The Evolution of Cultural Evolution

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Humans are unique in their range of environments and in the nature and diversity of their behavioral adaptations. While a variety of local genetic adaptations exist within our species, it seems certain that the same basic genetic endowment produces arctic foraging, tropical horticulture, and desert pastoralism, a constellation that represents a greater range of subsistence behavior than the rest of the Primate Order combined. The behavioral adaptations that explain the immense success of our species are cultural in the sense that they are transmitted among individuals by social learning and have accumulated over generations. Understanding how and when such culturally evolved adaptations arise requires understanding of both the evolution of the psychological mechanisms that underlie human social learning and the evolutionary (population) dynamics of cultural systems.

In 1860, aiming to be the first Europeans to travel south to north across Australia, Robert Burke led an extremely well-equipped expedition of three men (King, Wills and Gray) from their base camp in Cooper's Creek in central Australia with five fully loaded camels (specially imported) and one horse. Figuring a maximum round trip travel time of three months, they carried twelve weeks of food and supplies. Eight weeks later they reached tidal swamps on the northern coast and began their return. After about ten weeks their supplies ran short and they began eating their pack animals. After twelve weeks in the bush, Gray died of illness and exhaustion, and the group jettisoned most of their remaining supplies. A month later, they arrived back in their base camp, but found that their support crew had recently departed, leaving only limited supplies. Still weak, the threesome packed the available supplies and headed to the nearest outpost of "civilization," Mt. Hopeless, 240km south. In less than a month, their clothing and boots were beyond repair, their supplies were again gone, and they ate mostly camel meat.

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Key words: social learning; human evolution; culture and cognition; coevolution; dual inheritance theory

Evolutionary Anthropology 12:123–135 (2003)
DOI 10.1002/evan.10110

Faced with living off the land, they began foraging efforts and tried, unsuccessfully, to devise means to trap birds and rats. They were impressed by the bountiful bread and fish available in aboriginal camps, in contrast to their own wretched condition. They attempted to glean as much as they could from the aboriginals about *nardoo,* an aquatic fern bearing spores they had observed the aboriginals using to make bread. Despite traveling along a creek and receiving frequent gifts of fish from the locals, they were unable to figure out how to catch them. Two months after departing from their base camp, the threesome had become entirely dependent on *nardoo* bread and occasional gifts of fish from the locals. Despite consuming what seemed to be sufficient calories, all three became increasingly fatigued and suffered from painful bowel movements. Burke and Wills soon died, poisoned and starved from eating improperly processed *nardoo* seeds. Unbeknown to these intrepid adventurers, *nardoo* seeds are toxic and highly indigestible if not properly processed. The local aboriginals, of course, possess specialized methods for detoxifying and processing these seeds. Fatigued and delusional, King wandered off into the desert where he was rescued by an aboriginal group, the Yantruwanta. He recovered and lived with the Yantruwanta for several months until a search party found him.

The planning for this expedition could not have been more extensive, and these men were not unprepared British schoolboys out on holiday. However, despite their big brains, camels, specialized equipment, training, and seven months of exposure to the desert environment prior to running out of supplies, they failed to survive in the Australian desert. This bit of history makes a simple point: Humans, unlike other animals, are heavily reliant on social learning to acquire large and important portions of their behavioral repertoire. No evolved cognitive modules, "evoked culture," or generalized cost-benefit calculators delivered to these men the knowledge of how to detoxify *nardoo* spores or how to make and use rat traps, bird snares, or fishing nets from locally available materials. Unlike social learning in other animals, human cultural abilities generate adaptive strategies and bodies of knowledge that accumulate over generations. Foraging, as it is known ethnographically, would be impossible without technologies such as kayaks, blowguns, bone tools, boomerangs, and bows. These technological examples embody skills and know-how that no single individual could figure out in his lifetime. Nonmaterial culture, such as seed processing techniques, tracking abilities, and medicinal plant knowledge, reveals similar locally adaptive accumulations. Interestingly, this adaptive information is often embodied in socially learned rules, techniques, and heuristics that are applied with little or no understanding of how or why they work.

Thus, understanding a substantial amount of human adaptation requires understanding the cultural learning processes that assemble our behavioral repertoires over generations. This is not, however, a call to separate humans from the rest of nature. A productive approach should seat humans within the broader context of mammalian and primate evolution while at the same time being able to explain how and why humans are so different in the diversity and nature of their behavioral adaptations. Our goal in this paper is to review recent developments in understanding both the evolution of the psychological mechanisms that make cultural evolution possible and the population-level consequences of those individually adaptive mechanisms. Most of the relevant work occurs within a pair of closely related approaches: gene-culture coevolution[1–5] and dual-inheritance theory.[6,7] These approaches examine the interactions between genetic and cultural inheritance systems. In these models, individual phenotypes are combinations of both genetic and socially transmitted characters, which in turn affect the transmission rates of different alleles and cultural variants. Early models explored, among other things, how different modes of cultural inheritance affect rates and outcomes of cultural evolution[2] and how natural selection acting on genes can produce a semi-autonomous inheritance system.[7] Like human behavioral ecology,[8] coevolutionary and dual-inheritance theories are concerned with adaptation. Unlike human behavioral ecology, however, these theories model the proximate mechanisms that produce adaptations. Like evolutionary psychology, these theories share an interest in the design of cognition. Unlike most evolutionary psychology, however, dual-inheritance and gene-culture models are rigorously formalized, take account of social learning, and explore population processes. For many questions, strictly outcome-oriented or culture-free models are sufficient and insightful. For many others, however, taking account of cultural dynamics is essential. As the Burke and Wills story illustrates, even hunter-gatherer adaptation is substantially reliant upon evolved cultural knowledge and technology. To understand adaptation in human societies with any time depth seems very difficult without some attempt to account for the evolutionary dynamics that produce such adaptations.

