CULTURAL EVOLUTION

Maciej Chudek
School of Human Evolution and Social Change
Arizona State University

Michael Muthukrishna
University of British Columbia
Department of Psychology

Joseph Henrich
University of British Columbia
Department of Psychology
Department of Economics

You and I are very unusual beasts. Our ancestors, mere African primates, spread across the globe tens of thousands of years ago, long before the origins of agriculture, cities or industrial technologies. More ecologically successful than any land mammal, human foragers came to inhabit most of the world's terrestrial ecosystems, from the frozen tundra of the Arctic to the arid deserts of Australia. Yet, despite our massive ecological success, our kind is physically weak, slow, and not particularly good at climbing trees; any adult chimp can kick our butts and any big cat can easily chase us down (though we are unusually good at long distance running). We can't distinguish edible plants from poisonous ones, and our gut can't detoxify the 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.

Sceptical about this last point? Imagine we took you and 19 of your coworkers or fellow students (without equipment) and pitted you against a troop of 20 capuchin monkeys from Costa Rica (also without equipment). We would parachute both teams into a remote part of the Ituri Forest in the Congo in central Africa. After six months, we return and count the survivors on each team. The team with the most survivors wins. Who would you bet on, the monkeys or your colleagues? 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 a foragers—which our ancestors have managed to do across a staggering variety of environments for thousands of generations—what's that big brain *for* anyway?

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. 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 include the Franklin Expedition (Boyd, Richerson, & Henrich, 2011; Lambert, 2009) of 1846, 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' foray into the Australian outback (Henrich & McElreath, 2003) in 1860, who despite their extensive preparations and equipment, died because they did not know the local aboriginal techniques for detoxifying plants. You might also consider watching the recent 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 lush and 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 over 35,000 years (Cosgrove et al., 2010), and eating each other. Only Pearce survived the slow cannibalistic attrition.

How does all this floundering by educated, technologically sophisticated explorers square with the massive ecological success of our species? How is it that you and I 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 so unusual compared to other animals is that we are a member of a cultural species that evolved by natural selection: an "evolved cultural species". Unlike all other species, our kind is addicted to culture. You and I are entirely reliant on a cumulative body of cultural know-how that is transmitted from one person to another, and accumulates over generations. Stripped of this non-genetic information, we are rather pathetic compared to other species (Boyd et al., 2011; Henrich, Boyd, & Richerson, 2008).

We need an evolutionary explanation for the existence and behavior of a cultural species. Over the last 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 "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 non-cultural individual could devise alone in their lifetime, regardless of how individually intelligent they were. 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, as our species has, 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 like:

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 did a species similar to extant, non-human apes come to possess such highly adaptive, but non-genetic, behavioural repertoires, and why haven't other species done the same?
3. What psychological processes and cognitive adaptations should we expect in a species whose survival depends so critically on mastering culturally transmitted know-how?
4. How does culture itself evolve? How do these cultural repertoires, or large bodies of know-how, 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?

Let's dive right in to the answers evolutionary researchers are finding to these questions.

How can 'culture' evolve? Doesn't evolution require discrete genes and replication?

Neither evolution nor adaptation requires discrete traits, "replicators", low mutation rates, vertical transmission or random variation (Henrich & Boyd, 2002; Henrich et al., 2008). Just because genes evolve, it does not 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 illustrate how culture can evolve, and exactly how this is like and unlike genetic evolution. Our emerging understanding of cultural evolution is actually closer to Darwin's original conception of evolution. Knowing nothing of genes, he reasoned about the inheritance of acquired habits, and was actually inspired by work on the cultural evolution of languages (Hayek, 1988).

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 adaptive. Culture also meets all three requirements, but in different ways. Like bacterial genes, cultural information spreads horizontally and need not be limited to parental transmission to offspring.

Although the basic idea of natural selection is simple enough, we have come a long way since Darwin's time. Developing rigorous hypotheses and plausible theories about evolution requires formal mathematical models. To demonstrate how culture and the capacity for culture can evolve, theorists have borrowed and extended tools from evolutionary biology. These models begin from simple descriptions of how individuals acquire their adult behavioral repertoires---by learning from others, learning individually (for instance, by trial and error), or by genetically encoding responses to specific stimuli ("evoked culture"). Then, using mathematical techniques drawn from population genetics, epidemiology, statistics and communications, they explore how the distribution of phenotypes---behaviours, motivations, beliefs, and so on---changes over time.

In these models when individuals are sufficiently reliant on learning from others, cultural evolution emerges. That is, populations adapt non-genetically, know-how accumulates and useful practices (and sometimes harmful ones) become widely shared.

Even the earliest models delved into the distinct nature of cultural evolution, taking seriously and formally investigating the ways it was unlike genetic evolution. Cavalli-Sforza and Feldman, for example, studied a wide range of models for learning, including ones involving continuous traits and “horizontal” learning from peers or “oblique” learning from older individuals besides one’s genetic parent e.g. (Cavalli-Sforza, 1981). Similarly, in their now classic treatise, Boyd and Richerson (1985; also see 2005) built 38 different models of cultural evolution or culture-gene coevolution. Eighteen of these models assumed cultural traits were continuous (not discrete) and contained arbitrary amounts of error in transmission---unlike genes, which mutate very rarely. They considered models in which innate and specialized "modules" competed against social learning and individual learning.

To get a handle on some of the similarities and differences between cultural and genetic evolution, consider an example of the kinds of events that occur in models of cultural evolution. Suppose a young hunter-gatherer wants to figure out the best length for his arrows. To accomplish this, he (or she) locates the 3 most successful hunters in the community, notes the lengths of their arrows, and then averages them. If the observed arrow lengths were 14cm, 15cm and 19cm, our learner would make his arrow 16cm.

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 (preferred arrow lengths) of the new generation will be correlated with those they learned from their ‘cultural parents’.

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

Will there be adaptive evolution? Yes, if everyone learns this way and if there is an optimal arrow length for hunting, eventually arrow lengths will converge to it. This will occur without anyone constructing a mental model of aerodynamics or performing cost benefit analyses of the effectiveness of different arrows on various prey types. This will generally occur unconsciously and unintentionally, since these biases generally operate outside conscious awareness.

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.

Below 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.

THE EVOLUTION OF OUR CAPACITIES FOR CULTURE

Many people still think that 'evolutionary' or 'biological' explanations are in opposition to 'cultural' explanations—the "Nature versus Nurture" debate. To a cultural evolutionary theorist, however, 'cultural explanations' are a type of evolutionary explanation that can compete with, or be complemented by, other non-cultural evolutionary explanations. In 1985, Boyd and Richerson extended the Darwinian umbrella to cover 'cultural' explanations by asking: under what conditions might natural selection favor individuals relying on social learning over their own experience or their genetically evolved intuitions; and, how might natural selection shape psychological mechanisms to allow individuals to most effectively extract ideas, beliefs, values, motivations and practices from others in their social milieu. Under this expanded umbrella, explanations involving social learning ('cultural explanations') can compete with non-cultural hypotheses within the same epistemological framework. Cultural evolutionary models investigate the details of how our genetically evolved psychology for social learning and attention interacts with other aspects of our evolved psychology, and the social and physical environments encountered by individuals and populations.

Of course, all explanations of behavior are 'biological' in the sense that they involve the output from our brains and nervous systems. Both genes and culture shape our brains and biology, as work in cultural neuroscience now makes inescapably clear. 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. Remember, there's much more to our biology than our genes.

HOW AND WHEN WILL 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. One key question is: will selection favor rare cultural learners in a population of mostly asocial learners? The answer: culture is adaptive when asocial learning is hard and environments fluctuate a lot, but not too much.

While the mathematical reasoning that generated and 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 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 cognitive machinery for cultural learning; that is, 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 your best bet.

Why did humans in particular make the transition to a cultural species and why only recently (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 re-conquered by each individual, and (c) a species have the cognitive pre-adaptations 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 five million years since our lineage split from chimpanzees (Potts, 1998; P. Richerson & R. Boyd, 2000; P. J. Richerson & R. Boyd, 2000; cf.Shultz, Nelson, & Dunbar, 2012).

Meanwhile archaeological evidence shows us that for over 1.5 million years we have relied on technologies that are hard to invent and master asocially. Our hominid ancestors relied on expertly produced Acheulean stone tools, which are hard to reinvent alone (Stout & Chaminade, 2012; Stout, Passingham, Frith, Apel, & Chaminade, 2011; Stout, Toth, Schick, & Chaminade, 2008). 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). When contemporary experts make Acheulean tools their patterns of brain activation overlap with language circuits and imply complex hierarchical planning (Stout et al., 2008). In the few remaining societies that use stone tools today, acquiring expertise requires many years of apprenticeship and social scaffolding (Stout et al., 2002).

A second question that naturally follows is: if selection favors cultural learning and since cultural learners are in a sense parasitic on the costly trial-and-error learning of others, won't groups and species where cultural learners are common eventually stagnate and suffer? Actually, there are several reasons why we wouldn't expect this to happen---circumstances that make cultural learning adaptive for both individuals and groups. This is true when (1) individuals cleverly combine cultural learning and individual innovation, using one to improve on the results of the other (Boyd & Richerson, 1985; Enquist, Eriksson, & Ghirlanda, 2007); (2) when cultural learners have cognitive adaptations that let them learn better-than-average information from their peers (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Henrich & Gil-White, 2001); or (3) when there is limited dispersal (Lehmann, Feldman, & Kaeuffer, 2010; Rendell, Fogarty, & Laland, 2010)—that is, if mostly individuals interact with people born near them, but reproduce with a broader population.

