION REQUIRE GENES OR REPLICATORS?

It's now clear that neither evolution nor adaptation requires discrete traits, "replicators," low mutation rates, vertical transmission, or random variation (Henrich & Boyd, 2002; Henrich, Boyd, & Richerson, 2008). Genes evolve, but it doesn't follow that all evolving things must be gene-like. Genetic evolution is just one way information can change and accumulate. A large body of formal mathematical models now illustrates how culture can evolve, and when and how this is like—and unlike—genetic evolution.

Evolutionary adaptation has three basic requirements: (1) individuals vary, (2) this variability is heritable (information transmission occurs), and (3) some variants are more likely to survive and spread than others. Genes have these characteristics, so they evolve and adapt. Culture also meets all three requirements, but in different ways. Like bacterial genes, cultural information spreads horizontally, not just from parent to child. Formal models of cultural evolution begin from simple descriptions of how individuals acquire behaviors—by learning from others, learning individually (e.g., trial and error), or by genetically encoded responses ("evoked culture"). Then, using mathematical techniques drawn from population genetics, epidemiology, statistics, and communications, they explore how the distribution of phenotypes—behaviors, motivations, beliefs, and so on—changes over time.

There's no analogy with genes. These models are built for culture, given what we know about human learning. Even the earliest models focused on the differences between cultural and genetic evolution: the transmission of continuous traits (like how long to make your spear), "horizontal" learning from peers, or "oblique" learning from older nonparents (Cavalli-Sforza & Feldman, 1973). Of the 38 different models in Boyd and Richerson (1985), roughly half explore cultural traits as continuous (not discrete) with transmission fidelity modeled as a parameter (so, no assumption of "replication"), and many also considered the influence of cognitive biases in learning and the impact of individual learning on cultural and gene–culture evolution.

To get a handle on these formal models, consider an example. Suppose a young hunter wants to figure out the best length for his arrows. He (or she) watches the three most successful hunters in the community, notes the lengths of their arrows, and then averages them.

Did anything replicate? No, but that's not a necessary or useful concept for cultural evolution.

Was something inherited? Yes, the learner didn't invent an arrow or pick an arrow length *de novo*; these were inherited from others by social learning. The phenotypes (arrow lengths) of the new generation will be correlated with those of their "cultural parents" (those they learned from).

Was there selection? Yes, the learner constrained the space of possible arrow lengths by choosing the three most successful hunters. This is selective cultural transmission.

Will there always be variability for selection to act on? Yes, even in this very simple model, as long as there are fluctuations in hunting success and individuals are imperfect copiers, arrow lengths will vary and learners will selectively imitate just some of them.

Will there be adaptive evolution? Yes, under many conditions. If everyone learns this way and if there is an optimal arrow length for hunting, eventually arrow lengths will converge to it. This kind of adaptation—the process of phenotypes (e.g., behaviors and technologies) becoming better suited to their environment—doesn't require genetic change or intelligence. It happens without anyone constructing a mental model of aerodynamics or performing cost-benefit analyses of the effectiveness of different arrows on various prey types.

Later we discuss emerging research on how cultural information evolves as it travels the landscape of the adapted minds of our cultural species. To really understand this, though, we'll need to start by understanding the cognitive adaptations that make cultural evolution possible in the first place.

HOW DID WE EVOLVE TO BE A CULTURAL SPECIES?

Many people still think that "evolutionary" or "biological" explanations oppose "cultural" explanations—"Nature versus Nurture." However, this approach shows how cultural explanations are merely one type of evolutionary explanation. In 1985, Boyd and Richerson extended the Darwinian umbrella to cover "cultural" explanations by asking, Under what conditions does natural selection favor social learning over individual exploration or genetic adaptation? How might natural selection shape psychology to most effectively acquire ideas, beliefs, values, motivations, and practices from others? Under this expanded umbrella, explanations involving social learning ("cultural explanations") can interface with noncultural hypotheses within one epistemological framework. Recognizing that social learning is part of the explanation of a phenomenon doesn't mean that genetically evolved aspects of psychology aren't also important parts of the explanation.

As neuroscience now makes inescapably clear, both genes and culture shape our brains. Growing up in different societies, learning and navigating different culturally evolved social norms, institutions, and technologies, results in different neurological and hormonal reactions (Han et al., 2013; Kitayama & Uskul, 2011; Na & Kitayama, 2012; Nisbett & Cohen, 1996), that propel different perceptions, judgments, motivations, and behaviors. Cultural evolution shapes our biology in the short term by influencing our development and our genes in the longer term. There's much more to our biology than our genes (Henrich, forthcoming).

How and When Did Capacities for Culture Evolve? When Is Cultural Learning Genetically Adaptive?

A great deal of theoretical work explores whether and when cultural learning improves genetic fitness. Will selection favor rare cultural learners in a population of mostly asocial learners? It often will: Culture is adaptive when asocial learning is hard and environments fluctuate a lot, but not too much.