Throughout this paper we will use "cultural learning" and "cultural transmission/acquisition" to refer to the subset of social learning capacities that allow for cumulative cultural evolution. We use "culture" to refer to the information acquired by individuals via social learning. Processing *nardoo* and making arrow poison, for example, are cultural practices because individuals learn them from other members of their social group. The mental representations that allow individuals to detoxify the fern spores or bring down large game with relatively lightweight bows and arrows do not come coded in their genes, nor are these continually relearned by each individual via trial-and-error experimentation or deduced solely by fitness-oriented cost-benefit analysis. Instead, such adaptations result from and embody the cumulative effects of the efforts, experiments, errors, insight, and interactions of many individuals across generations.

Conceptualizing culture as socially learned information stored in people's brains opens up new sets of evolutionary questions. We will review the research on five of these: How does social learning in humans increase adaptability and thereby allow our species to successfully occupy such an enormous range of environments? If cultural learning mechanisms are so adaptive, why are such mechanisms seemingly rare in nature? What cognitive processes guide human social learning? If cultural variants do not replicate like genes, can culture evolve? How does the coevolution of genes and culture influence human psychology and the histories of human societies? These five questions build a natural progression of puzzles, from the genetic origins of cultural inheritance to the dynamics of modern cultural and societal evolution.

WHY IS CULTURAL LEARNING ADAPTIVE?

To understand the evolution of social learning, theorists have developed formal models to study how temporally and spatially changing environmental conditions affect the evolutionary trade-offs between capacities for individual learning (for example, trial and error), social learning, and "hardwired" behavioral responses.[1,5,7,9–15] Most of these models are very abstract and apply to a wide range of animal social learning, not just human cultural transmission. They show that social learning is favored throughout a large intermediate range of environmental fluctuation, especially when environments are highly autocorrelated. The intuition behind these results is that social learning allows organisms to respond more quickly to environmental changes than do hardwired responses, but only by exploiting a body of adaptive knowledge that is stored in the learned behavioral repertoire of the population. At one extreme, when environments fluctuate on the order of thousands of generations, social learning serves no purpose since raw natural selection acting on genes can, on average, do just as well without paying for expensive social learning machinery. At the other extreme, when fluctuations occur on the order of single generations, there is little adaptive knowledge for social learners to exploit. However, with intermediate rates of change, on the order of tens or hundreds of generations, social learning mechanisms both outpace genetic adaptation and have sufficient time between environmental changes to accumulate a body of adaptive knowledge in the population.

When viewed alongside a growing pool of empirical evidence, this theoretical work suggests that both individual and social learning from an intertwined adaptive response to increasing amounts of environmental variability[16,17]—what Potts[18] calls variability selection. First, there is new evidence that increases in brain size relative to body size are correlated with both social and individual learning abilities across species. In primates, brain size corrected for body size correlates most strongly with social learning abilities, but also with individual learning ("innovation") and tool use, all three of which are highly intercorrelated.[19] As far as we know, no similar studies exist for mammals in general, although there are similar findings for birds.[20,21] Second, these data suggest that increases in brain size in the paleontological record have been partly driven by increases in social learning abilities. Right up to the present, the record shows that several mammalian lineages have undergone increases in brain size relative to body size. Finally, over the same period, ice-core data show increasing degrees of climatic variation: Over the last fourteen million years, which is the limit of the time depth of the data, increases in climatic variability are mirrored by increases in brain ratio. This combination of evidence, alongside the formal theory that independently implicates environmental variation with increases in social learning abilities, suggests that human cultural capacities may be a hypertrophied subset of a larger class of learning abilities that have evolved in many species.[22]

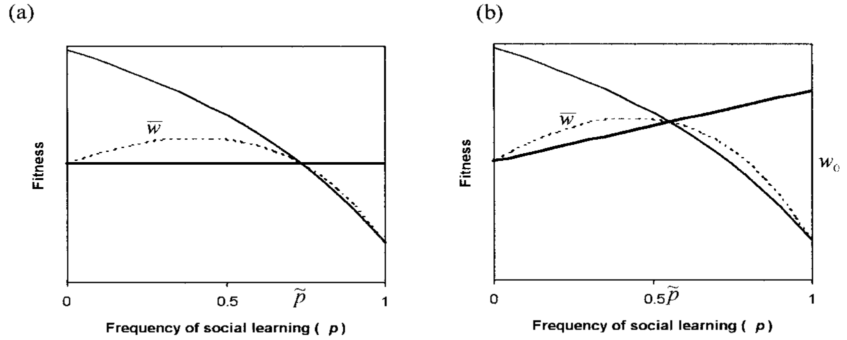
Yet humans stand out in the number and diversity of environments they inhabit. What is the role of social learning in human adaptability, and how have these abilities permitted a tropical primate to spread so rapidly and successfully into so many habitats—from the dry savannahs and tropical forests of equatorial Africa to the Arctic tundra and humid swamps of New Guinea—while most other mammals with plausibly well-developed social learning abilities show comparably restricted ranges? Prior to a clever paper by Rogers,[23] several researchers had argued that social learning improves human adaptability by exempting individuals from the costs of individual learning.[5,7,24] The argument seems cogent enough: Time costs and potential mistakes can make individual learning quite expensive. If another individual or group of individuals has already paid those costs, learning from that behavior may be considerably cheaper. Imagine the task of selecting among mushroom varieties through individual learning. Because some mushrooms are poisonous, the price of choosing the wrong mushroom is quite high. However, an individual who learns from others which mushrooms are poisonous spares herself those potential costs, provided that the behavior of others is adaptive.

Without any individual learners, social learners cannot track changes in the environment, and the first individual learner entering a group of social learners always has higher fitness than the others. This means that at equilibrium the mean fitness of the population as a whole is the same as that in a population of purely individual learners. Social learning alone does not increase adaptability.