Questions like these recently led Luke Rendell and his collaborators (Rendell, Boyd, et al., 2010) to run a social-learning tournament with a €10,000 prize. Stepping into the shoes of our evolving genome, researchers from across the world submitted computer-based strategies describing how their organism would learn, either individually or culturally, in an unknown, varying environment. The winning strategy relied almost exclusively on cultural learning.

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; J. F. Coleman, Blake, & Mouton, 1958; T. Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). Even infants socially reference adults more when confronted with more ambiguous stimuli (Kim & Kwak, 2011).

One development that makes this theoretical work---which originally attempted to explain the evolutionary dynamics that gave rise to culture in humans---particularly compelling, is how successful it has been at predicting the social learning strategies of other animals. Biologists have observed increased reliance on social information when individual experience and evolved intuitions produce uncertainty across many domains, including foraging, mate choice and aggression, and across diverse species, including fish (Laland, Atton, & Webster, 2011; Webster & Laland, 2008), birds, rodents (Galef Jr & Whiskin, 2008), deer and primates (Kendal, Coolen, van Bergen, & Laland, 2005). For an application of these idea to chimpanzee culture, see Henrich and Tennie (under review).

Theory and observation both suggest that as global climates began to increasingly fluctuate over the last five 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 do it so faithfully and consistently, that it crossed the threshold to cumulative cultural evolution and became a cultural species.

Building from this bedrock of evolutionary theory, further investigations of cultural evolution have honed in on the details of how natural selection would shape the psychology of a cultural species. These investigations weave formal evolutionary theory together 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).

Who to learn from

Some of the people around you are just better at certain things than others. No doubt this was also true for your distant ancestors. Natural selection favored learners who chose better cultural models. Our psychology may be rife with biases and dispositions whose ancestral purpose was to make it more likely we learned from the right people. The learning behavior of children and infants is a particularly good testing ground for these kinds of hypotheses.

Skill, Success and Prestige

Sometimes a learner can just identify the most skilled people around them. When identifying skill is easy, selection should favor a bias for learning from more skilled models (for a review see Maciej Chudek, Heller, Birch, & Henrich, 2012; Henrich & Gil-White, 2001). Supporting this evolutionary logic, children preferentially imitate more skilful models when learning object names (Koenig & Harris, 2005; Scofield & Behrend, 2008), artefact functions (S. A. Birch, Vauthier, & Bloom, 2008) and even causal properties (Sobel & Corriveau, 2010). They do this (1) even when the more skilled individual is a stranger rather than a familiar teacher from their preschool (Corriveau & Harris, 2009a), (2) even a week later (Corriveau & Harris, 2009b), (3) even when the more skilful model acts in bizarre and unconventional ways (Scofield, Gilpin, Pierucci, & Morgan, 2013) or has an unfamiliar accent (Corriveau, Kinzler, & Harris, 2013), and (4) even when they have witnessed the skilful model being intentionally deceitful (Liu, Vanderbilt, & Heyman, 2013). Gelman (2009) and Mills (2012) provide additional examples.

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 strangers than their own mother (Kim & Kwak, 2011; Stenberg, 2009; Walden & Kim, 2005) when the stranger appears more knowledgeable or competent of the novel environment.

Perhaps as an indirect mechanism to the same end, young children also preferentially learn from more confident individuals (S. A. Birch, Akmal, & Frampton, 2010; Jaswal & Malone, 2007; Sabbagh & Baldwin, 2001). Interestingly, children who speak languages with obligate evidential markers---which grammatically indicate the source of the information when a speaker makes a statement (e.g. Turkish)---seem to respond more to skill cues at a younger age (Lucas, Lewis, Pala, Wong, & Berridge, 2013), suggesting that culture itself can shape our social learning biases.

Sometimes skill differences aren't that easy to assess. Even today it's hard to know whether fad diets improve or worsen your health because their consequences aren't apparent for many years; even with decades of research, it's still not clear what the optimal diet contains, though many people below they know. Imagine how much harder these judgments were for our prehistoric ancestors. In such uncertain circumstances, you can sometimes make more adaptive learning choices on the basis of success (Boyd & Richerson, 1985; Henrich & Gil-White, 2001) by imitating whoever seems to have the most positive life outcomes in general—many wives, greater hunting success, more resources, etc.—even if you do not understand why. Consistent with this, young children seem to prefer individuals who experience entirely random positive outcomes (Olson, Banaji, Dweck, & Spelke, 2006; Olson, Dunham, Dweck, Spelke, & Banaji, 2008).

Assessing success differences can be difficult or costly and may take a long time; but children need to make learning decisions right now! In these situations, if everyone else is also trying to make adaptive learning choices, you can sometimes exploit information they have (but you don't) by preferring to learn from whomever everyone else is learning from ("prestige bias"). For an in-depth exploration of these ideas, see Henrich & Gil-White (2001). This approach explains why, when children see strangers paying more attention to one model than others, they are in fact more likely to learn from the model receiving more attention, i.e. the more prestigious model (Maciej Chudek et al., 2012; Fusaro & Harris, 2008).

Similarly, when adult experimental participants faced a computer simulation of a challenge relevant to our Pleistocene ancestors – designing a stone arrowhead for hunting – they also show these patterns of biased learning. They preferentially imitate both prestigious models (those who others have paid attention to) and successful models (those who's 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 all about picking the most skilled individuals overall. Sometimes someone is a better model for you in particular. For instance, a three-year-old might be more likely to acquire behaviors adapted to their personal ecology—the skills it takes to be a successful three-year-old—from a four-year-old than by trying to imitate a fifty-year-old. Young children do seem to prefer learning from similar or slightly older aged peers in a variety of domains (Hilmert, Kulik, & Christenfeld, 2006; Shutts, Banaji, & Spelke, 2010; VanderBorght & Jaswal, 2009), while in others they prefer older models, unless the older models are obviously unskilled (Jaswal & Neely, 2006). Even 14-18-month old infants seem to have better recall for actions when they are modelled by three-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 (Rosekrans, 1967; Shutts et al., 2010; Wolf, 1973). Adults, meanwhile, seem more susceptible to social influence by those who share their existing beliefs (Hilmert et al., 2006).

Another important theoretical result is that the existence of an evolving cultural corpus can readily give rise to ethnicities—i.e., 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 (Maciej 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 co-ethnics. In fact, any interaction governed by social norms (Henrich & Henrich, 2007) spontaneously generates just these kinds of ethnic correlations between an arbitrary signal (e.g. dialect) and their behaviors (Efferson, Lalive, & Fehr, 2008) and preferentially interact with co-ethnics. Effectively testing these predictions, recent developmental work has shown that children and infants pay careful attention to others' accents and prefer interacting with and learning from people with familiar ones (Kinzler, Corriveau, & Harris, 2011; Kinzler, Dupoux, & Spelke, 2007; Kinzler, Shutts, DeJesus, & Spelke, 2009; Shutts, Kinzler, McKee, & Spelke, 2009).

One vivid demonstration that we are a cultural species adapted for a world containing fitness relevant, but arbitrarily marked ethnicities is the potency and ubiquity of “minimal group paradigms” in social psychology research, originally developed by Tajfel (1971) but used by countless researchers since. Sometimes researchers want to experimentally measure people's group-relevant psychological traits, such as in-group favouritism. So strong is our disposition to notice and use information about arbitrary, symbolically marked groupings that researchers don’t need to recruit people from different ethnic groups, they can observe the same effects by recruiting anyone at all and assigning them to entirely arbitrary groups (Kurzban, Tooby, & Cosmides, 2001).

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 five most of us found ourselves faced with compulsory attendance in a micro-society of same-aged, mostly unrelated peers—each an evolved cultural learner, each trying to make sense of the world, each 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 first-hand experience of conformist transmission (people preferentially adopting the most common behaviour) and even anti-conformity (preferentially avoiding the most common behaviour).

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 anti-conform. 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 (Andrés Guzmán, Rodríguez-Sickert, & Rowthorn, 2007; Boyd & Richerson, 1985; Henrich & Boyd, 1998; Nakahashi et al., 2012; Perreault, Moya, & Boyd, 2012), others imply a more limited scope (Eriksson, Enquist, & Ghirlanda, 2007). The question is hard because whether the majority are likely to be right depends on what everyone else's learning strategy is (including their own conformity biases), and on how recently the environment has changed, rendering old cultural adaptations obsolete.

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; T. 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).

There is some indication that conformity biases may be present in young children (Corriveau, Fusaro, & Harris, 2009; Corriveau & Harris, 2010), but there are not yet tests for conformity-bias in the narrow cultural evolution sense. Conformity biases have also been observed in fish (Pike & Laland, 2010).

