The cultural niche: Why social learning is essential for human adaptation

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In the last 60,000 y humans have expanded across the globe and now occupy a wider range than any other terrestrial species. Our ability to successfully adapt to such a diverse range of habitats is often explained in terms of our cognitive ability. Humans have relatively bigger brains and more computing power than other animals, and this allows us to figure out how to live in a wide range of environments. Here we argue that humans may be smarter than other creatures, but none of us is nearly smart enough to acquire all of the information necessary to survive in any single habitat. In even the simplest foraging societies, people depend on a vast array of tools, detailed bodies of local knowledge, and complex social arrangements and often do not understand why these tools, beliefs, and behaviors are adaptive. We owe our success to our uniquely developed ability to learn from others. This capacity enables humans to gradually accumulate information across generations and develop well-adapted tools, beliefs, and practices that are too complex for any single individual to invent during their lifetime.

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In its brief evolutionary history, *Homo sapiens* has come to occupy a larger range than any other terrestrial vertebrate species. Earlier hominins, such as *Homo heidelbergensis* and Neanderthals, were limited to Africa and the temperate regions of southern Eurasia. Behaviorally modern humans were living in Africa by 70,000 y ago (1). Between 50,000 and 60,000 y ago, people left Africa, crossing into southwest Asia (2). From there they spread rapidly through southern Eurasia, reaching Australia by 45,000 y ago, a feat that only one other terrestrial mammal (a murid rodent) was able to accomplish (3). Soon after this, people penetrated far north, reaching the latitude of Moscow by 40,000 y ago and the Arctic Ocean by 30,000 y ago. People had spread almost as far south as the southern tip of South America 13,000 y ago, and by 5,000 y ago humans occupied virtually every terrestrial habitat except Antarctica and some islands in Oceania (2). Even the most cosmopolitan bird and mammal species have substantially smaller ranges (4–6).

This global expansion required the rapid development of a vast range of new knowledge, tools, and social arrangements. The people who moved out of Africa were tropical foragers. Northern Eurasia was an immense treeless steppe, relatively poor in plant resources and teeming with unfamiliar prey species. The people that roamed the steppe confronted a hostile climate—temperatures fell to −20 °C for months at a time, and there were often high winds. Surviving in such environments requires a whole new suite of adaptations—tailored clothing (7), well-engineered shelters, local knowledge about game, and techniques for creating light and heat. This is just the northern Eurasian steppe; each of the other environments occupied by modern human foragers presented a different constellation of adaptive problems. Ethnographic and historical accounts of 19th and 20th century foraging peoples make it clear that these problems were solved through a diverse array of habitat-specific adaptations (8). Although these adaptations were complex and functionally integrated, they were mainly cultural, not genetic, adaptations. Much evidence indicates, in fact, that local genetic changes have played only a relatively small part in our ability to inhabit such a diverse range of environments (9, 10).

Why are humans so much better at adapting to novel environments than other mammals? There have been many different answers to this question, but the most influential are rooted in the idea that people are simply smarter than other creatures. We have bigger brains and more computing power, and this allows us to adapt to a wider range of environments than other animals. One of the clearest statements of this hypothesis comes from a series of papers by Tooby, Cosmides, Pinker, and collaborators (11–14). Other animals, they argue, are limited to what they call "dedicated intelligence," domain-specific learning and decision-making mechanisms that are adapted to particular environments. Humans, by contrast, have evolved "improvisational intelligence," a suite of uniquely flexible cognitive capacities that allow our species to acquire locally adaptive behavior in a wide range of environments. In short, we are adapted to the "cognitive niche" (11, 14). These capacities are augmented by our species' ability to learn from each other, especially using grammatical language.

This hypothesis flows from a nativist, modularist view of cognition. Its central premise is that broad general problems are much more difficult to solve than narrow specialized ones, and therefore the minds of all animals, including humans, are built of many special-purpose mechanisms dedicated to solving specific adaptive problems that face particular species. These mechanisms are modular in that they take inputs and generate outputs relevant to problems in particular domains such as mate choice, foraging, and the management of social relationships. These authors are nativists because they believe that evolved mechanisms depend on a considerable amount of innate information about the relationships between cues and outcomes in particular domains for particular species. For example, mechanisms that regulate decisions about mate choice in human males may be based on the assumption that long-term mating is likely, and thus selection favored a psychology that leads men to be attracted to young women. Analogous mechanisms in chimpanzees, which do not form long-term bonds, have produced a psychology that causes males to prefer older females, perhaps because they are better mothers (15). Mechanisms regulating social exchange are specialized in other ways. The innate content is built up because learning and decision mechanisms have been shaped by natural selection to solve the important recurrent adaptive problems that confronted the species.