However, Rogers showed that this argument is insufficient to explain the adaptive success of our cultural species. Using a very simple model, he proved that sparing individuals the costs of individual learning will not, on its own, lead to increased overall adaptability in the population—the mean fitness of the population is not increased. While social learners do very well when they are rare, they do poorly when they are common. Without any individual learners, social learners cannot track changes in the environment, and the first individual learner entering a group of social learners always has higher fitness than the others. This means that at equilibrium the mean fitness of the population as a whole is the same as that in a population of purely individual learners. Social learning alone does not increase adaptability. Box 1 explains this mathematical argument in more detail. Boyd and Richerson[11] extended Rogers' result to more complicated models in which social learners can identify and preferentially copy individual learners, the environment varies spatially as well as temporally, imitation generates errors, and there are more than two behaviors. None of these changes alter the result that the evolution of social learning does not lead to a more fit population. Cultural capacities, as represented in these models, do not raise the overall fitness of the population, so they are unlikely to explain the adaptive success of our species in the last 200,000 years.

In the same paper, however, Boyd and Richerson[11] showed that social learning can lead to higher mean fitness provided either that it allows the accumulation of behaviors that no individual learner could acquire in its lifetime or improves the efficiency of individual learning. When either is the case, social learning may increase the mean fitness of the population. The first condition is in fact the question we started the paper with, and we will discuss it at length in the next section. The second condition is satisfied if learners use individual learning when it is cheap and reliable, and switch to social learning when individual learn-

Box 1. Mathematical Argument



As we explain in the text, Rogers'[23] model demonstrates that social learning alone will not increase the average fitness of a population of cultural organisms. A simple graph can make the argument much clearer.

Figure (a) plots the fitnesses of individual learners (w_I, dark line) and social learners (w_S, thin line), as well as the population mean fitness ($\bar{w}$, dotted line), for all frequencies of social learning in the population (p). When social learners are rare, they do significantly better than individual learners, since most potential models are practicing the correct behavior. As social learning becomes more common, however, the population lags behind the environment more and more until individual learning pays just as well as social learning, at $\tilde{p}$. Natural selection will stabilize the population at this equilibrium, at which both social and individual learners receive fitness $\tilde{w}$, which is the same as the average population fitness when $p = 0$, when there are no social learners.

But if we allow the frequency of social learning to reduce the costs of individual learning, a new equilibrium arises at which the population mean fitness is greater than that of a population of individual learners. Figure (b) shows the modified model in which the costs of individual learning decrease as the frequency of social learning increases. Now the population mean fitness $\bar{w}$ is greater than the mean fitness in a population of individual learners, w_0. In order for social learning to increase adaptability, the mean fitness of the population, it must also somehow increase the fitness of individual learning. In the text, we discuss plausible mechanisms for this effect.

ing is expensive.[7,14] We think both are at work in human cognition. However, the adaptive gains possible through the second mechanism alone seem modest in comparison to those produced by cumulative cultural evolution.

WHY ARE CAPACITIES FOR CUMULATIVE CULTURAL TRANSMISSION RARE?

Several of our colleagues are fond of the "Why not baboons?" stratagem: If an evolutionary scenario is meant to explain some unique (or at least nearly unique) feature of humans, then it must also be able to explain why baboons—and many other animals—do not fall under the same evolutionary logic. We have seen many clever theories crumble before this interrogation. The story we outlined earlier is vulnerable to the same criticism. Although human cultural capacities can be seen as part of a more general pattern of adaptation for learning in variable environments, their immense adaptiveness and apparent uniqueness poses an evolutionary puzzle: Why haven't the social learning capacities that generate cumulative cultural adaptations repeatedly evolved along with other individual and social learning abilities in many mammalian lineages over the last fourteen million years? Thus, here we attempt to explain why human-like cultural capacities should be rare in nature, as we believe they are, despite being extremely adaptive.

While an increasing amount of field evidence suggests that other animals, particularly chimpanzees, may maintain traditions that result from social learning,[25–28] there is little reason to believe that nonhuman social learning capacities can generate cumulative adaptation.[7,29,30] In contrast, accumulated cultural skills and knowledge are characteristics of all human societies. While the psychological mechanisms that make cumulative culture possible are unclear, there are some promising ideas. Tomasello, Kruger, and Ratner[29] suggested that true imitation, or observational learning—the direct and accurate copying of behaviors, strategies or symbolic knowledge—is necessary for cumulative cultural evolution. Other kinds of social learning may lead to traditions, but not to the accumulation of adaptive information. Imagine that individuals are capable of a modest amount of individual learning, so that interaction with the environment slowly generates adaptive behavior. If naive individuals tend to hand around other individuals, and some of these individuals prefer to hang around certain kinds of food sources, because they have individually learned how to exploit those food sources (for example, cracking nuts or termiting), then naive individuals would be more likely to devise a means to exploit that resource. This would be social learning, but since individuals have to reinvent the details of the behavior for themselves, albeit accelerated by proximity to conspecifics, the behavior cannot become more complex across generations beyond a certain point. Naive individuals do not get a "head start," and thus cannot begin where previous learners left off. If, instead, individuals acquire their behavior by directly observing and copying the details of others' techniques, then individual learning can build atop previous innovations.[31] A version of this distinction that allows for more continuity with chimpanzees would be that chimps possess modest true imitative capacities, but the complexity of the skills and technologies they can represent and the fidelity of their transmission is less than that of humans.

True imitation is probably not the whole story, however, at least not in the long run. In modern humans, a suite of social learning abilities contributes to the maintenance and accumulation of culture. Simpler forms of observational learning (of physical skills, for example) likely provided a foundation for more complex kinds of social learning and inference, such as those associated with symbolic communication and language. Symbolic communication through proverbs, stories, and myths allows for a great deal of cultural transmission without "observation" in the usual sense.[31,32] For example, !Kung hunters knew a great deal of natural history, including the fact that porcupines are monogamous.[33] It is hard to imagine that knowledge of this kind is preserved through observational learning alone. However, Tomasello[30] argues that true imitation, rooted in a genetically evolved capacity for Theory of Mind, generates both linguistic and nonlinguistic forms of cultural evolution, and that linguistic symbols (including grammatical structures) have gradually accumulated, improved, and adapted through a cultural evolutionary process analogous to that observed in the domain of material culture and technology.