Credibility Enhancing Displays (CREDs)

Imagine yourself as a young person in an ancient Pleistocene society. You pay attention to what members of your tribe are doing and you notice that some are more successful than others. Big Bruce is a highly successful and prestigious member of your tribe – he's a highly productive hunter and as a result, very rich, gets all the ladies and people pay attention to him when he speaks. Although you know that there's something about Big Bruce that makes him successful, you don't know exactly what it is. Maybe Bruce is successful because of the spears he uses, or where he hunts, or what time of day he goes out. Or maybe it's because of the animal skins he dons, how he shaves his head, or the gods he worships. In this situation you can often improve your fitness if you copy everything about Bruce. Cultural evolutionary scientists argue that this helps explain why even today, celebrities are able to increase the sale of milk or cologne, have their fashion-sense copied and influence popular trends that have nothing to do with their success (Maciej Chudek et al., 2012). NBA star Lebron James, who went directly from high school to the pros, gets paid millions for telling people which car insurance to buy.

Of course, if we're paying attention to prestigious or successful individuals we're potentially subject to exploitation. If Bruce notices that everyone is listening to him, he might offer them self-serving information, for example, tell them to hunt in the wrong spots or that they are more likely to succeed if they give him half of their meat. In this case it would pay to discriminate on cultural content.

The Credibility Enhancing Displays hypothesis (CREDs; Joseph Henrich, 2009) proses an evolved defence against such exploitation. Some evidence suggests that people have evolved to be sensitive to costly displays that reveal if a person really does believe what they're claiming. For example, if Bruce were to tell everyone that the land across the river was the best hunting spot, but then not hunt there himself, people would be less likely to believe Bruce. CREDs can also help us understand how religious beliefs can be transmitted in the absence of direct experience – a child would be more likely to become a believer if her parents professed belief in God and also attended weekly services and gave money to charity than if her parents only professed belief in God (Lanman, 2012). Without the CREDs associated with the time and cost of religion, a learners should be sceptical of claims about invisible agents who monitor people for proper behavior since her parents might make up such a story to better control her.

Recently, Aiyana Willard and her collaborators experimentally observed CREDs changing people's behavior. Their participants were willing to bet actual money that an implausible news story---for instance, that scientists can now teleport small particles---was true if someone who was endorsing the story actually bet their own money. What's more, they were more likely to voluntarily choose to eat real insects if someone nearby both claimed the bugs were nutritious and backed up that claim by sampling some (Willard, Norenzayan, & Henrich, n.d.).

Do these matter in the real world?

One of the starkest demonstrations of prestige and self-similarity biases—and particularly relevant for students of evolutionary psychology—is the *Werther effect* (Phillips, 1974); the phenomenon of copycat suicides. In 1774, the German author Goethe's published *The Sorrows of Young Werther*, whose main protagonist, driven to sorrow by unrequited love, shoots himself in the head. The subsequent spate of copycat suicides by young men led authorities to ban the book in Italy, Leipzig and Copenhagen. Since then, spikes in copycats of well-publicized suicides of famous individuals (L. Coleman, 2004; Mesoudi, 2009), by similar victims and using similar methods, have been documented in the United States (Phillips, 1974), Germany (Jonas, 1992) and Japan (Stack, 1996). 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.

At first glance from an evolutionary vantage, 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. These disturbing patterns make more sense if you recognize that humans are an obligate cultural species. We are equipped with a cultural learning psychology which, on average, sifts out better models and more adaptive information, and predisposes us to acquire this information. Sadly however, these cognitive mechanisms sometimes tragically misfire (Henrich & Henrich, 2007: Chapter 2).

A less harrowing demonstration of our self-similarity bias is the fact that students attain better grades and are less likely to drop out of classes when taught by same-sex (Hoffmann & Oreopoulos, 2009) and same-race instructors (Fairlie, Hoffmann, & Oreopoulos, 2011). These studies strive to separate these 'learning' biases created by instructors on their students from other more studied effects, such as those related to ethnic or racial prejudices.

Systematic fieldwork in small-scale societies also makes it clear that cultural learning biases emerge there as well, which helps establish both the cross-cultural generalizability and ecological validity of the above-described laboratory findings. Henrich and Broesch (2011) collected data in three subsistence farming and fishing villages on Yasawa Island in Fiji. They asked villagers from age 7 to 81 who they would talk to if they had a question about (1) fishing, (2) planting yams, and (3) using a medicinal plant. They then used these data to create "advice networks" for the village. The researchers asked what theoretically important variables predicted seeking someone out for advice in these locally important domains. By far, the most important factor was the seekers perceptions of how successful or knowledge a person was. However, independent of this, age, sex and proximity (being in the same village) were also important predictors. Interestingly, there were also cross-domain prestige effects. For example, being a successful fishermen caused one to be sought out more for advice on yam planting, even after controlling for people's beliefs about a person's yam success and know-how. For work in other small-scale communities see Reyes-Garía et al.(2009) and Tehrani et. al. (2010).

WHAT TO LEARN

Of course, not all cultural information is equal—you can often learn more by ignoring some things and focusing on others. Natural selection ought to have attuned people to attend to fitness-relevant forms of information. These include information about animals and plants, dangers, fire, reputation, social norms, and social groupings.

Children not only keenly attend to information about animals, but they are selective in what they store in memory. For example, Clark 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, forthcoming).

Similarly, recent investigations of infants responses to plants suggests that even at around one 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:

1) Reputation information: Mesoudi, Whiten and Dunbar(2006) has demonstrated that gossipy information—about others misdeeds and affairs—gets transmitted more faithfully through laboratory social networks.
2) Fire: Fessler(2006) has drawn on diverse evidence to argue that children's psychology may be calibrated for attending to and learning about fire .
3) 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 (Rakoczy, Brosche, Warneken, & Tomasello, 2009; Schmidt, Rakoczy, & Tomasello, 2011; Schmidt & Tomasello, 2012).

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, forthcoming).

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 might natural selection 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 this cultural learning psychology, how does the 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. Each of us only very recently transformed from helpless, squirming infants to adults capable of surviving, reproducing, bicycling, queuing, completing sudokus and many other amazing feats. To successfully make that transformation we had to absorb a tremendous amount of information from the people around us—words, concepts, skills, beliefs, practices, norms, motivation, tastes, strategies, and habits. When we are young we don't have the time, let alone the necessary motivation, background knowledge or resources, to also deduce where this cultural knowledge originally came from. Though in some societies children torment their parents with never-ending choruses of "why, why, why?", they usually move on moments later without any clear answers. As we age, we acquire intuitions that black is the color of mourning, that "d" comes before "e" in the alphabet, that skipping to the front of the queue is a major transgression, and that neck ties look professional rather than ridiculous, because that's just the way things are. If asked, our childhood selves might have answered that "in the olden times" someone very smart decided that this was just how things were going to be. As adults, when our children press us with their chorus of "whys" we, like our parents, often lack good answers.

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 or billions of individuals with evolved, biased psychologies learning, forgetting, applying, and transmitting information over generations. Those dynamic processes work 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 visit small scale societies and with the benefit of modern science, see that people's culturally-acquired practices are extraordinarily well-adapted to local environmental challenges; yet, the people themselves merely claim it's just "our custom"(Henrich, 2002; Henrich & Henrich, 2010).

In Sardinia, for example, many people traditionally made their living by herding goats and sheep. Typically, in mountainous terrain like Sardinia, people live in the valley and take their flock up into the mountains when the pasture is good. This setup means that water sources are near the house, and the animals are in the valley, near home, during the shearing and milking season. But Sardinians traditionally did it the opposite way; they lived in the mountains and took their flocks down to the valley, where they had to get water and do all the shearing and milking. Anthropologist Peter Brown puzzled over this, and when he put it together with an array of otherwise peculiar practices, like closing windows on hot nights, he realized that he was likely at looking at an adaptive cultural package of anti-malarial practices (Brown, 1998).

How could these, and many other groups, have come to act so adaptively without anyone understanding why their actions are useful? Must we assume that each culture's history is peppered with savant shamans, who secretly shaped these traditions, and for some unknown reason people listened to them without understanding why?

No need, which is good given the flaws and biases in human reasoning (Henrich, 2002). Mechanisms such as the success bias, prestige bias, conformist bias, CREDs, content biases and intergroup competition allows cultural information to improve and aggregate over generations, without most or any individuals ever needing to understand why or how it is happening, or why a given cultural practice or tradition is effective (J. Henrich, 2009; Henrich & Broesch, 2011; Henrich & Henrich, 2010).

CULTURAL EVOLUTION SHAPES PREFERENCES AND PSYCHOLOGY

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 chilli peppers. However, despite this aversive content bias, many populations in the New World have incorporated chillies and other strong spices as essential ingredients in their cuisine. Billings and Sherman (1998) conducted an extensive survey of the recipes from across the world, along with a survey of the anti-microbial 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 anti-microbial 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 each 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 (chilli peppers provide anti-microbial defence despite genetic predispositions against them). But how does culture override our genetically encoded preferences?

Experimental works shows how this can work at the micro-level: children adopt the food choices and preferences held by their peers (L. L. Birch, 1987; Duncker, 1938), and exercise those preferences in both their private rankings and public behaviour. Evidence from neuroscience indicates that seeing cultural models prefer something actually makes a learner enjoy it or desire it more themselves, even if they are alone (Zaki, Schirmer, & Mitchell, 2011). The available evidence indicates that cultural learning alters our brains to change our preferences for, or tastes in, wine, mates and music (Goldstein et al., 2008; T. J. H. Morgan & Laland, 2012; Plassmann, O'Doherty, Shiv, & Rangel, 2008; Watts, 2012).