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This view of cognitive evolution seems to preclude flexible, widely applicable cognitive abilities; or, as Cosmides and Tooby put it, "…on first inspection, there appear to be only two biologically possible choices for evolved minds: either general ineptitude or narrow competences" (12). However, these authors believe that humans, and only humans, have undergone an evolutionary breakthrough that gives them "the computational ability to improvise solutions in developmental time to evolutionarily novel problems" (13). The key ability is the use of cause-and-effect reasoning to make inferences about local environmental contingencies. As Pinker puts it,

> These inferences are played out internally in mental models of the world.…It allows humans to invent tools, traps, and weapons, to extract poisons and drugs from other animals and plants.…These cognitive stratagems are devised on the fly in endless combinations suitable to the local ecology. They arise by mental design and are deployed, tested, and fine-tuned by feedback in the lifetime of individuals… (14, pp 8993–8994)

These inferential capacities are augmented by a second evolutionary innovation, the ability to learn from each other, a capacity that dramatically lowers the cost of acquiring information necessary for local, contingent adaptations.

It seems likely that the average human is smarter than the average chimpanzee, at least in domains like planning, causal reasoning, and theory of mind. However, we do not think this is sufficient to explain our ecological success. The cognitive niche hypothesis overestimates the extent to which individual human cognitive abilities allow people to succeed in diverse environments and misunderstands the role that culture plays in a number of important ways. We suggest, instead, that our uniquely developed ability to learn from others is absolutely crucial for human ecological success. This capacity enables humans to gradually accumulate information across generations and develop well-adapted tools, beliefs, and practices that no individual could invent on their own. We have entered the "cultural niche," and our exploitation of this niche has had a profound impact on the trajectory of human evolution. In the remainder of this article, we will develop this argument in more detail.

Culture Is Essential for Human Adaptation

It is easy to underestimate the scope, sophistication, and importance of the pool of culturally transmitted information that supports human subsistence, even in what seem to be the "simplest" foraging societies. The archaeological record makes it clear that modern humans adapted to life above the Arctic Circle early in their expansion but tells us little about their way of life. However, ethnographic studies of the Netsilik and Copper Inuit, collectively known as the Central Inuit, give us a sense of the complexity of the adaptations that allow foragers to thrive in the Arctic. These people occupy a habitat that is harsh and unproductive, even by Arctic standards. Their groups were small, and their lifeways were simple compared with foragers living on the coasts of Alaska and Greenland. To focus your mind on the crucial adaptive challenges, imagine that you are marooned on a beach on the coast of King William Island (68.935N, 98.89W). It is November and it is very cold.

Your first problem is to stay warm. Monthly average temperatures in the winter months are between −25 °C and −35 °C. Even well-acclimatized people rapidly succumb to hypothermia below −1 °C, so you need warm clothes. If there were no wind and you could remain motionless, a cloak would do, but this is a windy place and you need to hunt, so you will need well-tailored clothes (7). In the winter, the Central Inuit wore elaborately constructed parkas and pants (16). The best were made from caribou skins harvested in the fall. Caribou skins insulate better than seal or polar bear fur because the individual hairs have an unusual air-filled structure, something like bubble wrap (17). Caribou skins harvested in autumn have fur that is just the right thickness. Hides were repeatedly stretched, scraped, moistened, and then stretched again to yield pliable skins (18). Parkas were assembled from multiple pieces to create a bell shape that captures heat, while also allowing moisture to dissipate when the hood is thrown back. Hoods were ruffed with a strip of fur taken from a wolverine's shoulders because its variable length makes it easier to clear the hoarfrost. Winter footwear was constructed with many layers: first the *alirsiik*, fur-lined caribou stockings, then the *ilupirquk*, short lightweight stockings with the fur outside, then a pair of *pinirait*, heavier stockings with the fur to the outside, then *kamiik*, boots with the fur outside, and finally *tuqtuqutiq*, short heavy double-soled boots of caribou skin. Clothing was stitched together with fine thread made from sinew taken from around the vertebrae of caribou. The sinew had to be cleaned, scraped, shredded, and twisted to make thread. Several different kinds of stitches were used for different kinds of seams. A complicated double stitch was used to make footwear waterproof. To make these stitches, Central Inuit women used fine bone needles that made holes that were smaller in diameter than the thread (16).