While the mathematical reasoning that supports this answer is sometimes subtle (Aoki & Feldman, 2014; Boyd & Richerson, 1985; Hoppitt & Laland, 2013; Nakahashi, Wakano, & Henrich, 2012), the logic of the conclusion is easy to appreciate. If asocial, individual learning (e.g., trial and error) is easy and effective, then metabolic energy and attention spent carefully observing others (cultural learning) is wasted. If environments don't vary much, genes that adapt directly to the environment can produce adaptive behavior more efficiently than ones that build metabolically expensive brains capable of carefully observing others, inferring their goals, copying their actions, and so on. If, on the other hand, environments vary so much that each generation faces dramatically different challenges, then your parents' generation's behaviors, strategies, and practices just aren't worth copying, and asocial learning or genetic programming is the best bet.

These theoretical insights fit well with empirical observations of human behavior. We are more influenced by others' behavior when individual experimentation is difficult, costly, or produces ambiguous results (Caldwell & Millen, 2010; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). Even infants socially reference adults more when confronted with more ambiguous stimuli (Kim & Kwak, 2011). Evolutionary models have allowed us to build theories of human learning.

Why did humans in particular become a cultural species, and why only in the past few million years (Henrich, forthcoming; Henrich & Tennie, under review)? One explanation suggested by these models is that only recently did (a) environments become too unpredictable for genes to track them, (b) fitness-relevant challenges become too hard to be easily, asocially reconquered by each individual, and (c) a species have the cognitive preadaptations to kick-start high-fidelity cultural learning. Consistent with this, ice-core evidence shows that the rate at which global climates (and consequently hominid habitats) fluctuated increased dramatically over the 5 million years since our lineage split from chimpanzees (Potts, 1998; Richerson & Boyd, 2000; cf. Shultz, Nelson, & Dunbar, 2012).

In terms of establishing when humans became cultural, the evidence is scarce, but archaeological findings show that for more than at least 1.8 million years, we have relied on technologies that are hard to invent and master asocially (for review of the evidence, see Henrich, forthcoming). Our hominid ancestors relied on expertly produced Acheulean stone tools, which are hard to reinvent alone (Stout & Chaminade, 2012). Contemporary, healthy, well-educated adults, with a completed example of a stone tool in hand and facing no time constraints, cannot produce stone tools like expert Acheulean stone tool makers did and contemporary experts still do (Geribàs, Mosquera, & Vergès, 2010). In the few remaining societies that use stone tools today, acquiring expertise requires many years of apprenticeship and social learning (Stout et al., 2002). This suggests that by 1.8 million years ago, our lineage already relied on social learning.

Theory and observation both suggest that as global climates began to increasingly fluctuate over the past 5 million years, selection drove many species to rely more on socially learned information. Ours, however, was the first to rely so heavily on social learning, and to do it so faithfully and consistently that we crossed the threshold to cumulative cultural evolution and became a cultural species. Why it was our species that crossed the threshold is just beginning to get scholarly attention, though some researchers argue the key lies in the social organization (e.g., pair bonding) and group sizes of our ancient ancestors (Burkart, Hrdy, & van Schaik, 2009; Chapais, 2008; Henrich, forthcoming).

THE PSYCHOLOGY OF A CULTURAL SPECIES

Building from this theoretical bedrock, scholars have honed in on the details of how natural selection shapes the psychology of a cultural species. These investigations weave formal evolutionary theory with careful empiricism to establish what cues cultural learners use to figure out who to learn from (model biases) and what to pay attention to (content biases).

Some people are just better at certain things, and natural selection favors cultural learners who imitate better models. By studying how children and infants learn, we can test hypotheses about which cultural learning biases were adaptive for our ancestors.

SKILL, SUCCESS, AND PRESTIGE

When learners can easily spot skilled models (that guy's spear goes further), selection should favor a bias for learning from them (for a review, see Chudek, Heller, Birch, & Henrich, 2012). Supporting this evolutionary logic, children preferentially imitate more skillful models when learning object names, artifact functions, and even causal properties. They do this (a) even when the more skilled individual is a stranger rather than a familiar teacher from their preschool, (b) even a week later, (c) even when the more skillful model acts in bizarre and unconventional ways (Scofield, Gilpin, Pierucci, & Morgan, 2013) or has an unfamiliar accent (Corriveau, Kinzler, & Harris, 2013), and (d) even when they have witnessed the skillful model being intentionally deceitful (Liu, Vanderbilt, & Heyman, 2013). Even infants are more likely to imitate a previously competent over a previously incompetent adult (Chow, Poulin-Dubois, & Lewis, 2008; Zmyj, Buttelmann, Carpenter, & Daum, 2010). In novel environments, infants are more likely to seek social cues from novel, competent strangers than their own mother (Kim & Kwak, 2011; Stenberg, 2009)

Young children also preferentially learn from more confident individuals (see review in Chudek, Brosseau, Birch, & Henrich, 2013). Interestingly, children who speak languages with obligate evidential markers—grammatical indicators of the source of information (e.g., Turkish)—respond more to skill cues at a younger age (Lucas, Lewis, Pala, Wong, & Berridge, 2013), suggesting that cultural information itself can shape cultural learning biases.