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) provide the close up details of this process, by examining how an adaptive repertoire of fish taboos, which protect pregnant women from dangerous marine toxins, have accumulated to address a local environmental challenge in Fiji.

In addition to preferences, ample evidence from diverse societies now makes it clear that important psychological variation exists across populations, even in seemingly basic psychological domains (Henrich, Heine, & Norenzayan, 2010a, 2010b). Anthropologists and cultural psychologists have documented differences in people's 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 a disciplined and systematic approach to building theories about how and why these (non-genetic) psychological differences emerge, and are maintained (Henrich, Ensminger, et al., 2010; Hruschka & Henrich, 2013a, 2013b; Leibbrandt, Gneezy, & List, 2013; Nisbett & Cohen, 1996; Slingerland, Henrich, & Norenzayan, 2013). Documenting cultural differences needn't be just an exercise in butterfly collecting; in the light of cultural evolution, patterns of cultural differences can make sense.

Sociality influences cultural evolution

The sociality of a population—its size and interconnectedness—also influences the process of cumulative cultural evolution. Historians, anthropologists, and archaeologists have long noticed a relationship between a population's size and its cultural and technological complexity. Larger populations tend to have more complex technology and culture (Edinborough, 2009; Kline & Boyd, 2010; Marquet et al., 2012; Powell, Shennan, & Thomas, 2009; Wadley et al., 2011). As a corollary, 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; Enquist, Strimling, Eriksson, Laland, & Sjostrand, 2010; Henrich, 2004; Hill et al., 2011; Kobayashi & Aoki, 2012; Lehmann, Aoki, & Feldman, 2011; Powell et al., 2009; Premo & Kuhn, 2010; Vaesen, 2012; van Schaik & Pradhan, 2003) have helped us understand the mechanisms behind this correlation, suggesting a causal relationship between a population's sociality and its technological sophistication and cultural complexity.

Imagine a population such as the village that Big Bruce, our hunter, lives in. Within this population, there is a distribution of skills—for example, some individuals, like Bruce, are better at making bows than others. The prestige and success biases lead people to copy Bruce, but on average, even copying, most people aren't as good as he is – whatever combination of skills and knowledge that Bruce has are difficult to transmit. Although most copiers don't' end up as good as Bruce, one or two end up better than he is. With a larger population, we are more assured that at least someone in the next generation is better than Bruce; and, with greater interconnectivity, people are more likely to have access to better models, learning from the best and integrating insights and techniques from more individuals. By corollary, if population size falls, the number of people better than Bruce decreases, and accumulated know-how or technical sophistication may be lost over generations. These models suggest a relationship between the number of cultural mentors that people have access to and the level of cultural and technological sophistication that can be sustained over generations.

Recently, two teams have confirmed these relationships using laboratory experiments. Muthukrishna and colleagues (2013) showed that students who had access to more cultural models were substantially better at editing images and tying a system of knots than those who had access to fewer cultural models. Within 10 generations, the worst member of the group with access to more models was better than the best member of the group that had access to fewer models. The group with access to more models also sustained greater cultural complexity. In addition, these results showed that while learners were preferentially focusing on the most skilled individual in the previous generation, they were also integrating knowledge from other individuals. In a similar experiment, Derex and colleagues (2013) had students play a game where they built nets and arrowheads. They found that larger groups were better able to maintain the original net design and improve on the arrowhead design more so than smaller groups, whose net design deteriorated over time.

Cultural Maladaptation

The psychological capacities that have led us into the realm of cumulative cultural evolution have allowed us to live in an astonishing array of environments and become the dominant species on Earth. 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. There is still so much more to discover, but here we review some of what we presently know about cultural maladaptations.

The classic example of an evolutionary runaway process is the peacock's tail. The peacock's elaborate tail evolved as peafowl preferentially mated with peacocks with more extravagant trains (Petrie, Tim, & Carolyn, 1991). These peahens' preferences became ever more common, since they were more likely to mate with bigger-tailed males, who had more descendants, including daughters who preferred bigger-tailed males, and so on in a runaway process that decreased peacocks' mobility and increased their visibility to predators.

An analogous process can occur in cultural evolution 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 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 (Veblen, 1899).

Our norm psychology (Maciej Chudek & Henrich, 2011)—our tendency to recognize, internalize, and copy norms—cannot readily distinguish between adaptive, neutral or even maladaptive norms. Mechanisms like reputation, signalling and costly punishment can sustain any costly behavior independent of whether the behavior contributes to others or the group. Indeed many non-adaptive 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 (Appiah, 2010; Durham, 1991; Edgerton, 1992). Edgerton (1992) reviews a wide range of these patterns.

Understanding the various ways that cultural evolution produces and maintains maladaptive practices is a rich area for future research, but important theoretical contributions have already been made. For example, the fact that ineffective medical treatments may often be used for longer periods (because they are ineffective) can favor their transmission, even though they are abandoned more frequently. This may explain the diffusion and persistence of homeopathic, chiropractic, and “natural” medicine (Tanaka, Kendal, & Laland, 2009). Similarly, theoretical work shows that our species’ aforementioned reliance on CREDs can maintain stable maladaptive behaviors under certain conditions. This may be relevant to explain some practices related to lifetime celibacy, reliance on prayer over modern medicine, or suicidal warfare (Joseph Henrich, 2009). Finally, models of cultural transmission in various network structures suggest that some types of networks make the persistence of maladaptive practices more likely (Yeaman, Schick, & Lehmann, 2012).

In the next section, we discuss how intergroup competition acts as a filter for the practices, norms and networks that sustain maladaptive behaviors.

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 have particularly important consequences for understanding the emergence of our sense of morality and prosocial dispositions.

Students of biology are typically sceptical of explanations that invoke “group selection” (even if they don’t know precisely why) and this has led to much confusion among psychologists who sometimes lack the experience in evolutionary modelling needed to make sense of the technical debate (see Henrich, 2012). Concerns about the importance of genetic group selection arises because in the long run, natural selection will eliminate genetic adaptations that cause individuals to behave cooperatively (i.e. in individually costly ways that benefit others or their group). Even if a genetic group out-competes others in the short term, in the long run the disadvantage that cooperative individuals have within their groups will often dominate because even small rates of migration will quickly make interacting groups genetically similar. This mixing process usually reduces the variation between groups and thereby saps the strength of intergroup competition.

Cultural group selection is an entirely different story. As a preliminary point, one must first drop the essentializing and entity-based conception of "cultures". We are tracking information stored in individual brains over time. There are no apriori "groups" out there. Nevertheless, cultural evolution often results in clumpy distributions of particular ideas, beliefs, values and practices that aggregate in space or in social networks—that is, sometimes groups form and come to share some set of ideas, practices, values and beliefs. This is well substantiated empirically, and understood theoretically. Importantly, though, populations may be similar on some traits and different on others. Westerners, for example, might possess distinct cultural traits vis-à-vis many East Asian populations, though Japanese and Americans may be more similar to each other than either is to Chinese on other traits (e.g. commitment to democratic institutions). It's crucial to partition "culture" (the information) from the "populations" (groups of people).

Cultural evolution, unlike genetic evolution, has a variety of mechanisms that sustain trait variation between populations. This persistent between-group variation means that intergroup competition, when it occurs, favors some ideas, norms, values, institutions and practices over others. Forces such as language barriers, conformity-bias, prestige and ethnocentric biases re-enforce behavioral differences between social groups, even if individuals migrate between them. Reputation and punishment make social norms self-re-enforcing and migrants have incentives to switch their behavior to meet local standards, sustaining variation between groups (Maciej Chudek & Henrich, 2011). In cultural evolution, the children of migrants will tend to adopt the cultural traits of the larger community they grow up in, yet they will still carry their parent's genes. Cultural group selection is plausible and even likely many circumstances where genetic group selection is not.

Empirical work by Bell and colleagues (2009) confirms these theoretical predictions: 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 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.

1. In the laboratory, economists Gürerk, Irlenbusch, and Rockenbach (2006)have shown how individuals migrate from lower payoff institutions to higher payoff ones, and adopt the local norms of that group (Henrich, 2006). This is cultural group selection in the lab, which tests this model (Boyd & Richerson, 2009).
2. Using quantitative data gleaned from New Guinea ethnographies, Soltis, Boyd, and Richerson (1995) have shown that even the slowest forms of cultural group selection (conquest) can occur in 500 to 1000 year time scales.
3. Using detailed experimental data from Hadza foragers, Apicella and her interdisciplinary team(2012)show that much of the variation in cooperative behavior occurs *between* Hadza bands. This creates the conditions for intergroup competition to influence cultural evolution, and violates then necessary conditions for ignoring the between-group components of selective processes.