Not even the best clothing is enough to protect you from winter storms, so you need shelter. During the winter most Inuit lived in substantial driftwood and sod houses, but the Central Inuit wintered on the sea ice, living in snow houses. These round vaulted structures were ≈3 m high, made of snow blocks cut with a serrated bone knife. The central room was built above a pit, with platforms for sleeping, and a long entrance tunnel below the level of the main room with several low doors to prevent heat loss. The walls were usually lined with skins suspended from toggles on the outside of the snow house. This design allowed the snow walls to stay near freezing, while the inside of the snow house could reach temperatures of 10–20 °C (19).

You need a source of heat and light in your snow house, for cooking and for melting sea ice for water. You cannot use wood fires because there are no trees. Instead, Arctic peoples carved lamps from soap stone and fueled them with rendered seal fat. These lamps were made from oblong stones between 30 cm and 1 m long; a shallow, sharp-sided depression was carved from the surface of the stone, and the lamp was equipped with a long, curtain-like wick made of moss. A well-managed lamp burned without producing any soot (16).

You also need food. Plants are easy to gather, but for most of the year this is not an option in the Arctic. During the winter, the Central Inuit hunted seals, mainly by ambushing them at their breathing holes. When the sea ice begins to freeze, seals claw a number of breathing holes in the ice within their home ranges. As the ice thickens, they maintain these openings, which form conical chambers under the ice. The Inuit camped in snowy spots near the seals' breathing holes. The ice must be covered with snow to prevent the seals from hearing the hunters' footsteps and evading them. Inuit hunted in teams, monitoring as many holes as possible. The primary tool was a harpoon approximately 1.5 m long. Both the main shaft and foreshaft were carved from antler. On the tip was a detachable toggle harpoon head connected to a heavy braided sinew line. The other end of the harpoon was made from polar bear bone honed to a sharp point. At each hole, the hunter opened the hard icy covering using the end of the harpoon, smelled the interior to make sure it was still in use, and then used a long, thin, curved piece of caribou antler with a rounded nob on one end to investigate the chamber's shape and plan his thrust. The hunter carefully covered most of the hole with snow and tethered a bit of down over the remaining opening. Then, the hunter waited motionless in the frigid darkness, sometimes for hours. When the seal's arrival disturbed the down, the hunter struck downward with all his weight. If he speared the seal, he held fast to the line connected to his harpoon's point; the seal soon tired and could be hauled onto the ice (20).

During the high summer, the Central Inuit used the leister, a special three-pronged spear with a sharp central spike and two hinged, backward-facing points, to harvest Arctic char in large numbers. Later in summer and the fall, they shifted to caribou hunting. On land, caribou were mainly stalked or driven into ambush, and kills had to be made from a substantial distance. This required a bow with the power to propel a heavy arrow at high velocity. The simplest way to accomplish this is to make a long bow using a dense elastic wood like yew or osage orange, a design common in South America, Eastern North America, Africa, and Europe. This solution was not available to the Inuit, who had only driftwood (mainly spruce), horn, and antler available. Instead, they made short bows and used every bowyer's trick to increase their power. A bow can be made more powerful by adding wood to the limbs. However, making the bow thicker increases the stress within the bow, leading to catastrophic and dangerous failure. This problem is exacerbated in short bows because the curvature is greater. Instead, the Inuit made bows that were thin front to back, wide near the center, and tapering toward the tips. These bows were also recurved, meaning that the unbraced bow formed a backward "C" shape. Bracing the bow leads to a compound curve, a geometry that stores more potential energy. Finally, the Inuit constructed a unique form of composite bow. When a bow is bent, the back (the side away from the archer) is stretched, whereas the belly (the side closer to the archer) is compressed. Wood, horn, and antler are stronger in compression than tension, so the ability of a bow to sustain strong bending forces can be enhanced by adding a material that is strong in tension to the back of the bow. In central Asia and western North America, sinew was glued to the back of the bow to strengthen short bows for use on horseback. The Inuit lashed a woven web of sinew to the backs of their bows, probably because they had no glues that would work in the moist, cold conditions of the arctic (21).