But sometimes skill differences aren't easy to assess. Even today it's hard to know whether fad diets improve or worsen your health; even with decades of research, it's still not clear what the optimal diet contains, though many people believe they know. Imagine how much murkier these choices were for our prehistoric ancestors. Even when skill is opaque, learners can make good choices by tracking success (Henrich & Gil-White, 2001): Imitate whomever has more positive life outcomes—more wives, more wealth, more friends, and so on. Consistent with this, young children seem to prefer individuals who experience entirely random positive outcomes (Olson, Dunham, Dweck, Spelke, & Banaji, 2008).

Assessing success differences can be difficult, can be costly, or can take a long time, but children need to make learning decisions right now! Luckily, you can also imitate your peers' learning choices ("prestige bias"). For an in-depth exploration of these ideas, see Henrich & Gil-White (2001). These insights explain why when children see strangers paying more attention to someone, they're more likely to learn from them (see review of evidence in Chudek et al., 2012), and when adults need to design a virtual stone arrowhead for hunting, they preferentially imitate both prestigious models (those others have paid attention to) and successful models (those whose stone tools reaped better payoffs), particularly when they themselves were struggling with the challenge (Atkisson, O'Brien, & Mesoudi, 2012).

Self-Similarity, Age, Sex, and Ethnicity

Of course, it's not just about picking the most skilled model; there are also better models for you in particular. A 3-year-old might be more likely to acquire behaviors adapted to his or her personal ecology—the skills it takes to be a successful 3-year-old—from a 4-year-old than by trying to imitate a 50-year-old. Young children do prefer learning from similar or slightly older-aged peers in a variety of domains (see review in Shutts, Banaji, & Spelke, 2010). Even 14- to 18-month-old infants seem to have better recall for actions when they are modeled by 3-year-olds than by adults (Ryalls, Gul, & Ryalls, 2000). It is also well established that children have strong same-sex biases in their learning preferences (Shutts et al., 2010; Wolf, 1973). Adults, meanwhile, seem more susceptible to social influence by those who share their existing beliefs (Hilmert, Kulik, & Christenfeld, 2006).

The existence of an evolving cultural corpus can also give rise to ethnicities—that is, symbolically marked groups (McElreath, Boyd, & Richerson, 2003). Once your fitness depends on culturally transmitted strategies for interaction, and all your peers' fitnesses do too, local norms can become critically important (Chudek & Henrich, 2011), and it makes sense to use arbitrary signals (like accent, dress style, tattoos, body mutilation, etc.) to preferentially identify, interact with, and learn from coethnics. In fact, any interaction governed by social norms (Henrich & Henrich, 2007) can spontaneously generate just these kinds of ethnic correlations between an arbitrary signal (e.g., dialect) and their behaviors (Efferson, Lalive, & Fehr, 2008). Recent developmental psychology has shown that children and infants pay careful attention to others' accents and prefer interacting with and learning from people with familiar ones (see review in Kinzler, Corriveau, & Harris, 2011).

Conformist Transmission

Most people today have lived through the historically bizarre phenomenon of "going to school." Though we grew up in very different parts of the world, at around age 5 most of us found ourselves faced with compulsory attendance in a microsociety of same-aged, mostly unrelated peers—each an evolved cultural learner, and each trying to make sense of the world and making countless choices about what to wear, how to behave, whom to affiliate with, and how to invest their time. So, chances are, you already have some pretty good firsthand experience of conformist transmission (people preferentially adopting the most common behavior) and even anticonformity (preferentially avoiding it).

The simplest null models of cultural evolution assume that—in a given domain, say, how early to wake up—learners carefully observe the beliefs and behaviors of their peers or parents and then pick one at random. These models imply that the probability of someone choosing a cultural variant is just the frequency of that variant in the preceding generation. A natural next step is to ask: Does it sometimes pay to be more or less likely to adopt a cultural variant than its population frequency? If it does, human psychology might be adapted to, all else being equal, conform or anticonform. A widespread conformist bias has profound implications for the long-term, large-scale patterns of cultural evolution we'd expect to see in history.

The question of whether and when conformist transmission pays continues to be the focus of nuanced theoretical analyses. While some models suggest that conformist transmission should be pervasive (see review in Nakahashi et al., 2012; Perreault, Moya, & Boyd, 2012), others imply a more limited scope (Eriksson, Enquist, & Ghirlanda, 2007).