4. Combining data on intergroup violence with basic evolutionary models, the economist Bowles (2006) shows that intergroup competition is likely to have had a big impact on selective processes over our species evolutionary history.
5. Using field data from three populations in Guatemala, an interdisciplinary team of anthropologists and psychologists (Scott Atran, 2002; Scott Atran et al., 2002)has shown how conservation-oriented ecological beliefs spread from locally prestigious Itza Maya to Ladinos in Guatemala, and how highland Q'eqchi' Maya, with tightly bound cooperative institutions and commercially-oriented economic production, are spreading at the expense of both Itza and Ladinos. This is cultural group selection at the regional level.
6. Using ethnohistorical data, the anthropologist Kelly (1985) has demonstrated how differences in culturally acquired beliefs about brideprice fuelled the Nuer expansion over the Dinka, and how different social institutions, underpinned by different cultural beliefs about segmentary lineages, provided the decisive competitive advantage. Converging with Kelly, Sahlins (1961) has argued that cultural beliefs about segmentary lineages facilitated both the Nuer and Tiv expansions.
7. At the global level, Diamond (1998) has made a cultural group selection case for the European expansion after 1500AD, as well as for the Bantu and Austronesian expansions.
8. Using historical data on ancient polities, the mathematical ecologist Turchin show how crucial intergroup competition is for understanding the rise and fall of empires and for the development of societal institutions (Peter Turchin, 2005; P. Turchin, 2009, 2010)
9. Using material culture, archaeologists are increasingly arguing for the importance of cultural group selection in prehistory (Flannery & Marcus, 2000; Spencer & Redmond, 2001), including competition among foragers (Bettinger & Baumhoff, 1982; Young & Bettinger, 1992).
10. Recently, Henrich, Boyd, and Richerson (2012) have argued that the rather unusual practice of normative monogamy has spread due to the societal level benefits it generates. The spread of monogamy has often occurred as less successful societies have copied the practices and institutions of more successful societies.

Because it spreads social norms and reputational systems that foster greater cooperation and internal harmony, cultural evolution driven by intergroup competition can create purely within-group selection pressures on genes, favoring psychological mechanisms related to prosociality, norm compliance and shame (Maciej Chudek & Henrich, 2011; M. Chudek, Zhao, & Henrich, 2013).

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 (Scott Atran & Norenzayan, 2004). 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 by invoking our second line of inheritance, and the mechanisms of cultural evolution that we have discussed thus far, we can begin to unravel this evolutionary enigma.

Understanding the cultural evolution of religion requires using (1) content biases, (2) credibility enhancing displays (CREDs), and (3) cultural group selection (S. Atran & Henrich, 2010; Norenzayan, 2013). First, research shows that our theory of mind abilities, which may have evolved to subserve high fidelity cultural learning, favor beliefs in supernatural agents (Scott Atran & Norenzayan, 2004). Building on this, cognitive scientists have long argued that religious representations, such as the concept of a ghost, is minimally counterintuitive and thus more easily remembered and retransmitted (Norenzayan, Atran, Faulkner, & Schaller, 2006). This means that certain kinds of representations of supernatural agents will tend to spread as a by-product of otherwise adaptive aspects of our cognition.

Second, however, nothing in this 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 counter-intuitive 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 & Henrich, 2010; Gervais, Willard, Norenzayan, & Henrich, 2011). CREDS provides one solution to this puzzle (Joseph Henrich, 2009). Watching Mum, 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.) actually deepen 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.

Of course, explaining widespread beliefs in supernatural agents does not account for why gods in the modern world are frequently concerned with moral behaviour, and with the rewarding and punishing people according to their behavior. This pattern is especially puzzling in light of the fact that the gods of hunter-gatherers are weak, whimsical and not morally concern. How did gods evolved to be such high and mighty moralizers, with power over the afterlife?

The final piece of the puzzle is intergroup competition. If some combinations of supernatural beliefs and rituals can galvanize cooperation and favor success in intergroup competition better than alternatives, then these can preferentially proliferate over centuries. Thus, we have an explanation for religion's association with both large scale cooperation and intergroup-conflict. 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 (limited geographic range and purview) and often non-moralizing deities typical of small-scale societies (S. 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 co-religionists. The work shows, for example, that unconsciously priming religious people with God, increases their fairness toward strangers and decreases cheating. However, the identical primes have no impact on atheists (Atkinson & Bourrat, 2011; Norenzayan & Shariff, 2008; Shariff & Norenzayan, 2007).

Culture-Gene Coevolution: The Cultural Brain Hypothesis

There's now little doubt that cultural evolution has shaped genetic evolution, especially over the last 10,000 years. Specific genes in the genome have been identified which 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; O'Brien & Laland, 2012; 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 re-transmit 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. 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 (Deaner, Isler, Burkart, & van Schaik, 2007; van Schaik & Burkart, 2011; van Schaik, Isler, & Burkart, 2012). Theoretical simulations 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, n.d.).

This approach neatly sets humans within the primate order while at the same time explaining our unique evolutionary trajectory.

STUDYING A CULTURAL SPECIES

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, economists and mathematicians from many different backgrounds. Psychologists are also playing a key role in this important episode of scientific 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.

REFERENCES

Andrés Guzmán, R., Rodríguez-Sickert, C., & Rowthorn, R. (2007). When in Rome, do as the Romans do: the coevolution of altruistic punishment, conformist learning, and cooperation. *Evolution and human behavior, 28*(2), 112-117.
Aoki, K., & Feldman, M. W. (2014). Evolution of learning strategies in temporally and spatially variable environments: a review of theory. *Theoretical Population Biology, 91*, 3-19.
Aoki, K., Lehmann, L., & Feldman, M. W. (2011). Rates of cultural change and patterns of cultural accumulation in stochastic models of social transmission. *Theoretical Population Biology, 79*(4), 192-202.
Apicella, C. L., Marlowe, F. W., Fowler, J. H., & Christakis, N. A. (2012). Social networks and cooperation in hunter-gatherers. *Nature, 481*(7382), 497-U109.
Appiah, A. (2010). *The honor code : how moral revolutions happen* (1st ed.). New York: W.W. Norton.
Atkinson, Q. D., & Bourrat, P. (2011). Beliefs about God, the afterlife and morality support the role of supernatural policing in human cooperation. *Evolution and human behavior, 32*(1), 41-49.
Atkisson, C., O'Brien, M. J., & Mesoudi, A. (2012). Adult learners in a novel environment use prestige-biased social learning. *Evolutionary psychology: an international journal of evolutionary approaches to psychology and behavior, 10*(3), 519.
Atran, S. (2002). Modular and cultural factors in biological understanding: an experimental approach to the cognitive basis of science. *The cognitive basis of science*, 41-72.
Atran, S., & Henrich, J. (2010). The Evolution of Religion: How Cognitive By-Products, Adaptive Learning Heuristics, Ritual Displays, and Group Competition Generate Deep Commitments to Prosocial Religions. *Biological Theory, 5*(1), 1-13.
Atran, S., Medin, D., Ross, N., Lynch, E., Vapnarsky, V., Ek, E., . . . GilWhite, F. (2002). Folkecology, Cultural Epidemiology, and the Spirit of the Commons: A Garden Experiment in the Maya Lowlands, 19912001 1. *Current anthropology, 43*(3), 421-450.
Atran, S., & Norenzayan, A. (2004). Religion's evolutionary landscape: Counterintuition, commitment, compassion, communion. *Behavioral and brain sciences, 27*(06), 713-730.
Barrett, H. C., & Broesch, J. (2012). Prepared social learning about dangerous animals in children. *Evolution and human behavior, 33*(5), 499-508.
Bell, A. V., Richerson, P. J., & McElreath, R. (2009). Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences, 106*(42), 17671-17674.
Bettinger, R. L., & Baumhoff, M. A. (1982). The Numic spread: Great Basin cultures in competition. *American Antiquity*, 485-503.
Billing, J., & Sherman, P. W. (1998). Antimicrobial functions of spices: why some like it hot. *Quarterly Review of Biology*, 3-49.
Birch, L. L. (1987). Children's food preferences: Developmental patterns and environmental influences. *Annals of child development, 4*, 171-208.
Birch, S. A., Akmal, N., & Frampton, K. L. (2010). Two-year-olds are vigilant of others' non-verbal cues to credibility. *Developmental science, 13*(2), 363-369.
Birch, S. A., Vauthier, S. A., & Bloom, P. (2008). Three-and four-year-olds spontaneously use others' past performance to guide their learning. *Cognition, 107*(3), 1018-1034.
Bowles, S. (2006). Group competition, reproductive leveling, and the evolution of human altruism. *Science, 314*(5805), 1569-1572.
Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*: University of Chicago Press.
Boyd, R., & Richerson, P. J. (2009). Voting with your feet: Payoff biased migration and the evolution of group beneficial behavior. *Journal of Theoretical Biology, 257*(2), 331-339.
Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences, 108*(Supplement 2), 10918-10925.
Broesch, J., Henrich, J., & Barrett, C. (forthcoming). Adaptive Content Biases in Learning about Animals Across the Lifecourse. *Human Nature*.

Brown, P. J. (1998). Cultural Adaptations to Endemic Malaria in Sardinia. In P. J. Brown (Ed.), *Understanding and Applying Medical Anthropology*. London: Mayfield Publishing Company.

Caldwell, C. A., & Millen, A. E. (2010). Conservatism in laboratory microsocieties: unpredictable payoffs accentuate group-specific traditions. *Evolution and human behavior, 31*(2), 123-130.

Cavalli-Sforza, L. L. L. (1981). *Cultural transmission and evolution: a quantitative approach*: Princeton University Press.

Chow, V., Poulin-Dubois, D., & Lewis, J. (2008). To see or not to see: Infants prefer to follow the gaze of a reliable looker. *Developmental science, 11*(5), 761-770.

Chudek, M., Heller, S., Birch, S. A., & Henrich, J. (2012). Prestige-biased cultural learning: bystander's differential attention to potential models influences children's learning. *Evolution and human behavior, 33*(1), 46-56.