Whatever the specific nature of the mechanisms—be they true imitation or not—it remains puzzling why they should be so rare. Boyd and Richerson[34] constructed a model of the evolution of cumulative cultural capacities designed to explore this puzzle. In their model, a population lives in a variable environment in which there is a unique optimal adaptive value of a quantitative trait. Each generation, there is some probability that the environment changes so that a new value of the trait is optimal. Individual phenotypes are a combination of genetic influences and cultural transmission. Other genes affect an individual's reliance on imitation, but carry an incremental fitness cost. All individuals engage in some individual learning, which moves their phenotypes a small amount toward the current optimum. But individuals with a substantial reliance on cultural learning can acquire phenotypes much closer to the optimum, once such phenotypes exist in the population. These phenotypes are then improved a small amount by individual learning. This process repeats every generation.

While an increasing amount of field evidence suggests that other animals, particularly chimpanzees, may maintain traditions that result from social learning, there is little reason to believe that nonhuman social learning capacities can generate cumulative adaptation. In contrast, accumulated cultural skills and knowledge are characteristics of all human societies.

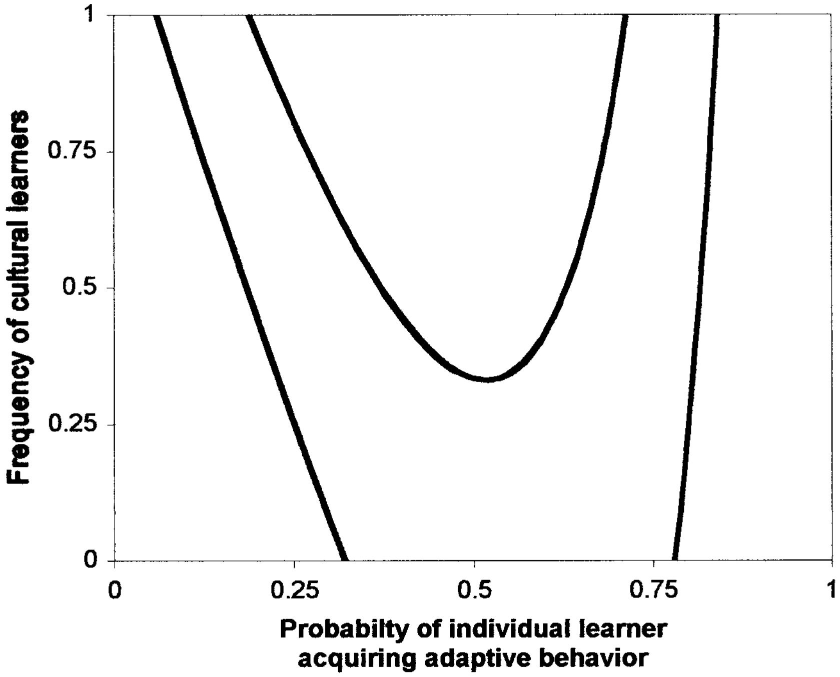
Unlike the simpler social learning models discussed in the previous section, this work demonstrates that a substantial reliance on cultural learning is unlikely to spread initially, but goes to fixation and is stable once a critical threshold frequency is surmounted (Box 2). Natural selection favors cultural learning only when the costs of developing and maintaining cultural learning mechanisms are smaller than the benefits gained by acquiring simple behaviors that could be learned on one's own. But, despite being difficult to get started, once a reliance on cultural learning is common in the population, it is easy to sustain. Provided that the environment is not too variable, the rate of accumulation of adaptive behavior through cultural learning can easily pay for the cost of the psychological capacities needed to make it possible: Cultural learning mechanisms provide access to the knowledge accumulated over generations that simple social learning does not. However, because cultural capacities are not favored when rare, we should not expect them to be widespread in nature. A population must traverse a fitness valley before the frequency of true imitation is high enough to make it individually advantageous. Because other forms of social learning are often built principally out of individual learning, and do not involve inferential reconstructions of behaviors and strategies, they do not face this dilemma—but they also cannot generate cumulative cultural adaptation.

Having offered an explanation of why cumulative cultural abilities might be rare in nature, we are left with the question of why it was specifically the human ancestral lineage that crossed the cultural threshold. One possibility is that ancestral humans just happened to drift genetically across the threshold. Random events of this kind were likely important in the evolutionary histories of many species. However, we think it is more productive to ask if there was something particular about the human lineage that made it more likely than other species to cross this cultural threshold. Perhaps our evolving cultural capacities depended first upon some other adaptation, which might have arisen for another reason entirely.[34] Good answers here are probably a long way off, but speculation based on the existing information will help direct future research.

WHAT COGNITIVE MECHANISMS GUIDE CULTURAL EVOLUTION?

Like evolutionary psychology, dual-inheritance theory combines evolutionary theory with empirically

Box 2. Cultural Learning



Regions for which cultural learning has an advantage over individual learning, for the Boyd and Richerson[34] model. The curves show the internal unstable equilibrium of cultural learners versus individual learners and represent the threshold frequency at which cultural learning becomes favored by selection. This is shown for two values of γ, the probability that the environment changes each generation and renders a new behavior adaptive. In each case, culture learners will increase in the region above the curve and decrease below it.

When individual learning is difficult (left side of plot), cultural learning cannot invade the population because too few individuals have the skilled behavior. When cultural learning is rare, the only behaviors that exist in the population are those that are solely the result of individual learning (those that could be figured out by one individual in his lifetime). The cost (for example, in adding metabolically costly brain tissue) does not easily outweigh the benefit because there is little adaptive information contained in the behavior of others that the animal cannot figure out on its own. It is important to keep in mind that the developmental or fitness costs of true imitation mechanisms may be quite high, even though, from our human perspective, imitation itself strikes us as being quite easy. It is "easy" because our cognition is "designed for" imitation and social learning (for example, infants show both sophisticated imitative and inferential abilities, as well as a strong desire to imitate[70]).

As we move toward slightly easier problems, cultural learning still cannot invade, but is stable once common. Once cultural capacities are common, population processes will begin to assemble complex adaptations, and individuals who have the ability to acquire them will do substantially better than those who cannot. Under these conditions, cultural learning does for genes what they cannot do directly for themselves.