Though psychologists have a long history of studying "conformity" in the broad sense, only recently has evidence begun accumulating on conformity in this narrow sense relevant to cultural evolution: how learning probabilities change as a function of the frequency of a cultural variant. Across several studies, researchers have observed that some individuals use conformist learning (Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; Morgan et al., 2012; Toelch, Bruce, Meeus, & Reader, 2010), among a diversity of other strategies, like ignoring frequency information entirely (Efferson, Lalive, Richerson, et al., 2008), copy the strategy whose frequency is increasing the fastest (Toelch et al., 2010), and increasing dependence on social information as the absolute number of demonstrators increases (which is consistent with theory; Perreault et al., 2012).

CREDIBILITY-ENHANCING DISPLAYS (CREDs)

Imagine yourself as a Pleistocene youth. You notice that Big Bruce is a great hunter, is very rich, has many wives, and that everyone pays attention to him. Something makes Bruce successful, but what is it exactly? Is it the spears he uses, where he hunts, what time of day he goes out, how he shaves his head, or the gods he worships? Since it's hard to know, selection can favor copying everything about Bruce. This logic helps explain why even today, sports or music celebrities are able to increase the sale of milk, cologne, or underpants (Chudek et al., 2012).

However, if we blindly imitated prestigious or successful people, they could easily exploit us. Bruce could tell us the secret to success is giving him half of our meat. The Credibility Enhancing Displays hypothesis (CREDs; Henrich, 2009) proposes an evolved defense: We doubt claims that aren't backed up by actions. CREDs help us understand patterns of religious belief transmission: More children become believers when their parents attend weekly services and give money to charity than if they merely profess belief (Lanman, 2012). In experiments, adult participants make costly commitments to new beliefs after witnessing others engaging in costly actions that only make sense in the light of particular underlying beliefs (Willard, Norenzayan, & Henrich, 2015).

Do These Cultural Learning Mechanisms Matter in the Real World?

One of the starkest demonstrations of prestige and self-similarity biases—particularly relevant for students of evolutionary psychology—is the *Werther effect* (Phillips, 1974): the phenomenon of copycat suicides. In 1774, the German author Goethe published *The Sorrows of Young Werther*, whose main protagonist, driven to sorrow by unrequited love, shoots himself. The subsequent spate of copycat suicides by young men led authorities to ban the book in Italy, Leipzig, and Copenhagen. Since then, spikes of copycats of well-publicized suicides of famous individuals (Coleman, 2004; Mesoudi, 2009), by similar victims and using similar killing methods, have been documented in the United States, Germany, and Japan. Besides the obvious prestige or success effect, copycats tend to match their models on gender and ethnicity and be somewhat younger. Statistical analyses show that many of these suicides were not individuals who would have committed suicide anyway, since the rate spikes are not followed by relative dips in the months following the celebrity's suicide (see review in Henrich & Henrich, 2007).

At first glance from an evolutionary vantage point, it seems inexplicably maladaptive that people should kill themselves, let alone that they should do so in imitation of strangers who only superficially resemble them. However, these disturbing patterns make more sense when you recognize that humans are an obligate cultural species. We are equipped with a cultural learning psychology that, on average, sifts out better models and more adaptive information and predisposes us to acquire this information, even if the behavior propelled by this information is individually costly in the short term. Sadly, these cognitive mechanisms can tragically misfire.

What to Learn (Content-Rich Mechanisms)

Not all cultural information is equal—it pays to ignore some things and focus on others. Natural selection ought to have attuned people to attend to fitness-relevant forms of information. These include information about animals and plants, kinship, dangers, mating, fire, reputation, social norms, and social groupings. In fact, many of the psychological adaptations studied by mainstream evolutionary psychology provide the rich cognitive architecture and shape the acquisition of cultural information, creating what we call content biases.

For example, children not only keenly attend to information about animals, but they are selective in what they store in memory. Barrett and his collaborators have demonstrated that children across societies are particularly savvy learners of social information about dangerous animals (Barrett & Broesch, 2012)—we're especially likely to remember when someone tells us that an animal is dangerous, and when children make mistakes they tend to err on the side of assuming animals are dangerous (Barrett & Broesch, 2012; Broesch, Henrich, & Barrett, 2014).

The information is then structured cognitively into hierarchical taxonomies, and information gleaned about one animal or one species is probabilistically extended to other species by category-based induction. If you learn that a particular pet parrot has hollow bones, you readily infer that all parrots have hollow bones, and that perhaps all birds have hollow bones. The combination of cultural learning and this folkbiological cognition provides adults in small-scale societies with an immense body of valuable and adaptive knowledge. However, without cultural input, this cognitive machinery corrodes and begins to malfunction, as it does in urban Western populations (Atran, Medin, & Ross, 2004; Medin & Atran, 2004).