Chudek, M., & Henrich, J. (2011). Culture–gene coevolution, norm-psychology and the emergence of human prosociality. *Trends in cognitive sciences, 15*(5), 218-226.

Chudek, M., Zhao, W., & Henrich, J. (2013). Culture-Gene Coevolution, Large-Scale Cooperation and the Shaping of Human Social Psychology. In R. Joyce, K. Sterelny & B. Calcott (Eds.), *Signaling, Commitment, and Emotion*. Cambridge: MIT Press.

Coleman, J. F., Blake, R. R., & Mouton, J. S. (1958). Task difficulty and conformity pressures. *The Journal of Abnormal and Social Psychology, 57*(1), 120.

Coleman, L. (2004). *The copycat effect: How the media and popular culture trigger the mayhem in Tomorrow's headlines*: Simon and Schuster.

Corriveau, K. H., Fusaro, M., & Harris, P. L. (2009). Going with the flow preschoolers prefer nondissenters as informants. *Psychological Science, 20*(3), 372-377.

Corriveau, K. H., & Harris, P. L. (2009a). Choosing your informant: Weighing familiarity and recent accuracy. *Developmental science, 12*(3), 426-437.

Corriveau, K. H., & Harris, P. L. (2009b). Preschoolers continue to trust a more accurate informant 1 week after exposure to accuracy information. *Developmental science, 12*(1), 188-193.

Corriveau, K. H., & Harris, P. L. (2010). Preschoolers (sometimes) defer to the majority in making simple perceptual judgments. *Developmental psychology, 46*(2), 437.

Corriveau, K. H., Kinzler, K. D., & Harris, P. L. (2013). Accuracy trumps accent in children's endorsement of object labels. *Developmental psychology, 49*(3), 470.

Cosgrove, R., Field, J., Garvey, J., Brenner-Coltrain, J., Goede, A., Charles, B., . . . O'Connell, J. (2010). Overdone overkill - the archaeological perspective on Tasmanian megafaunal extinctions. *Journal of Archaeological Science, 37*(10), 2486-2503.

Deaner, R. O., Isler, K., Burkart, J., & van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution, 70*(2), 115-124.

Derex, M., Beugin, M.-P., Godelle, B., & Raymond, M. (2013). Experimental evidence for the influence of group size on cultural complexity. *Nature, 503*(7476), 389-391.

Deutscher, G. (2011). *Through the language glass: Why the world looks different in other languages*: Random House.

Diamond, J. M. (1998). *Guns, germs and steel: a short history of everybody for the last 13,000 years*: Random House.

Duncker, K. (1938). Experimental modification of children's food preferences through social suggestion. *The Journal of Abnormal and Social Psychology, 33*(4), 489.

Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*: Stanford University Press.

Edgerton, R. B. (1992). *Sick societies: Challenging the myth of primitive harmony*: Simon & Schuster.

Edinborough, K. (2009). Population history, abrupt climate change, and evolution of arrowhead technology in Mesolithic south Scandinavia (pp. 191-202): Berkeley, CA: University of California Press.

Efferson, C., Lalive, R., & Fehr, E. (2008). The coevolution of cultural groups and ingroup favoritism. *Science, 321*(5897), 1844-1849.

Efferson, C., Lalive, R., Richerson, P. J., McElreath, R., & Lubell, M. (2008). Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evolution and human behavior, 29*(1), 56-64.
Enquist, M., Eriksson, K., & Ghirlanda, S. (2007). Critical social learning: A solution to Rogers's paradox of nonadaptive culture. *American Anthropologist, 109*(4), 727-734.
Enquist, M., Strimling, P., Eriksson, K., Laland, K., & Sjostrand, J. (2010). One cultural parent makes no culture. *Animal Behaviour, 79*(6), 1353-1362.
Eriksson, K., Enquist, M., & Ghirlanda, S. (2007). Critical points in current theory of conformist social learning. *Journal of Evolutionary Psychology, 5*(1), 67-87.
Fairlie, R., Hoffmann, F., & Oreopoulos, P. (2011). A community college instructor like me: Race and ethnicity interactions in the classroom: National Bureau of Economic Research.
Fessler, D. M. (2006). *A burning desire: steps toward an evolutionary psychology of fire learning*: Springer.
Flannery, K. V., & Marcus, J. (2000). Formative Mexican chiefdoms and the myth of the "Mother Culture". *Journal of Anthropological Archaeology, 19*(1), 1-37.
Fogarty, L., Strimling, P., & Laland, K. N. (2011). The evolution of teaching. *Evolution, 65*(10), 2760-2770.
Fusaro, M., & Harris, P. L. (2008). Children assess informant reliability using bystanders' non-verbal cues. *Developmental science, 11*(5), 771-777.
Galef Jr, B. G., & Whiskin, E. E. (2008). Use of social information by sodium-and protein-deficient rats: test of a prediction (Boyd & Richerson 1988). *Animal Behaviour, 75*(2), 627-630.
Gelman, S. A. (2009). Learning from others: Children's construction of concepts. *Annual review of psychology, 60*, 115.
Geribàs, N., Mosquera, M., & Vergès, J. M. (2010). What novice knappers have to learn to become expert stone toolmakers. *Journal of Archaeological Science, 37*(11), 2857-2870.
Gervais, W. M., & Henrich, J. (2010). The Zeus problem: Why representational content biases cannot explain faith in gods. *Journal of Cognition and Culture, 10*(3-4), 3-4.
Gervais, W. M., Willard, A. K., Norenzayan, A., & Henrich, J. (2011). The cultural transmission of faith: Why innate intuitions are necessary, but insufficient, to explain religious belief. *Religion, 41*(3), 389-410.
Goldstein, R., Almenberg, J., Dreber, A., Emerson, J. W., Herschkowitsch, A., & Katz, J. (2008). Do more expensive wines taste better? Evidence from a large sample of blind tastings. *Journal of Wine Economics, 3*(01), 1-9.
Gürerk, Ö., Irlenbusch, B., & Rockenbach, B. (2006). The competitive advantage of sanctioning institutions. *Science, 312*(5770), 108-111.
Han, S. H., Northoff, G., Vogeley, K., Wexler, B. E., Kitayama, S., & Varnum, M. E. W. (2013). A Cultural Neuroscience Approach to the Biosocial Nature of the Human Brain. *Annual Review of Psychology, Vol 64, 64*, 335-359.
Hayek, F. (1988). The Fatal Conceit. In W. W. Bartley (Ed.), *The Collected Works of F.A Hayek Vol I*. Chicago: University of Chicago Press.
Henrich, J. (2002). Decision-making, cultural transmission and adaptation in economic anthropology. In J. Ensminger (Ed.), *Theory in Economic Anthropology* (pp. 251-295). Walnut Creek, CA: AltaMira Press.
Henrich, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *American Antiquity*, 197-214.
Henrich, J. (2006). Cooperation, punishment, and the evolution of human institutions. *Science, 311*(5769), 60-61.
Henrich, J. (2009). The evolution of costly displays, cooperation and religion: Credibility enhancing displays and their implications for cultural evolution. *Evolution and human behavior, 30*(4), 244-260.
Henrich, J. (2009). The Evolution of Innovation-Enhancing Institutions. In S. J. Shennan & M. J. O'Brien (Eds.), *Innovation in Cultural Systems: Contributions in Evolution Anthropology*. Cambridge: MIT.
Henrich, J. (2012). Too late: models of cultural evolution and group selection have already proved useful. *The False Allure of Group Selection.* from http://edge.org/conversation/the-false-allure-of-group-selection
Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and human behavior, 19*(4), 215-241.