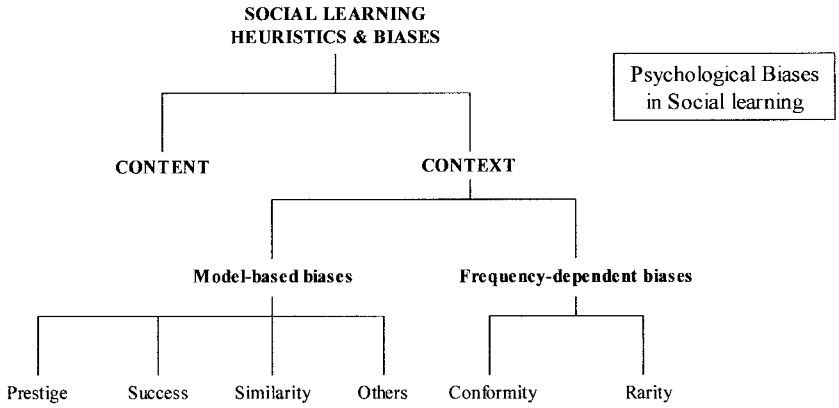
Looking at the far right side of the plot, where individual learning is easy, essentially everyone acquires highly adaptive behavior without paying the additional costs of cultural learning capacities, so cultural learning is rarely adaptive.

In all cases, there are many more combinations of parameters for which cultural learning is stable when common, but cannot invade the population when rare. In the case where $\gamma = 0.4$, implying that the optimal behavior changes in 40% of generations, there is no difficulty of individual learning for which cultural learning invades, but a wide range for which cultural learning is stable.

grounded assumptions about the environments inhabited by ancestral human populations to make predictionsa about the details of human psychology—details that often specify cognitive mechanisms people use to extract adaptive ideas, beliefs, and practices from their social environments. However, the approach diverges from mainstream evolutionary psychology in emphasizing the costly information hypothesis. This hypothesis focuses on the evolutionary tradeoffs between acquiring accurate behavioral information at high cost and obtaining less accurate information at low cost. When accurate information is unavailable or too costly, individuals may exploit the information stored in the behavior and experience of other members of their social group.

By exploring how the costly information hypothesis generates tradeoffs in the evolution of our cognitive capacities, we can generate productive theories about the details of human cultural psychology. When information is costly, natural selection will favor cognitive mechanisms that allow individuals to extract adaptive information, strategies, practices, heuristics, and beliefs from other members of their social group at a lower cost than through alternative individual mechanisms. Human cognition probably contains numerous heuristics and learning biases that facilitate the acquisition of useful knowledge, practices, beliefs, and be-

Box 3. Cultural Learning Mechanisms



Content biases and heuristics arise from the interaction of human psychology and the characteristics or "cues" associated with the thing being transmitted (the idea, representation, or behavior). These biases affect the likelihood of a particular mental representation being transmitted because of the content of the representation. Content effects can take many forms. They may reflect the direct action of natural selection on our "prepared learning" abilities, such as language, folk biology, and color categories. They may also arise as by-products of cognitive evolution: Boyer's[38] approach to cultural phenomena like ghosts and gods is one example. Or they may emerge from a kind of more generalized cost-benefit calculation: People prefer steel axes to stone axes because it is much less work to cut down trees with steel. Such biases may result for either genetically transmitted cognitive structures (as in Boyer's argument) or culturally acquired mental representations. Context heuristics arise from the learning environment or context. Model-based biases result from cues or characteristics of the potential model ("an individual who may be imitated") and make the ideas, mental representations, or behavior of their possessor more likely to transmit than those held by other individuals. Other model-based biases may include age, sex, ethnicity, and healthful appearance. Frequency biases use the commonality or rarity of a behavior as a cue.

havior ("cultural traits" or "representations"). These mechanisms can be usefully modeled at the algorithmic level, much as some cognitive scientists investigate other kinds of information processing.

Such cultural learning mechanisms, all of which build atop other social and cultural learning abilities, can be categorized into content biases and context biases. Box 3 organizes the various forms of cultural learning mechanisms. Content biases, or what Boyd and Richerson[7] called direct biases, exploit informative cues of an idea, belief, or behavior itself, and thereby influence the likelihood of imitation. An equivalent perspective prefers to discuss cultural learning as adaptive inferences triggered by content biases for cues provided in the behavior of others.[35] Many such biases may have evolved because they facilitate the acquisition of fitness-enhancing cultural traits.[2,4,7] Because content biases are likely numerous and generally confined to particular domains of culture, for space considerations we have omitted any substantial discussion of them here. However, in thinking about content biases, it is important to keep in mind a number of things. First, jury-rigged evolutionary products, like human minds, are likely to contain accidental by-products and latent structures that create biases for fitness-neutral behaviors, ideas, beliefs, and values.[36,37] Boyer[38] detailed one kind of by-product content bias in his explanation for the universality of religious concepts (like ghosts). Second, even content biases that arose because they led to the adoption of fitness-enhancing behavior in ancient environments may now promote the adoption of quite maladaptive practices. Third, content biases may be either reliably developing products of our species-shared genetic heritage or they may be culture specific. People may learn valuable content cues via cultural learning or, having acquired one idea or practice via cultural transmission, may be more likely to acquire another because the two "fit together" in some cognitive sense.

Context biases, on the other hand, exploit features of potential models or the frequencies of alternative behaviors or strategies, rather than features of the alternatives themselves, to guide social learning. There is a great deal of adaptive information embodied in both who holds ideas and how common the ideas are. A large amount of modeling effort has been expended in exploring the conditions under which different context biases evolve and how strong natural selection would prefer they be. These models derive from first principles about how individual cognitive biases affect both individual fitness (when they evolve) as well as the patterns of information in the population (what they evolve). Our remaining discussion of psychological mechanisms focuses on two categories of context biases in cultural learning: success and prestige bias and conformity bias.