Similarly, recent investigations of infants' responses to plants suggests that even at around 1 year of age we recognize plants as something special that should be approached cautiously (Wertz & Wynn, 2014) and have a special sensitivity to information about whether they are edible (Wertz & Wynn, in press). Infants, who seem to immediately put almost anything in their mouths, will pause when encountering a plant and wait to see if anyone else tastes or eats it (a CRED) before putting it in their own mouth.

Here's a small sampling of work in other content domains of cultural learning:

Reputation information: Mesoudi, Whiten, and Dunbar (2006) have demonstrated that gossipy information—about others misdeeds and affairs—gets transmitted more faithfully through laboratory social networks.

Fire: Fessler (2006) has drawn on diverse evidence to argue that children's psychology may be calibrated for attending to and learning about fire.

Norms: Tomasello and his colleagues have experimentally demonstrated that young children are particularly attuned to notice others' behavioral regularities and interpret them as injunctive social norms, spontaneously enforcing them on a "norm-violating" behaving puppet (Schmidt, Rakoczy, & Tomasello, 2011; Schmidt & Tomasello, 2012).

By focusing on content mechanisms, cultural evolution can interface in important ways with mainstream evolutionary psychology. For example, much work on human mating preferences has shown reliable patterns across societies as well as interesting cross-population variation and historical change over time (Buss, Shackelford, Kirkpatrick, & Larsen, 2001; Henrich, Heine, & Norenzayan, 2010). Consistent with this, increasing evidence now shows how humans use the forms of biased cultural learning discussed above not only in assigning mate values to individuals but also in assigning mate vales to attributes, like hair style or dress (see review in Henrich, forthcoming; Little, Jones, DeBruine, & Caldwell, 2011; Zaki, Schirmer, & Mitchell, 2011). Of course, this doesn't imply that mate preferences are merely culturally learned, since there ample and reliable preferences across diverse societies and mate preference variation may be due to factors besides cultural learning. It does, however, begin to suggest how an evolutionary psychology that fully incorporates cultural evolution can provide a more complete account of human nature and diversity.

Finally, one important and emerging area of work is the evolution of teaching, which is the flip side of cultural transmission (Fogarty, Strimling, & Laland, 2011). Evolutionary approaches to teaching have already begun to generate important insights in small-scale societies (Kline, Boyd, & Henrich, 2013).

CULTURAL EVOLUTION

So far we've explored scientific terrain that should be familiar to someone reading a handbook of evolutionary psychology. We've asked how natural selection might have adapted our modern minds for navigating a particularly important challenge our ancestors faced—the challenge of cultural learning. Now we take an exciting step further by asking: Given our evolved psychology, how does culture itself evolve? How can we, as researchers, describe, model, test, and understand the ways in which the information we transmit between individuals and between generations changes over decades, centuries, and millennia?

Cultural Evolution Builds Adaptations

Cultural adaptations are all around us, but they can be hard to see, let alone understand. In a few cases, such as the metric system, our cultural corpus was honed by smart minds making deliberate choices. For the most part, though, the behaviors we acquire—how we tie our shoes, give directions, and even divide the color spectrum (Deutscher, 2011)—have been dynamically shaped by many millions of evolved, biased minds learning, forgetting, applying, and transmitting information over generations. These dynamics play out on scales far larger than our individual lives, and so, like genetic evolution, are difficult to perceive with the naked eye.

There are, however, rare and valuable moments when the consequences of these processes are cast into stark relief. For instance, when anthropologists study small-scale societies through the lens of modern science, they see culturally acquired practices extraordinarily well adapted to local environmental challenges, yet the people themselves merely claim it's just "our custom" (Henrich, 2002; Henrich & Henrich, 2010). How can we explain this? Must we assume that each culture's history is peppered with long-lost savant shamans, who secretly, consciously crafted these traditions?

We needn't, which is good given the many flaws in human reasoning (Henrich, forthcoming). Mechanisms such as the success bias, prestige bias, conformist bias, CREDs, content biases, and intergroup competition allow cultural information to improve and aggregate over generations, without anyone ever needing to understand why or how it is happening, or why a given cultural practice or tradition is effective.

Cultural Evolution Shapes Preferences and Thinking

Don't make the mistake of thinking that culture is a passive thing—merely a message that is distorted by our biased minds as it is whispered between generations. Culture isn't just shaped by our minds; our minds are shaped by culture.

Consider this case: Like other primates, humans are born with a taste aversion to spicy chili peppers. However, despite this aversive content bias, many populations in the New World have incorporated chilies and other strong spices as essential ingredients in their cuisine. Billing and Sherman (1998) conducted an extensive survey of the recipes from across the world, along with a survey of the antimicrobial properties of different spices. They found a strong relationship: Societies in climates that posed the greatest pathogen risk due to food spoilage also had the greatest preponderance of antimicrobial spices in their food.