Henrich, J., & Boyd, R. (2002). On modeling cognition and culture. *Journal of Cognition and Culture, 2*(2), 87-112.
Henrich, J., Boyd, R., & Richerson, P. J. (2008). Five misunderstandings about cultural evolution. *Human Nature, 19*(2), 119-137.
Henrich, J., Boyd, R., & Richerson, P. J. (2012). The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1589), 657-669.
Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 1139-1148.
Henrich, J., Ensminger, J., McElreath, R., Barr, A., Barrett, C., Bolyanatz, A., . . . Henrich, N. (2010). Markets, religion, community size, and the evolution of fairness and punishment. *Science, 327*(5972), 1480-1484.
Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and human behavior, 22*(3), 165-196.
Henrich, J., Heine, S. J., & Norenzayan, A. (2010a). Most people are not WEIRD. *Nature, 466*(7302), 29-29.
Henrich, J., Heine, S. J., & Norenzayan, A. (2010b). The weirdest people in the world? *Behavioral and brain sciences, 33*(2-3), 61-83.
Henrich, J., & Henrich, N. (2007). *Why humans cooperate: A cultural and evolutionary explanation*: Oxford University Press.
Henrich, J., & Henrich, N. (2010). The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society B: Biological Sciences, 277*(1701), 3715-3724.
Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News, and Reviews, 12*(3), 123-135.
Henrich, J., & Tennie, C. (under review). Cultural Evolution in Chimpanzees and Humans. In M. Muller, R. Wrangham & D. Pilbream (Eds.), Chimpanzees and Human Evolution. Cambridge: Harvard University Press.
Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science, 317*(5843), 1360-1366.
Hill, K. R., Walker, R. S., Božičević, M., Eder, J., Headland, T., Hewlett, B., . . . Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science, 331*(6022), 1286-1289.
Hilmert, C. J., Kulik, J. A., & Christenfeld, N. J. (2006). Positive and negative opinion modeling: The influence of another's similarity and dissimilarity. *Journal of Personality and Social Psychology, 90*(3), 440.
Hoffmann, F., & Oreopoulos, P. (2009). A professor like me the influence of instructor gender on college achievement. *Journal of Human Resources, 44*(2), 479-494.
Hoppitt, W., & Laland, K. N. (2013). *Social Learning: An Introduction to Mechanisms, Methods, and Models*: Princeton University Press.
Hruschka, D. J., & Henrich, J. (2013a). Economic and evolutionary hypotheses for cross-population variation in parochialism. *Frontiers in human neuroscience, 7*.
Hruschka, D. J., & Henrich, J. (2013b). Institutions, parasites and the persistence of in-group preferences. *PloS one, 8*(5), e63642.
Jaswal, V. K., & Malone, L. S. (2007). Turning believers into skeptics: 3-year-olds' sensitivity to cues to speaker credibility. *Journal of Cognition and Development, 8*(3), 263-283.
Jaswal, V. K., & Neely, L. A. (2006). Adults Don't Always Know Best Preschoolers Use Past Reliability Over Age When Learning New Words. *Psychological Science, 17*(9), 757-758.
Jonas, K. (1992). Modelling and suicide: a test of the Werther effect. *British Journal of Social Psychology, 31*(4), 295-306.
Kelly, R. C. (1985). *The Nuer conquest: The structure and development of an expansionist system*: University of Michigan Press.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior, 35*, 333-379.
Kim, G., & Kwak, K. (2011). Uncertainty matters: Impact of stimulus ambiguity on infant social referencing. *Infant and child development, 20*(5), 449-463.
Kinzler, K. D., Corriveau, K. H., & Harris, P. L. (2011). Children’s selective trust in native-accented speakers. *Developmental science, 14*(1), 106-111.
Kinzler, K. D., Dupoux, E., & Spelke, E. S. (2007). The native language of social cognition. *Proceedings of the National Academy of Sciences, 104*(30), 12577-12580.
Kinzler, K. D., Shutts, K., DeJesus, J., & Spelke, E. S. (2009). Accent trumps race in guiding children’s social preferences. *Social Cognition, 27*(4), 623.
Kitayama, S., & Uskul, A. K. (2011). Culture, Mind, and the Brain: Current Evidence and Future Directions. *Annual Review of Psychology, Vol 62, 62*, 419-449.
Kline, M. A., & Boyd, R. (2010). Population size predicts technological complexity in Oceania. *Proceedings of the Royal Society B: Biological Sciences, 277*(1693), 2559-2564.
Kline, M. A., Boyd, R., & Henrich, J. (forthcoming). Teaching and the life history of cultural transmission in Fijian villages. *Human Nature*.
Kobayashi, Y., & Aoki, K. (2012). Innovativeness, population size and cumulative cultural evolution. *Theoretical Population Biology, 82*(1), 38-47.
Koenig, M. A., & Harris, P. L. (2005). Preschoolers mistrust ignorant and inaccurate speakers. *Child development, 76*(6), 1261-1277.
Kurzban, R., Tooby, J., & Cosmides, L. (2001). Can race be erased? Coalitional computation and social categorization. *Proceedings of the National Academy of Sciences of the United States of America, 98*(26), 15387-15392.
Laland, K. N., Atton, N., & Webster, M. M. (2011). From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 958-968.
Laland, K. N., Odling-Smee, J., & Myles, S. (2010). How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics, 11*(2), 137-148.
Lambert, A. D. (2009). *The Gates of Hell: Sir John Franklin's Tragic Quest for the North West Passage*: Yale University Press.
Lanman, J. A. (2012). The importance of religious displays for belief acquisition and secularization. *Journal of Contemporary Religion, 27*(1), 49-65.
Lehmann, L., Aoki, K., & Feldman, M. W. (2011). On the number of independent cultural traits carried by individuals and populations. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1563), 424-435.
Lehmann, L., Feldman, M., & Kaeuffer, R. (2010). Cumulative cultural dynamics and the coevolution of cultural innovation and transmission: an ESS model for panmictic and structured populations. *Journal of Evolutionary Biology, 23*(11), 2356-2369.
Leibbrandt, A., Gneezy, U., & List, J. A. (2013). Rise and fall of competitiveness in individualistic and collectivistic societies. *Proceedings of the National Academy of Sciences, 110*(23), 9305-9308.
Liu, D., Vanderbilt, K. E., & Heyman, G. D. (2013). Selective trust: Children's use of intention and outcome of past testimony. *Developmental psychology, 49*(3), 439.
Lucas, A. J., Lewis, C., Pala, F. C., Wong, K., & Berridge, D. (2013). Social-cognitive processes in preschoolers' selective trust: Three cultures compared. *Developmental psychology, 49*(3), 579.
Marquet, P. A., Santoro, C. M., Latorre, C., Standen, V. G., Abades, S. R., Rivadeneira, M. M., . . . Hochberg, M. E. (2012). Emergence of social complexity among coastal hunter-gatherers in the Atacama Desert of northern Chile. *Proceedings of the National Academy of Sciences, 109*(37), 14754-14760.
McElreath, R., Boyd, R., & Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current anthropology, 44*(1), 122-130.
Mesoudi, A. (2009). The cultural dynamics of copycat suicide. *PloS one, 4*(9), e7252.

Mesoudi, A., Whiten, A., & Dunbar, R. (2006). A bias for social information in human cultural transmission. *British Journal of Psychology, 97*(3), 405-423.
Mills, C. M. (2012). Knowing when to doubt: Developing a critical stance when learning from others.
Morgan, T., Rendell, L., Ehn, M., Hoppitt, W., & Laland, K. (2012). The evolutionary basis of human social learning. *Proceedings of the Royal Society B: Biological Sciences, 279*(1729), 653-662.
Morgan, T. J. H., & Laland, K. N. (2012). The biological bases of conformity. *Frontiers in neuroscience, 6*.
Muthukrishna, M., Chudek, M., & Henrich, J. (n.d.). *The Cultural Brain Hypothesis: Explaining the Human Brain Expansion During the Pleistocene*.
Muthukrishna, M., Shulman, B. W., Vasilescu, V., & Henrich, J. (2013). Sociality influences cultural complexity. *Proceedings of the Royal Society B: Biological Sciences, 281*(1774), 20132511.
Na, J., & Kitayama, S. (2012). Will people work hard on a task they choose? Social-eyes priming in different cultural contexts. *Journal of Experimental Social Psychology, 48*(1), 284-290.
Nakahashi, W., Wakano, J. Y., & Henrich, J. (2012). Adaptive social learning strategies in temporally and spatially varying environments. *Human Nature, 23*(4), 386-418.
Nisbett, R. E., & Cohen, D. (1996). *Culture of honor: The psychology of violence in the South*: Westview Press.
Norenzayan, A. (2013). *Big gods: How religion transformed cooperation and conflict*: Princeton University Press.
Norenzayan, A., Atran, S., Faulkner, J., & Schaller, M. (2006). Memory and mystery: The cultural selection of minimally counterintuitive narratives. *Cognitive Science, 30*(3), 531-553.
Norenzayan, A., & Shariff, A. F. (2008). The origin and evolution of religious prosociality. *Science, 322*(5898), 58-62.
O'Brien, M. J., & Laland, K. N. (2012). Genes, Culture, and Agriculture. *Current anthropology, 53*(4), 434-470.
Olson, K. R., Banaji, M. R., Dweck, C. S., & Spelke, E. S. (2006). Children's biased evaluations of lucky versus unlucky people and their social groups. *Psychological Science, 17*(10), 845-846.
Olson, K. R., Dunham, Y., Dweck, C. S., Spelke, E. S., & Banaji, M. R. (2008). Judgments of the lucky across development and culture. *Journal of Personality and Social Psychology, 94*(5), 757.
Perreault, C., Moya, C., & Boyd, R. (2012). A Bayesian approach to the evolution of social learning. *Evolution and human behavior, 33*(5), 449-459.
Petrie, M., Tim, H., & Carolyn, S. (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour, 41*(2), 323-331.
Phillips, D. P. (1974). The influence of suggestion on suicide: Substantive and theoretical implications of the Werther effect. *American Sociological Review*, 340-354.
Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology letters, 6*(4), 466-468.
Plassmann, H., O'Doherty, J., Shiv, B., & Rangel, A. (2008). Marketing actions can modulate neural representations of experienced pleasantness. *Proceedings of the National Academy of Sciences, 105*(3), 1050-1054.
Potts, R. (1998). Variability selection in hominid evolution. *Evolutionary Anthropology: Issues, News, and Reviews, 7*(3), 81-96.
Powell, A., Shennan, S., & Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science, 324*(5932), 1298-1301.
Premo, L. S., & Kuhn, S. L. (2010). Modeling effects of local extinctions on culture change and diversity in the Paleolithic. *PloS one, 5*(12), e15582.
Rakoczy, H., Brosche, N., Warneken, F., & Tomasello, M. (2009). Young children's understanding of the context-relativity of normative rules in conventional games. *British Journal of Developmental Psychology, 27*(2), 445-456.
Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., . . . Laland, K. N. (2010). Why copy others? Insights from the social learning strategies tournament. *Science, 328*(5975), 208-213.
Rendell, L., Fogarty, L., & Laland, K. N. (2010). Rogers' paradox recast and resolved: Population structure and the evolution of social learning strategies. *Evolution, 64*(2), 534-548.