Success and Prestige Bias

If individuals vary in skills (for example, tool making), strategies (tracking techniques), or preferences (for example, for foods) in ways that affect fitness, and at least some components of those differences can be acquired via cultural learning, then natural selection may favor cognitive capacities that cause individuals to learn preferentially from more successful individuals. The greater the variation in acquirable skills among individuals, and the more difficult those skills are to acquire via individual learning, the greater the pressure to preferentially focus one's attention on and imitate the most skilled individuals. If individuals evaluate potential "cultural models" (individuals they may learn from) along dimensions associated with competence in underlying skills (such as hunting returns), and focus their social learning attention on those who are more successful, they will be more likely to acquire adaptive strategies.[31] Interestingly, while the ability to rank individuals by foraging success is observed in nonhumans (for better scrounging),[39] there is no evidence that individuals in these species acquire strategies from successful foragers. With the rise of cultural capacities in the human lineage, natural selection needed only to connect these learning abilities with preexisting ranking capacities.

A bias of this kind is a standard assumption in evolutionary game theory,[40] where a preference for copying the strategies of successful individuals generates an evolutionary dynamic that is usually mathematically indistinguishable from natural selection acting on genes. However, uncertainty about the payoffs and success of other individuals complicates success-biased learning. Schlag[41,42] has explored the exact form that such an adaptive bias should take in the presence of noisy feedback about the success of other individuals, finding that a linear weighting of models by their observed payoffs may be more adaptive than simply imitating the individual with the highest observed payoff. Another solution is for individuals to use aggregate indirect measures of success, such as wealth, health, or family size, which integrate over many instances and smooth out perceptual and stochastic errors. This may explain the widespread observation that people copy successful individuals, as defined by local standards. (See Henrich and Gil-White[31] for a summary of the laboratory and field evidence.)

However, an additional problem created by using indirect indicators of successful strategies is that it is often very unclear which of an individual's many traits have led to success. Are people successful because of how they tend their farms, cook their food, or make sacrifices to the spirits, or all three? Because of this ambiguity, humans may have evolved the propensity to copy successful individuals across a wide range of cultural traits, only some of which may actually relate to the individuals' success.[7,31,43] If information is costly, it turns out that this strategy will be favored by natural selection even though it may allow neutral and maladaptive traits to hitchhike along with adaptive cultural traits. In a world of costly information, cognitive adaptations do not always produce adaptive behavior from the point of view of genes, even in ancestral environments. Nevertheless, the theory does allow for predictions about the conditions under which maladaptive cultural traits will spread.

The evolution of a success bias may also be able to explain the formation of prestige hierarchies. Once success-biased transmission has spread through a population, highly skilled individuals will be at a premium, and social learners will need to compete for access to the most skilled individuals. This creates a new selection pressure on success-biased learners to pay deference to those they assess as highly skilled (those judged most likely to possess adaptive information) in exchange for preferred access and assistance in learning. Deference benefits may take many forms, including coalitional support, gifts, general assistance (house-building), and caring for offspring.[31]

With the spread of deference for high skilled individuals, natural selection can take advantage of these observable patterns of deference to further save on information-gathering costs. Naive entrants (say immigrants or children), who lack detailed information about the relative skill of potential cultural models, may take advantage of the existing pattern of deference by using the amounts and kinds of deference different models receive as cues of underlying skill. Assessing differences in deference provides a best guess of the skill ranking until more information can be accumulated. This also means that skilled individuals will prefer deference displays that are easily recognized by others (in public). Thus, along with the ethological patterns dictated by the requirements for high fidelity social learning (proximity and attention), deference displays also include diminutive body positions and sociolinguistic cues. The end point of this process gives us the psychology, sociology, and ethology of "prestige," which must be distinguished from those associated with phylogenetically older "dominance" processes.[31]

From this theory, Henrich and Gil-White[31] derived twelve predictions about the interrelationships between preferential imitation or influence, deference, and other ethological patterns, individual characteristics (like age and sex), and memory. A review of data from psychology, economics, and ethnography turned up a sizable amount of evidence consistent with these predictions.

Conformist Bias

It is unlikely that success and prestige biases solve all costly information problems, however. What do you do when any observable differences in success and prestige among individuals do not covary with the observable differences in behavior? For example, suppose everyone in your village uses blowguns for hunting except one regular guy who uses a bow and arrow and obtains fairly average hunting returns. Do you adopt the bow or the blowgun?

One solution for dealing with such information-poor dilemmas is to copy the behaviors, beliefs, and strategies of the majority.[7,14] Termed conformity bias, this mechanism allows individuals to aggregate information over the behavior of many individuals. Because these behaviors implicitly contain the effects of each individual's experience and learning efforts, conformist transmission can be the best route to adaptation in information-poor environments. To see this, suppose every individual is given a noisy signal (a piece of information) from the environment about what the best practice is in the current circumstances. This information, for any one individual, might give them a 60% chance of noticing that blowguns bring back slightly larger returns than bows. Thus, using individual learning alone, individuals will adopt the more efficient hunting practice with probability 0.6. But, if an individual samples the behavior of 10 other individuals, and simply adopts the majority behavior, his chances of adopting the superior blowgun technology increase to 75%.

Obviously, if everyone uses only conformist transmission, no adaptation or cultural evolution occurs, but models of interaction among different learning mechanisms indicate that natural selection will very often favor a mix of social and individual learning with a substantial reliance on conformity. Extending Boyd and Richerson's[7] original model, Henrich and Boyd[14] used simulation to investigate the interaction and coevolution of vertical transmission (parent-offspring transmission), individual learning, and conformist transmission in spatially and temporally varying environments. These results confirm that conformist transmission is likely to evolve under a very wide range of conditions. In fact, these results show that the range of conditions that favor conformist transmission are wider than those for vertical transmission alone, suggesting that if advanced social learning via vertical transmission evolves at all, we should also expect to observe a substantial conformist bias.

The model of the combination of conformity bias with individual learning and vertical transmission leads to three predictions: 1. Individuals will prefer conformist transmission over vertical transmission, assuming it is possible to access a range of cultural models at low cost, which is often, but not always the case; 2. As the accuracy of information acquired through individual learning decreases, reliance on conformist transmission over individual learning will increase; 3. Individuals should be sensitive to substantial shifts in the relevant environments so that they decrease their reliance on conformist transmission after recent fluctuations or increase it after immigrating.