How did these societies come to have such conveniently adaptive culinary tastes? It is implausible that individuals recognized that the bad taste of plant toxins was outweighed by their value in fighting disease and decided to overcome their innate aversions and incorporate spices into their diets. Most individuals just try different foods and imitate others' dietary choices as children. What tastes good is a combination of genetics (sweet items provide glucose) and culture (chili peppers provide antimicrobial defense despite genetic predispositions against them). But how does culture override our genetically encoded preferences?

Experiments show that children readily adopt the food choices and preferences held by their peers (Birch, 1987; Duncker, 1938), and exercise those preferences in both their private food rankings and public behavior. Consistent with this, evidence from neuroscience indicates that seeing cultural models prefer something actually makes a learner enjoy it or desire it more himself, even if he is alone (Zaki et al., 2011). The available evidence indicates that cultural learning alters our brains to change our preferences for, or tastes in, wine, men, and music (see review in Henrich, forthcoming, Chapter 16).

These cultural adaptations, modifications of our tastes in this case, are the long-term outcomes of population-level evolutionary processes, guided by the adaptive learning biases we described above. When many people across many generations are more inclined to learn from their slightly healthier and more successful peers, the entire population's dietary preferences and culinary repertoire will gradually become more adaptive. The same processes sometimes shape food taboos. Henrich and Henrich (2010) fill out the details of this process by examining how an adaptive repertoire of fish taboos, which protect pregnant women from dangerous marine toxins, has accumulated to address a local environmental challenge in Fiji.

In addition to preferences, ample evidence from diverse societies documents variation across populations in seemingly basic psychological domains (Henrich, Heine, et al., 2010). Across cultures, people differ in susceptibility to visual illusions, notions of fairness, motivations to punish, morality, endowment effects, spatial and folkbiological reasoning, conformity, IQ, underwater vision, and analytic thinking. In some cases, these psychological differences may arise from jukebox-like adaptive responses to distinct environmental cues, but the strength of these cues is almost always shaped by culturally constructed environments, including both institutions and technologies. Cultural evolution provides an evolutionarily grounded approach to building theories about how and why these (nongenetic) psychological differences emerge and are maintained (Henrich, Ensminger, et al., 2010; Hruschka & Henrich, 2013; Leibbrandt, Gneezy, & List, 2013; Nisbett & Cohen, 1996).

Documenting societal differences needn't be just an exercise in butterfly collecting (for this, see cultural psychology); in the light of cultural evolution, patterns of cultural differences can be theorized within a Darwinian framework.

Sociality Influences Cultural Evolution

The sociality of a population—its size and interconnectedness—also influences the process of cumulative cultural evolution. Larger populations tend to have more complex technology and culture (Edinborough, 2009; Kline & Boyd, 2010; Powell, Shennan, & Thomas, 2009). When populations shrink, cultural and technological complexity seems to also decline (Boyd et al., 2011; Henrich, 2004). Models of cultural evolution (Aoki, Lehmann, & Feldman, 2011; Kobayashi & Aoki, 2012; Lehmann, Aoki, & Feldman, 2011; Powell et al., 2009) explain why.

Each society has a distribution of skills—some individuals, like Bruce, are better at making bows than others. Prestige and success biases lead people to copy Bruce. On average, most imitators don't become as good as Bruce, but the larger the population, the higher the chance that one or two may be better. In a more interconnected population, people are more likely to have access to better models, learning from the best and integrating insights and techniques from more individuals. If populations shrink, the number of people better than Bruce decreases, and even with adaptive learning biases, on average, accumulated know-how or technical sophistication may be lost over generations. Recently, two teams have confirmed these predicted relationships using laboratory experiments (Derex, Beugin, Godelle, & Raymond, 2013; Muthukrishna, Shulman, Vasilescu, & Henrich, 2013). Psychology-style laboratory experiments can teach us about long-term cultural evolution.

Cultural Maladaptation

Our transition to cumulative cultural evolution has allowed us to live in an astonishing array of environments and become Earth's dominant species. But just as genetic evolution doesn't always lead to perfect solutions—from runaway selection (peacock tails), to the previously adaptive (sickle cells), to the vestigial (wisdom teeth)—so too can cultural evolution lead to cultural maladaptations.

Runaway cultural evolution can occur when naïve learners preferentially learn from prestigious individuals, identified by an arbitrary marker, leading to an arms race for more potent versions of the marker. Boyd and Richerson (1985) give the example of tattooing in Polynesia. Without the benefits of a modern tattoo parlor, tattooing in Polynesia was painful and somewhat dangerous, such that only about a foot of the body could be tattooed in one sitting. The recovery from each sitting involved 8 to 12 days of local inflammation and fever, which sometimes proved fatal. Tattooing was also very expensive, taking 6 months for the initial tattoo and requiring the supply of food and shelter for the artist and his family for the duration. Why would such a maladaptive practice evolve?