Reyes-García, V., Broesch, J., Calvet-Mir, L., Fuentes-Peláez, N., McDade, T. W., Parsa, S., . . . Martínez-Rodríguez, M. R. (2009). Cultural transmission of ethnobotanical knowledge and skills: an empirical analysis from an Amerindian society. *Evolution and human behavior, 30*(4), 274-285.
Richerson, P., & Boyd, R. (2000). The Pliestocene and the Origins of Human Culture: Built for Speed. In F. Tonneau & N. Thompson (Eds.), *Perspectives in Ethology* (Vol. 13, pp. 1-45).
Richerson, P. J., & Boyd, R. (2000). Climate, Culture and the Evolution of Cognition. In C. M. Heyes (Ed.), *The evolution of cognition* (pp. 329-345). Cambridge: MIT Press.
Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*: University of Chicago Press.
Richerson, P. J., Boyd, R., & Henrich, J. (2010). Gene-culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences, 107*(Supplement 2), 8985-8992.
Rosekrans, M. A. (1967). Imitation in children as a function of perceived similarity to a social model and vicarious reinforcement. *Journal of Personality and Social Psychology, 7*(3p1), 307.
Ryalls, B. O., Gul, R. E., & Ryalls, K. R. (2000). Infant imitation of peer and adult models: Evidence for a peer model advantage. *Merrill-Palmer Quarterly (1982-)*, 188-202.
Sabbagh, M. A., & Baldwin, D. A. (2001). Learning words from knowledgeable versus ignorant speakers: Links between preschoolers' theory of mind and semantic development. *Child development, 72*(4), 1054-1070.
Sahlins, M. D. (1961). The Segmentary Lineage: An Organization of Predatory Expansion1. *American Anthropologist, 63*(2), 322-345.
Schmidt, M. F., Rakoczy, H., & Tomasello, M. (2011). Young children attribute normativity to novel actions without pedagogy or normative language. *Developmental science, 14*(3), 530-539.
Schmidt, M. F., & Tomasello, M. (2012). Young children enforce social norms. *Current Directions in Psychological Science, 21*(4), 232-236.
Scofield, J., & Behrend, D. A. (2008). Learning words from reliable and unreliable speakers. *Cognitive Development, 23*(2), 278-290.
Scofield, J., Gilpin, A. T., Pierucci, J., & Morgan, R. (2013). Matters of accuracy and conventionality: Prior accuracy guides children's evaluations of others' actions. *Developmental psychology, 49*(3), 432.
Shariff, A. F., & Norenzayan, A. (2007). God is watching you priming God concepts increases prosocial behavior in an anonymous economic game. *Psychological Science, 18*(9), 803-809.
Shultz, S., Nelson, E., & Dunbar, R. I. M. (2012). Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. *Philosophical Transactions of the Royal Society B-Biological Sciences, 367*(1599), 2130-2140.
Shutts, K., Banaji, M. R., & Spelke, E. S. (2010). Social categories guide young children's preferences for novel objects. *Developmental science, 13*(4), 599-610.
Shutts, K., Kinzler, K. D., McKee, C. B., & Spelke, E. S. (2009). Social information guides infants' selection of foods. *Journal of Cognition and Development, 10*(1-2), 1-17.
Slingerland, E., Henrich, J., & Norenzayan, A. (2013). The evolution of prosocial religions. In P. J. Richerson & M. H. Christiansen (Eds.), *Cultural Evolution: Society, Technology, Language and Religion*. Cambridge: MIT Press.
Sobel, D. M., & Corriveau, K. H. (2010). Children monitor individuals' expertise for word learning. *Child development, 81*(2), 669-679.
Soltis, J., Boyd, R., & Richerson, P. J. (1995). Can group-functional behaviors evolve by cultural group selection?: An empirical test. *Current anthropology*, 473-494.
Spencer, C. S., & Redmond, E. M. (2001). Multilevel selection and political evolution in the Valley of Oaxaca, 500–100 BC. *Journal of Anthropological Archaeology, 20*(2), 195-229.
Stack, S. (1996). The effect of the media on suicide: evidence from Japan, 1955–1985. *Suicide and Life-Threatening Behavior, 26*(2), 132-142.
Stenberg, G. (2009). Selectivity in infant social referencing. *Infancy, 14*(4), 457-473.

Stout, D., Bril, B., Roux, V., DeBeaune, S., Gowlett, J., Keller, C., . . . Stout, D. (2002). Skill and Cognition in Stone Tool Production: An Ethnographic Case Study from Irian Jaya 1. *Current anthropology, 43*(5), 693-722.

Stout, D., & Chaminade, T. (2012). Stone tools, language and the brain in human evolution. *Philosophical Transactions of the Royal Society B-Biological Sciences, 367*(1585), 75-87.

Stout, D., Passingham, R., Frith, C., Apel, J., & Chaminade, T. (2011). Technology, expertise and social cognition in human evolution. *European Journal of Neuroscience, 33*(7), 1328-1338.

Stout, D., Toth, N., Schick, K., & Chaminade, T. (2008). Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*(1499), 1939-1949.

Tajfel, H., Billig, M. G., Bundy, R. P., & Flament, C. (1971). Social categorization and intergroup behaviour. *European journal of social psychology, 1*(2), 149-178.

Tanaka, M. M., Kendal, J. R., & Laland, K. N. (2009). From traditional medicine to witchcraft: why medical treatments are not always efficacious. *PloS one, 4*(4), e5192.

Tehrani, J. J., Collard, M., & Shennan, S. J. (2010). The cophylogeny of populations and cultures: reconstructing the evolution of Iranian tribal craft traditions using trees and jungles. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1559), 3865-3874.

Toelch, U., Bruce, M. J., Meeus, M. T., & Reader, S. M. (2010). Humans copy rapidly increasing choices in a multiarmed bandit problem. *Evolution and human behavior, 31*(5), 326-333.

Turchin, P. (2005). *War and peace and war : the life cycles of imperial nations*. New York: Pearson Education distributor.

Turchin, P. (2009). A theory for formation of large empires. *Journal of Global History, 4*(2), 191-217.

Turchin, P. (2010). Warfare and the Evolution of Social Complexity: A Multilevel-Selection Approach. *Structure and Dynamics, 4*(3).

Vaesen, K. (2012). Cumulative cultural evolution and demography. *PloS one, 7*(7), e40989.

van Schaik, C. P., & Burkart, J. M. (2011). Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 1008-1016.

van Schaik, C. P., Isler, K., & Burkart, J. M. (2012). Explaining brain size variation: from social to cultural brain. *Trends in cognitive sciences, 16*(5), 277-284.

van Schaik, C. P., & Pradhan, G. R. (2003). A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *Journal of Human Evolution, 44*(6), 645-664.

VanderBorght, M., & Jaswal, V. K. (2009). Who knows best? Preschoolers sometimes prefer child informants over adult informants. *Infant and child development, 18*(1), 61-71.

Veblen, T. (1899). *The Theory of the Leisure Class: an Economic Study in the Evolution of Institutions*. New York: Macmillan Company.

Wadley, L., Sievers, C., Bamford, M., Goldberg, P., Berna, F., & Miller, C. (2011). Middle Stone Age bedding construction and settlement patterns at Sibudu, South Africa. *Science, 334*(6061), 1388-1391.

Walden, T. A., & Kim, G. (2005). Infants' social looking toward mothers and strangers. *International Journal of Behavioral Development, 29*(5), 356-360.

Watts, D. J. (2012). *Everything Is Obvious: How Common Sense Fails Us*: Random House LLC.

Webster, M., & Laland, K. (2008). Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proceedings of the Royal Society B: Biological Sciences, 275*(1653), 2869-2876.

Wertz, A. E., & Wynn, K. (2014). Thyme to touch: Infants possess strategies that protect them from dangers posed by plants. *Cognition, 130*(1), 44-49.

Wertz, A. E., & Wynn, K. (in press). Selective social learning of plant edibility in 6- and 18-month-old infants. *Psychological Science*.

Willard, A., Norenzayan, A., & Henrich, J. (n.d.). *Do as I Do, Not as I Say: Credibility Enhancing Displays as indicators of belief*.

Wolf, T. M. (1973). Effects of live modeled sex-inappropriate play behavior in a naturalistic setting. *Developmental psychology, 9*(1), 120.

Yeaman, S., Schick, A., & Lehmann, L. (2012). Social network architecture and the maintenance of deleterious cultural traits. *Journal of the Royal Society Interface, 9*(70), 848-858.
Young, D. A., & Bettinger, R. L. (1992). The Numic spread: A computer simulation. *American Antiquity*, 85-99.
Zaki, J., Schirmer, J., & Mitchell, J. P. (2011). Social influence modulates the neural computation of value. *Psychological Science, 22*(7), 894-900.
Zmyj, N., Buttelmann, D., Carpenter, M., & Daum, M. M. (2010). The reliability of a model influences 14-month-olds' imitation. *Journal of Experimental Child Psychology, 106*(4), 208-220.