This sampler of Inuit lifeways represents only a tiny fraction of the immense amount of habitat-specific knowledge that is necessary for humans to survive and prosper in the Central Arctic. To stay warm and get enough to eat, you have to know how to make and use clothes, snow houses, lamps, harpoons, leisters, and bows. We have omitted other crucial tools like kayaks, dog sleds, and sun goggles, and of course, we have had to omit most of the details necessary to make and use the tools we did mention. Moreover, there is still much more you have to know to stay alive. Predicting storms, understanding the habits of game species, making baskets, building sledges, and managing dogs—all require extensive knowledge. Traveling on ice is essential, but also treacherous, and there is much to know about how the current temperature, recent weather, and the color and texture of the ice tell you where and when it is safe to travel. [Nelson (22) devotes four chapters to ice lore in his book on hunting among the Inupiaq of northern Alaska.]

So, here is the question: do you think that you could acquire all of the local knowledge necessary to survive in the arctic on your own? If superior cognitive ability alone is what allows humans to adapt to diverse habitats, then it should be possible. Moreover, to a first approximation, this is the only way that other animals have to learn about their environments—they must rely mainly on innate information and individual experience to figure out how to find food, build shelters, and in some cases to make tools. It is true that some species have simple traditions, probably maintained by learning mechanisms like stimulus enhancement and emulation. However, in every case, the traditions involve behaviors that individuals can and do learn on their own, or combine a handful of elements learned by multiple individuals (23). There are no convincing examples in which social learning allows the gradual cumulative cultural evolution of complex, locally adaptive behaviors that individuals could not learn on their own.

Could you make it? We don't think so.

Two different kinds of natural experiments support the intuition that forager adaptations are beyond the inventive capacities of individuals. The first, which might be called "the lost European explorer experiment," has been repeated many times during the past several centuries. Typically some explorers get stranded in an unfamiliar habitat in which an indigenous population is flourishing. Despite desperate efforts and ample learning time, the explorers die or suffer terribly owing to the lack of crucial information about how to adapt to the habitat. If they survive, it is often due to the hospitality of the indigenous population. The Franklin Expedition of 1845–1846 provides a good example (24). Sir John Franklin, a Fellow of the Royal Society and an experienced Arctic traveler, set out with two ships to explore the northern coast of North America and find the North West Passage. It was the best-equipped expedition in the history of British polar exploration, furnished with an extensive library, manned by a select crew, and stocked with a 3-y supply of food. The expedition spent the winter of 1846 at King William Island, where it became trapped in the ice. When food ran short, the explorers abandoned their ships and attempted to escape on foot. Everyone eventually perished from starvation and scurvy, perhaps exacerbated by lead poisoning from their tinned food.

King William Island is the heart of Netsilik territory, and the Netsilik have lived there for almost a millennium. King William Island is rich in animal resources—the main harbor is named *Uqsuqtuuq* which means "lots of fat." The British sailors starved because they did not have the necessary local knowledge and, despite being endowed with the same improvisational intelligence as the Inuit and having 2 y to use this intelligence, failed to learn the skills necessary to subsist in this habitat. Interestingly, the Norwegian explorer Roald Amundsen spent two winters on King William Island in 1903–1904. Amundsen sought out the Netsilik and learned from them how to make skin clothing, hunt seals, and manage dog sleds. He and his crew survived and completed the first successful traverse of the Northwest Passage. Later he would put these Inuit skills to good use in his race with Scott to the South Pole. Results from this lost European explorer experiment, and many others, suggest that intelligence alone is not enough. For a similar discussion of the ill-fated Burke and Wills expedition into the Australian outback, see ref. 25.

A second line of evidence comes from the loss of beneficial technologies in small, isolated populations. For instance, the Tasmanian tool kit gradually lost complexity after isolation from mainland Australia at the end of the Holocene (26). Other Pacific island groups have apparently lost useful technologies, such as canoes, pottery, and the bow and arrow (27). The best documented example comes from the isolated Polar Inuit of northwest Greenland. Explorers Elisha Kane and Isaac Hayes wintered with the Polar Inuit in 1853 and 1861, respectively, and reported that the Polar Inuit lacked kayaks, leisters, and bows and arrows and that their snow houses did not have the long heat-saving entryways that were seen among other Inuit populations. They could not hunt caribou, could only hunt seals during part of the year, and were unable to harvest arctic char efficiently, although char were plentiful in local streams (28). Apparently the population was struck by an epidemic in the 1820s that carried away the older, knowledgeable members of the group, and according to custom, their possessions had to be buried with them (29). The Polar Inuit lived without these tools until about 1862, when they were visited by a group of Inuit who migrated to Greenland from Baffin Island (28, 29). There is every reason to believe that these tools would have been useful between 1820 and 1862. The Polar Inuit population declined during this period, and the tools were immediately adopted once they were reintroduced. After their introduction, population size increased. It is also telling that the kayaks used by the Polar Inuit around the turn of the century closely resemble the large, beamy kayaks used by Baffin Island Inuit and not the small sleek kayaks of the West Greenland Inuit. Over the next half century the Polar Inuit kayak design converged back to the West Greenland design (30). If this inference is correct it means that for 40 years (nearly two generations) the Polar Inuit could have benefitted from the lost knowledge. Moreover, they collectively remembered kayaks, leisters, and bows and arrows, but did not know how to make them and could not recreate that knowledge.