Being both expensive and dangerous, tattoos became a marker of prestige, and tattooed individuals were more likely to be imitated by others, including their preference for tattooing and tattooed cultural models. As people competed for prestige, tattoos became larger and more elaborate, increasing their danger and cost in a runaway process, where individuals spent more and more resources they could otherwise use for food, shelter, and other immediately adaptive benefits. Similar processes may explain why poorer people spend money on luxury goods, and knock-offs, well beyond what they can afford.

Our norm psychology (Chudek & Henrich, 2011)—our tendency to recognize, internalize, and copy norms—cannot readily distinguish between adaptive, neutral, or even maladaptive norms. Mechanisms like reputation, signaling, and costly punishment can sustain any costly behavior independent of whether the behavior contributes to others or the group. Indeed, many nonadaptive traditions have stabilized in some cultures—from New Guineans eating the brains of their dead relatives and developing the fatal brain disease kuru to some Africans and Middle Easterners removing the clitori of their girls (Durham, 1991; Edgerton, 1992).

How cultural evolution produces and maintains maladaptive practices is a rich area for future research. Early insights include why ineffective medical treatments spread (they are used for longer periods, so have more chance to be imitated even though they are abandoned more frequently [Tanaka, Kendal, & Laland, 2009]); how lifetime celibacy, reliance on prayer over modern medicine, or suicidal warfare spread (Henrich, 2009); and the network structures that make maladaptive practices more likely (Yeaman, Schick, & Lehmann, 2012).

Intergroup Competition Shapes Cultural Evolution

We have discussed learning biases, such as prestige, success, and conformity biases that allow individual-level choices to shape population-level outcomes. However, sometimes cultural differences between competing populations can have their own potent influences on cultural evolution. Such processes are usually called *cultural group selection*, and may have particularly important consequences for understanding the emergence of our sense of morality and prosocial motivations.

Many biologists are skeptical of "genetic group selection," and many psychologists are rather confused by the highly technical and mathematical nature of the debates (see Henrich, 2012). Here's a necessarily too-brief introduction. Natural selection operating within groups usually eliminates genes that cause individuals to behave cooperatively (i.e., paying costs to benefit other group members). Even if a cooperative group outcompetes others in the short term, cooperative individuals are at a disadvantage *within* their group. This disadvantage usually dominates because even small rates of migration quickly make interacting groups genetically similar, sapping the genetic importance of intergroup competition. This is why biologists are skeptical of genetic group selection.

Cultural group selection is an entirely different story. Unlike genetic evolution, it has a variety of mechanisms that sustain trait variation between populations. These relate to language barriers, conformity bias, prestige, ethnocentric biases, reputation, CREDs, punishment, and norm psychology, just for a start. This persistent between-group variation means that intergroup competition, when it occurs, favors some ideas, norms, values, institutions, and practices over others. Since the children of migrants adopt the cultural traits of their community yet still carry their parents' genes, cultural group selection is plausible under many circumstances where genetic group selection is not. Cultural evolution and intergroup competition can also generate purely within-group selection pressures on genes, favoring psychological mechanisms for prosociality, norm compliance, and shame (Chudek & Henrich, 2011; Chudek, Zhao, & Henrich, 2013).

Empirical work by Bell, Richerson, and McElreath (2009) confirms these theoretical expectations: Globally, the amount of cultural variation among groups is much greater than the amount of genetic variation among groups. This is precisely the evidence that convinces evolutionary theorists that cultural group selection could very well be a major force in cultural evolution.

The importance of intergroup competition in shaping cultural evolution is further supported by a rich combination of experimental work, field studies, historical cases, and archaeological research. For recent reviews, see Richerson and Boyd (2005), Richerson et al. (2014), and Henrich (forthcoming).

The Cultural Evolution of Religion

Religion is an evolutionary puzzle. Supernatural beliefs, devotions, and rituals are universal, but variable, and often demand costly commitments to beliefs and practices that violate logical consistency and intuitive expectations (Atran & Norenzayan, 2004; Boyer, 2001). From an evolutionary perspective, a purely genetic account would be hard-pressed to explain these costly and often fitness-reducing beliefs and practices. However, our species has (at least) two lines of inheritance—genetic and cultural—and the mechanisms of cultural evolution we've discussed can begin to unravel this evolutionary enigma.

The cultural evolution of religion involves (a) content biases, (b) CREDs, and (c) cultural group selection (Atran & Henrich, 2010; Norenzayan, 2013). First, our theory of mind abilities, which may have evolved for high-fidelity cultural learning, favor beliefs in supernatural agents (Atran & Norenzayan, 2004). Cognitive scientists have argued that religious agents, such as spirits, are "minimally counterintuitive" and thus more easily remembered and retransmitted (Norenzayan, Atran, Faulkner, & Schaller, 2006)—a content bias. So, you can't explain religion without reference to reliably developing features of mind.