Work combining these models with empirical investigations is growing. Kameda and Nakanishi[44] have further extended the Henrich and Boyd[14] model to predict how human psychology should respond to changes in the cost of individual learning and designed experiments to test their predictions. By analyzing the temporal dynamics of historical cases of the diffusion of innovations, Henrich[45] has found evidence that is consistent with a strong role for both conformity- and success-biased transmission and inconsistent with a strong role for individual learning. We imagine future work will illuminate the complex interactions among conformist and other social learning biases in environments in which the costs and qualities of information vary.

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IF CULTURAL VARIANTS DO NOT REPLICATE LIKE GENES, CAN CULTURE EVOLVE?

So far, we have treated the inheritance of cultural variants as unproblematic. However, because much of the initial work in coevolutionary theory involved tools from population genetics and theoretical evolutionary biology, there are good reasons to examine the strength of the analogy between genes and "memes." Dawkins, in *The Extended Phenotype,*[46] described what he saw to be the necessary characteristics of any replicating entity: longevity, fecundity, and fidelity. The structure of this argument has been used to support the analogy between genetic and cultural (or "memetic") evolution: Cultural ideas can be replicators as well, and hence culture may evolve as do populations of alleles. Some cognitive and evolutionary anthropologists, however, have severely criticized the power of this analogy, arguing that cultural ideas are rarely if ever replicated during social learning and that culture is substantially transformed by human psychology so that ideas are rarely transmitted intact so there are no or few discrete units in culture.[35,38,47,48] For these reasons, they argue, cultural variants ("memes" or "representations") have little fidelity and so cannot evolve in a Darwinian sense. Essentially, if cultural inheritance involves continuously blending (nondiscrete) traits and mutation-like processes are powerful, memes will not fulfill Dawkins' requirements for a replicator. Without a replicator, the argument goes, there can be no cultural evolution.

These arguments should be taken seriously. If culture is not an evolving system in the Darwinian sense, then many coevolutionary theories (and, of course, substantial portions of this paper) require serious rethinking. Building on the preceding points, Sperber,[35] Boyer,[48] and Atran[47] have argued that many existing models of cultural evolution are inappropriate, transmission cannot explain the persistence of behavioral variation in humans, and cultural evolution cannot produce adaptations. If these arguments are correct, the story we told earlier about culture accumulating powerful locally adapted skills and technologies is somehow mistaken.

We think the arguments we reviewed earlier are valid in this respect, however. There are good reasons to suppose that culture is an evolutionary system, even if the three claims above are true. In two recent articles, Henrich and coauthors[49,50] use three mathematical models and several other lines of argument to show that the objections mentioned here do not follow from their assumptions. Through these analyses, the authors demonstrate how Dawkins' original claims about replicators and Darwinian evolution were wrong—replicators are sufficient for cumulative evolution, but not necessary.

In their first model, Henrich and Boyd[49] address two complaints: that culturally transmitted ideas are rarely if ever discrete and that inferential biases in learning (Sperber's "strong attractors") swamp the effects of selective transmission and prevent Darwinian adaptation. This model assumes that individuals' possess mental representations ("cultural variants," beliefs, and scripts) that are influenced by selectively learning from some individuals (for example, from successful individuals). These mental representations are continuous (nondiscrete or quantitative), so each individual may possess a somewhat different variant of the representation. There are no "copies" of variants, only social "influence." Furthermore, in learning these representations, individuals use inferential processes that strongly bias the final form of the representation. Their analysis shows that these complaints are deductively invalid. If cognitive inferential influences are sufficiently strong relative to selective forces (selective learning), a continuous (quantitative) model reduces to a discrete-trait replicator model commonly used in population models of both culture and genes. In fact, the stronger the effects of inferential bias on learning, the better is the discrete trait approximation. Moreover, this means that it is the weak effects of selective transmission that determine the final equilibrium of the system.

In the second and third models, the authors construct systems that allow for large amounts of transmission error to show that accurate individual-level replication of cultural variants is not necessary for selective forces to generate either cultural inertia or cumulative cultural adaptation. The second model shows how conformist transmission can act to drastically reduce the effect of transmission errors and still generate either cultural inertia or diffusion of successful variants. The third model combines all the potential problems with models of cultural evolution—continuous (nondiscrete) mental representations, incomplete transmission, and substantial inferential transformations—and shows not only that adaptive cultural evolution may still occur under empirically plausible conditions, but that it also predicts when such adaptive evolution will not occur.

Many of the insights from these formal models have been known for some time but, unlike Dawkins' replicator argument, have not successfully spread. While Sperber, Boyer and Atran's criticisms apply to the informal theorizing of some memeticists,[46,51,52] they are wide of the mark for much formal gene-culture coevolutionary theory. Continuous trait models go back to the very beginning of the field. Boyd and Richerson[7] argued in 1985 that there is no need to assume particulate "units" in order to build evolutionary models, in fact showing that blending models best produce heritable variation exactly when transmission is inaccurate. In fact, nineteen of the thirty-eight models presented in their book are continuous (nondiscrete) trait models that allow for an arbitrary amount of transmission error. Similarly, Cavalli-Sforza and Feldman[2] devoted one of their five chapters entirely to continuous trait models. These continuous models allow for substantial error and other forms of nonreplication. Similar to cognitivist critics, Boyd and Richerson also explicitly distinguish public representations from mental representations (though using different terminology) throughout their book, and repeatedly specify the inferential transformation between observed behavior and representation formed. They also make explicit reference to much research in psychology on the nature of social learning and propose the following pathway for the transmission of cultural variants: Modeled events → Attention Processes → Retention Processes → Motor Reproduction → Motivation Processes → Matching. Chapters 4 and 5 in Boyd and Richerson's book discuss how cognitive structures—what Sperber[35] would later call "attractors"—bias cultural change so that some outcomes are more likely than others, and even use some of the same examples as Boyer.[48]

An understanding of cultural evolution requires studying both the evolved cognitive abilities and inferential mechanisms that allow for cultural learning, as well as the population processes to which they give rise through social interaction. Culture can have heritable properties and evolve in a Darwinian sense even if it is continuous, error-prone, and individually ephemeral.