Cultural Adaptation Is a Population Process

We think that this body of evidence rules out the idea that superior cognitive ability *alone* explains human adaptability; the ability to cumulatively learn from others must play a crucial role. Although advocates of the cognitive niche hypothesis focus on cognition, they do not ignore social learning. They argue that the ability to learn from others reduces the average cost of acquiring locally adaptive information. For example, Barrett et al. (13) write:

> Cognitive mechanisms underlying cultural transmission coevolved with improvisational intelligence, distributing the costs of the acquisition of nonrivalrous information over a much greater number of individuals, and allowing its cost to be amortized over a much greater number of advantageous events and generations. Unlike other species, cultural transmission in humans results in a ratchet-like accumulation of knowledge. (p 244)

On the surface this seems to be a logical argument. It may be costly for individuals using improvisational intelligence to discover locally adaptive information, but once it is acquired, others can get it by teaching or imitation at relatively low cost. As a result, social learning acts to spread the cost of innovations over all who benefit. Innovations accumulate, leading to an accumulation of knowledge.

However, this reasoning is mistaken. It is probably true that learning from others either by teaching or imitation is usually cheaper than learning on your own. It is like cheating on a test: you do as well as the person you copy from but avoid all that tedious studying. However, evolutionary models show that if this is the only benefit of social learning, there will be no increase in the ability of the population to adapt (31–34). This surprising result emerges from the coevolutionary processes that affect the kinds of behaviors that are available to imitate and the psychology that controls learning and imitation. These evolutionary models of social learning rest on two assumptions. First, the propensities to learn and to imitate are part of an evolved psychology shaped by natural selection. This means that the balance between learning and imitating will be governed by the relative fitness of the two modes of behavior—the average fitness of the population is irrelevant. When few individuals imitate, imitators will acquire the locally adaptive behavior with the same probability as individual learners. Because they do not pay the cost of learning, imitators have higher fitness, and the propensity to imitate spreads. As the number of imitators increases, some imitate individuals who imitated other individuals, who imitated other individuals, and so on until the chain is rooted in someone who extracted the information from the environment. As the fraction of imitators in the population increases, these chains extend further.

The second assumption is that the environment varies in time or space. This means that as chains of imitation get longer, there is a greater chance that the learner who roots the chain learned in a different environment than the current environment, either because the environment has changed since then or because someone along the chain migrated from a different environment. The upshot is that on average imitators will be less likely to acquire the locally adaptive behavior than learners. The propensity to imitate will continue to increase until this reduction in fitness exactly balances the benefit of avoiding the costs of learning. At evolutionary equilibrium, the population has the same average fitness as a population without any imitation. There will be no increase in the ability to adapt to varying environments, and cumulative cultural adaptation will not occur.

Although this treatment is very simple, the basic result holds in more realistic models. The primary insight that emerges from these models is that imitation is a form of free riding—imitators scrounge information without producing anything of value. Free riders increase until they destroy the benefits of free riding. Realistic levels of relatedness among models and imitators do not qualitatively change the result (34). The advocates of the cognitive niche hypothesis err because they take it as unproblematic that once a beneficial innovation arises, it will spread, and as a result, the capacities for imitation will be favored by selection. However, to understand the evolution of social learning psychology you have to know what is available to learn, and this in turn is affected by the nature of the learning psychology. If imitators are simply information scroungers, then they will spread until selection no longer favors imitation.