However, nothing in this (so far) purely content-based approach explains why some people believe in and are committed to a particular supernatural agent or agents while others are not. Folktales may spread widely because they are minimally counterintuitive, but people need not be deeply committed to those folktales. Similarly, Christians may come to entirely acquire the concept of Shiva or Zeus, but not come to believe in either (Gervais, Willard, Norenzayan, & Henrich, 2011). A proper theory needs to explain the existence of faith or committed belief. CREDs provide one solution to this puzzle (Henrich, 2009). Watching Mom, Dad, and members of one's community engage in costly displays of self-sacrifice (animal sacrifices, fasting, prayer time, charitable giving, celibacy, time-consuming rituals such as church services, etc.) deepens observers' commitment to the beliefs underlying these practices. Gods who demand costly sacrifices from believers are transmitted more effectively because learners, seeing those costly sacrifices, will themselves come to deepen their faith.

Finally, why are gods in the modern world frequently concerned with rewarding and punishing people for (im)moral behavior? Why are the gods of hunter-gatherers typically weak, whimsical, and not morally concerned? The final puzzle piece is intergroup competition. Supernatural beliefs and rituals that galvanize cooperation and favor success in intergroup competition preferentially proliferate over centuries. The rise of big moralizing gods (such as Yahweh and Allah) may have been pivotal for the evolution of larger societies of anonymous but prosocial individuals compared to the smaller and often nonmoralizing deities typical of small-scale societies (Atran & Henrich, 2010; Norenzayan, 2013). A large body of experiments now supports that belief in religions with big moralizing gods, but not other religions or atheism, promotes prosocial behavior with strangers who are coreligionists (Atkinson & Bourrat, 2011; Norenzayan & Shariff, 2008). Cultural group selection helps us understand the variation in religions over space and time.

CULTURE-GENE COEVOLUTION

There's now little doubt that cultural evolution has shaped genetic evolution, especially over the past 10,000 years. Specific genes in the genome have been identified that show evidence of positive selection as a consequence of cultural practices. Examples of genes selected by pressures created by cultural evolution include genes for milk drinking (lactase persistence; gene LCT), alcohol processing (alcohol dehydrogenase, ADH), and blue eyes (HERC2), not to mention a host of genes related to brain growth, dietary diversity, and pathogen resistance (Laland et al., 2010; Richerson et al., 2010).

Building on this, some researchers have argued that cultural evolution has been driving genetic changes in the human lineage for hundreds of thousands or even millions of years, back to the origins of the genus Homo (Henrich & McElreath, 2003; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007). Variously termed the Cultural Brain Hypothesis or Cultural Intelligence Hypothesis, the idea is this: By generating an ever-expanding body of cultural know-how, including knowledge and skills related to tool making, animal tracking, plant processing, fire making, cooking, and shelter construction, cultural evolution created the key selection pressures driving recent human evolution and ignited an autocatalytic interaction between genes and culture that drove the rapid expansion of human brains in a relatively short period of evolutionary time. Once culture began to accumulate, selection would have increasingly favored brains equipped to acquire, organize, store, and retransmit the available cultural information. However, as brains got bigger and better at cultural learning, cultural evolution would have responded by expanding the pool of adaptive information available to the learner. The better learners got, the faster culture evolved and the larger the pool of cultural information grew. The cultural brain hypothesis claims that big brains are *for* cultural learning, not generalized intelligence, individual problem solving, or Machiavellian deception and strategizing.

The importance of culture may have implications beyond the autocatalytic culture-gene coevolutionary spiral of the human lineage. Researchers have also considered how social learning may have shaped primate brains, group size, sociality, and life history (van Schaik & Burkart, 2011; van Schaik, Isler, & Burkart, 2012). Theoretical models of these hypothesized gene-culture coevolutionary processes successfully reproduce the empirical patterns of relationships between brain size, group size, and juvenile periods observed in primates (Muthukrishna, Chudek, & Henrich, 2015).

Gene-culture coevolution neatly sets humans within the primate order while at the same time explains our unique evolutionary trajectory.

CONCLUSION

Understanding humans from an evolutionary perspective isn't easy. Not only do we have countless psychological adaptations and peculiarities, honed to environments long vanished, but we are an evolved cultural species, the inheritors of two different and very complex systems of evolving information. Like most discoveries in our information age, the evolutionary science of our cultural species hasn't emerged *sui generis* from the mind of a great thinker. Rather, it has and continues to coalesce at the intersection of an ever-ballooning body of work by biologists, anthropologists, and economists from many different backgrounds. Psychologists play a key role in this important episode of discovery, as the many citations above attest. In our view, this approach unites and synthesizes exciting lines of research in developmental psychology, social psychology, cultural psychology, and evolutionary psychology under a broad Darwinian umbrella. The emerging science of cultural evolution is building an understanding of our species from its origin to the present day, from the genetic evolutionary emergence of cultural learning in our species to the many fascinating phenomena produced by cultural evolution around us today, such as religions with big moralizing gods, markets, normative monogamy, ethnicity, castes, and technological change.

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