The force of arguments like those of Sperber, Atran and Boyer seems to be that cultural learning requires innate, domain-specific psychological mechanisms (we agree!), and therefore that most of the action is in individual psychologies and not in the population dynamics. This conclusion is unfounded: An understanding of cultural evolution requires studying both the evolved cognitive abilities and inferential mechanisms that allow for cultural learning, as well as the population processes to which they give rise through social interaction. Culture can have heritable properties and evolve in a Darwinian sense even if it is continuous, error-prone, and individually ephemeral.

HOW DOES COEVOLUTION INFLUENCE PSYCHOLOGY AND SOCIETY?

A persistent debate in the social sciences is whether the chief causal level in social phenomena is the individual or the social. Instead of arguing that primary causation exists at either level, gene-culture population models take seriously and treat explicitly forces at both levels, and sometimes more. From this perspective, classic features of human cultures and societies, such as culture being shared by members of self-ascribed groups, become results to derive, rather than *a priori* assumptions. These dialectical models have helped us to understand how interactions between cognition and population processes give rise to ethnically marked groups[53,54] and ethnic psychology,[55] large-scale cooperation, prosocial psychologies, and group-beneficial cultural norms.[7,16,56–60] Rather than attempting to summarize this large literature, we focus only on one of the most recent models.

The Coevolution of Ethnically Marked Groups and Ethnic Psychology

In almost all ethnographically known regions and historical periods, humans have organized themselves into self-ascribed groups marked by arbitrary symbols.[61] For example, in both historical and modern East Africa, different pastoralist groups wear differently colored clothing, which serves as ethnic markers. In one region of modern Tanzania, Maasai wear red, Sukuma wear blue, and Taturu wear black. Since no other primate forms such symbolically marked groups, and existing rates of mixing among such groups would quickly erode differences of this kind if they were transmitted from parent to offspring in any fashion (culturally or genetically), some explanation of their formation and maintenance is needed.

Prior efforts to explain ethnicity have proved theoretically unsound. First, the standard approach to ethnic actors as strategic manipulators requires that some other processes generate and maintain ethnic groups and their markings. If ethnicity were solely the product of strategic consideration or a coalitional psychology,[62] ethnicity would rapidly disappear as a phenomenon and there would not be anything to manipulate.[54,63] A more serious idea is that ethnic markers allow actors to select individuals with whom to cooperate.[64,65] These efforts fail because, unless some process prevents out-group members from adopting the same markers, individuals who wear the markers but do not cooperate will destroy the signal value of the symbols.[66,67] So the question remains: How do such markers arise and what are their functions?

In addressing this puzzle, McElreath, Boyd, and Richerson[54] constructed a model of the emergence of ethnic marking in which markers function to provide coordination (not cooperation, so there is no free-rider problem) with other individuals who share one's norms. Coordination means that individuals are better off when they practice complementary behaviors. The familiar example of this occurs in cross-cultural communication,[68] where different expectations in many aspects of interaction routinely lead to lower payoffs for all parties. The coaching book market for international business people attests to the severity of these problems. It is likely that the same phenomenon occurs in many other aspects of culturally inherited behavior. Having the same norms about child rearing, barter, marriage, inheritance, and conflict resolution can be crucial for successful social relations. Since the number of domains of this kind is likely large and many such rules are held unconsciously, the mutual costs of interactions between individuals with different sets of norms can be substantial.

The model is sketched as follows. First, imitation of the successful and social interaction produces culturally differentiated communities. In each social group, whatever norm is initially most common leads to the highest payoffs, making it more common. Then, provided individuals are biased to interact with people who share the same arbitrary symbolic markers as themselves, symbolically marked groups that possess different cultural norms arise endogenously in the model. Furthermore, even if there is initially no genetically transmitted psychological bias to interact with other individuals who share your same marker, natural selection, operating in this culturally constructed environment, will favor genes that reliably produce this bias since individuals who prefer to interact with those with the same marker are more likely to interact with someone with the same norms as themselves, and therefore profit more from social interaction.

The model also makes some unexpected predictions about the nature of ethnic marking. While the model requires spatial variation in norms to evolve the association between norms and markers, once markers are associated with underlying norms, and provided other processes permit a tight linkage between them, spatial variation in norms is no longer needed to maintain functional ethnic markers. Instead, the "ethnic" groups in the model merge, forming one large multiethnic community in which individuals still coordinate their interactions based on markers delineating distinct ethnic divisions. Since markers in such a situation allow individuals to assort nearly perfectly with others who share their norms, members of smaller norm communities are not at a disadvantage relative to the normative majority. Situations like this resemble in an abstract way modern multiethnic cities like Los Angeles or Detroit,[69] in which many ethnic groups live intermixed but preferentially interact among themselves.

The model makes predictions about both evolved psychological propensities and sociological patterns, and explicitly links them. Ethnic marking arises as a side effect of other psychological mechanisms—which themselves have solid individual-level selective advantages—that happen to generate behaviorally distinct groups. The strategy of using arbitrary symbolic markers to choose interactants then evolves because of features of the culturally evolved environment. Cultural transmission mechanisms may create statistically reliable regularities in the selective environments faced by genes.[4,57] Thus, explaining many important aspects of human psychology and behavior will require examining how genes under the influence of natural selection responded to the regularities produced by culture. This means that understanding the behavior of a highly cultural species like humans will sometimes demand a culture-gene coevolutionary approach. Phenotypic optimality models and models that ignore the population dynamics of social learning certainly have their place, and have proven very useful. But satisfying answers to many important questions concerning human behavior, from the cultural microevolution of foraging adaptations to the coevolution of human psychology and cultural variation, will remain elusive unless dual inheritance or some similar approach is taken seriously.

ACKNOWLEDGMENTS

This paper coevolved with valuable feedback from Robert Boyd, Natalie Henrich, Pete Richerson, Eric Smith, Peter Todd, Annika Wallin, and two anonymous reviewers.

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BOOK REVIEW

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