Thinking about the coevolution of the cultural pool of observable behavior and the genes that control the individual and cultural learning suggests that cultural learning can increase average fitness only if it increases the ability of the population to create adaptive information (32). The propensity to imitate evolves because it is directly beneficial to the individual, but it may, nonetheless, also benefit the population as a side effect. We have thought of three ways in which this could happen. First, cultural learning can allow individuals to learn selectively—using environmental cues when they provide clear guidance and learning from others when they do not. Second, cultural learning allows the gradual accumulation of small improvements, and if small improvements are cheaper than big ones, cultural learning can reduce the population's learning costs. Finally, by comparing "teachers" and learning selectively from those that seem most successful, "pupils" can acquire adaptive information without making any inferences based on environmental cues. If individuals acquire information from multiple teachers and recombine this information, this process can create complex cultural adaptations without any intelligence, save that required to distinguish among more- and less-successful teachers.

The ability to learn or imitate selectively is advantageous because opportunities to learn from experience or by observation of the world vary. For example, a rare chance observation might allow a hunter to associate a particular spoor with a wounded polar bear, or to link the color and texture of ice with its stability on windy days just after a thaw. Such rare cues allow accurate low-cost inferences about the environment. However, most individuals will not observe these cues, and thus making the same inference will be much more difficult for them. Organisms that cannot imitate must rely on individual learning, even when it is difficult and error prone. They are stuck with whatever information that nature offers. In contrast, an organism capable of cultural learning can afford to be choosy, learning individually when it is cheap and accurate, and relying on cultural learning when environmental information is costly or inaccurate. We have shown (32, 35) that selection can lead to a psychology that causes most individuals to rely on cultural learning most of the time, and also simultaneously increases the average fitness of the population relative to the fitness of a population that does not rely on cultural information. These models assume that our learning psychology has a genetically heritable "information quality threshold" that governs whether an individual relies on inferences from environmental cues or learns from others. Individuals with a low information quality threshold rely on even poor cues, whereas individuals with a high threshold usually imitate. As the mean information quality threshold in the population increases, the fitness of learners increases because they are more likely to make accurate or low-cost inferences. At the same time, the frequency of imitators also increases. As a consequence, the population does not keep up with environmental changes as well as a population of individual learners. Eventually, an equilibrium emerges in which individuals deploy both individual and cultural learning in an optimal mix. At this equilibrium, the average fitness of the population is higher than in an ancestral population lacking cultural learning. When most individuals in the population observe accurate environmental cues, the equilibrium threshold is low, individual learning predominates, and culture plays little role. However, when it is usually difficult for people to learn individually, the equilibrium threshold is high, and most imitate, even when the environmental cues that they do observe indicate a different behavior than the one they acquire by cultural learning. We take the evidence on Inuit adaptations as indicating that many of the problems that faced the Inuit are far too difficult for most individuals to solve. As a result, we interpret this logic as predicting that selection should have favored a psychology that causes individuals to rely heavily on cultural learning.

The ability to learn culturally can also raise the average fitness of a population by allowing acquired improvements to accumulate from one generation to the next. Many kinds of traits admit successive improvements toward some optimum. Bows vary in many dimensions that affect performance—such as length, width, cross section, taper, and degree of recurve. It is typically more difficult to make large improvements by trial and error than small ones for the same reasons that Fisher (36) identified in his "geometric model" of genetic adaptation. In a small neighborhood in design space, the performance surface is approximately flat, so that even if small changes are made at random, half of them will increase the payoff (unless the design is already at the optimum). Large changes will improve things only if they are in the small cone that includes the distant optimum. Thus, we expect it to be much harder to design a useful bow from scratch than to tinker with the dimensions of a reasonably good bow. Now, imagine that the environment varies, so that different bows are optimal in different environments, perhaps because the kind of wood available varies. Sometimes a long bow with a round cross section is best, other times a short flat wide bow is best. Organisms that cannot imitate must start with whatever initial guess is provided by their genotype. Over their lifetimes, they can learn and improve their bow. However, when they die these improvements disappear with them, and their offspring must begin again at the genetically inherited initial guess. In contrast, cultural species can learn how to make bows from others after these have been improved by experience. Therefore, cultural learners start their search closer to the best design than pure individual learners and can invest in further improvements. Then, they can transmit *those* improvements to the grandkids, and so on down through the generations until quite sophisticated artifacts evolve. Historians of technology have demonstrated how this step-by-step improvement gradually diversifies and improves tools and other artifacts (37, 38). Even "great insights" often result from lucky accidents or the recombination of elements from different technological traditions rather than the work of a creative genius who buckles down and racks his brain (39, 40).

The evolution of kayak keels by West Greenland Inuit provides an instructive example of how innovations arise and spread (41). When hunting marine mammals from a kayak, Inuit hunters always paddled their kayak hard toward the prey, then picked up their harpoon and hurled it directly over the bow. This increased the momentum transferred to the harpoon and prevented capsizing. When firearms first spread in West Greenland, the Inuit found that they could not pick up and aim their guns before the kayak veered off course, and thus could only use them from land or ice floes. In 1824, a prominent Inuit hunter named Jens Reimer began to experiment with methods to stabilize kayaks for firearm use. He tried trailing a line behind the kayak, but this did not work. He then fastened a partially submerged wooden plate to the kayak's stern, in imitation of the rudders of European ships. This did not work very well either—it was noisy, and the fastenings tended to fail. Nonetheless, a number of younger hunters imitated Reimer, perhaps owing to his local success and prestige. They were not able to produce a quality *ayût* (the Greenlandic word for both a ship's rudder and a kayak keel), and out of "bashfulness" (41, p 27) hid their crude rudders under the waterline. They soon discovered that this unintentional innovation allowed them to use guns from their kayaks, and over the next 50 y the *ayût* underwent a series of further small improvements, eventually creating the modern form.

Finally, if learners can compare the success of individuals modeling different behaviors, then a propensity to imitate the successful can lead to the spread of traits that are correlated with success, even though imitators have no causal understanding of the connection. This is obvious when the scope of traits being compared is narrow. You see that your uncle's bow shoots farther than yours and notice that it is thicker, but less tapered, and uses a different plait for attaching the sinew. You copy all three traits, even though in reality it was just the plaiting that made the difference. As long as there is a reliable statistical correlation between plaiting and power, plaiting form trait will change so as to increase power. Causal understanding is helpful because it permits the exclusion of irrelevant traits like the bow's color. However, causal understanding need not be very precise as long as the correlation is reliable. Copying irrelevant traits like thickness or color will only add noise to the process. By recombining different components of technology from different but still successful individuals, copiers can produce both novel and increasingly adaptive tools and techniques over generations, without any improvisational insights. An Inuit might copy the bow design from the best bowyer in his community but adopt the sinew plaiting used by the best hunter in a neighboring community. The result could be a better bow than anyone made in the previous generation without anyone inventing anything new.

Consistent with this, laboratory and field evidence suggests that both children and adults are predisposed to copy a wide range of traits from successful or prestigious people (42). Advertisers clearly know this. After all, what does Michael Jordan really know about underwear? Recent work in developmental psychology shows that young children readily attend to cues of reliability, success, confidence, and attention when choosing who to learn from (43, 44). Even infants selectively attend to knowledgeable adults rather than their own mothers in novel situations (45). This feature of our cultural learning psychology fits a priori evolutionary predictions, emerges spontaneously in experiments, develops early without instruction, and operates largely outside conscious awareness.

These models predict that an adaptive evolved psychology will often cause individuals to acquire the behaviors they observe used by in others even though inferences based on environmental cues suggest that alternative behaviors would be better. In a species capable of acquiring behavior by teaching or imitation, individuals are exposed to two different kinds of cues that they can use to solve local adaptive problems. Like any other organism, they can make inferences based on cues from the environment. However, they also observe the behaviors of a sample of their population. When most individuals can solve the adaptive problem using environmental cues alone, the models predict that an optimal learning psychology will result in social learning playing a significant but relatively modest role. Many people will rely on their own inferences, but some will copy to avoid learning costs. However, often only a minority will be able to solve the adaptive problem on the basis of environmental cues alone, because the appropriate environmental cues are rare or the adaptive problem is too complex. Then, if the environment is not too variable, an adaptive psychology will evolve in which most people ignore environmental cues and adopt behaviors that are common in the sample of the population they observe. They modify these behaviors rarely, or only at the margin, and as a result local adaptations evolve gradually often over many generations.

Evidence for Cultural Adaptation

The cultural niche hypothesis and the cognitive niche hypothesis make sharply different predictions about how local adaptations are acquired and understood. The cognitive niche hypothesis posits that technologies are adaptive because improvisational intelligence allows some individuals to figure out how they work and why they are better than alternatives. These acquired understandings of the world are then shared, allowing others to acquire the same causal understanding without costly individual investigation. In contrast, we argue that cultural evolution operating over generations has gradually accumulated and recombined adaptive elements, eventually creating adaptive packages beyond the causal understanding of the individuals who use them. In some cases elements of causal understanding may be passed along, but this is not necessary. Often individuals will have no idea why certain elements are included in a design, nor any notion of whether alternative designs would be better. We expect cultural learners to first acquire the local practices and occasionally experiment or modify them. At times this will mean that cultural learning will overrule their direct experience, evolved motivations, or reliably developing intuitions.

Several lines of evidence support the cultural learning hypothesis.

The anthropological literature on child development (46–48) indicates that children and adolescents acquire most of their cultural information by learning from older individuals who typically discourage questions from young learners and rarely provide causal explanations of their behavior. Kids practice adult behaviors, often using toy versions of adult tools, during mixed-age play, and little experimentation is observed, except that necessary to master the adult repertoire (49, 50).

The reliance of young learners on carefully observing and imitating the local repertoires revealed in the anthropological record converges with recent experiments on imitation (51, 52). In these experiments, an adult performs a behavior like opening a complex puzzle box to get a reward. The adult's behavior includes both necessary and unnecessary actions. A subject, either a child or a chimpanzee, observes the behavior. Children's performance on such tasks in both western and small-scale societies differs in important ways from that of chimpanzees. Children accurately copy all steps, including steps that direct visual inspection would suggest are unnecessary. Children seem to implicitly assume that if the model performed an action, it was probably important, even if they do not understand why. Chimpanzees do not seem to make this assumption; they mainly skip the unnecessary steps, leading them to develop more efficient repertoires than children (53) in these experimental settings.

Many examples indicate that people often do not understand how adaptive practices work or why they are effective. For example, in the New World, the traditional use of chili peppers in meat recipes likely protected people from food-borne pathogens (54). This use of chili peppers is particularly interesting because they are inherently unpalatable. Peppers contain capsaicin, a chemical defense evolved in the genus *Capsicum* to prevent mammals (especially rodents) from eating their fruits. Nonhuman primates and human infants find peppers aversive because capsaicin stimulates pain receptors in the mouth. Efforts to inculcate a taste for chilies in rats using reinforcement procedures have failed (55). However, human food preferences are heavily influenced by the preferences of those around us (56), so we overcome our innate aversion and actually learn to enjoy chilies. Psychological research indicates that people do not get accustomed to the chemical burning sensation. Instead, observational learning leads people to reinterpret their pain as pleasure or excitement (57). So, New World peoples learned to appropriately use and enjoy chili peppers without understanding their antimicrobial properties, and to do this they had to overcome an instinctive aversion that we share with other mammals.

Fijian food taboos provide another example of this process. Many marine species in the Fijian diet contain toxins, which are particularly dangerous for pregnant women and perhaps nursing infants. Food taboos targeting these species during pregnancy and lactation prohibit women from eating these species and reduce the incidence of fish poisoning during this period. Although women in these communities all share the same food taboos, they offer quite different causal explanations for them, and little information is exchanged among women save for the taboos themselves (58). The taboos are learned and are not related to pregnancy sickness aversions. Analyses of the transmission pathways for these taboos indicate the adaptive pattern is sustained by selective learning from prestigious women.

Culture and Maladaptation

Cultural adaptation comes with a built-in tradeoff. The cumulative cultural evolution of complex, hard-to-learn adaptations requires individuals to adopt the behavior of those around them even if it conflicts with their own inferences. However, this same propensity will cause individuals to acquire *any* common behavior as long as it is not clearly contradicted by their own inferences. This means that if there are cognitive or social processes that make maladaptive ideas common, and these ideas are not patently false or harmful, people will adopt these ideas as well. Moreover, it is clear that several such processes exist. Here are a couple of examples. For a longer discussion, see ref. 10.

Weak Cognitive Biases Can Favor the Spread of Maladaptive Beliefs or Practices over Generations. Laboratory diffusion chain studies clearly document that biases that have undetectable effects on individual decisions can have very strong effects when iterated over "generations" in the laboratory (59). The same effect may lead to the spread of false beliefs in natural populations. For example, Boyer (60) argues that a number of cognitive biases explain the spread of supernatural beliefs and account for the widespread occurrence of folktales about ghosts and zombies.

Adaptive Social Learning Biases Can Lead to Maladaptive Outcomes. A model's attributes provide indirect evidence about whether it is useful to imitate her. If she is successful, then by imitating her you can increase your chances of acquiring traits that gave rise to her success. If she is more similar to you than alternative models, her behavior may work better in your situation. If her behavior is more common than alternatives, then it is likely to be adaptive because learning increases the frequency of adaptive behaviors. An evolved cultural learning psychology that incorporates such biases increases the chance of acquiring beneficial beliefs and behaviors. However, these same biases can sometimes lead to the spread of maladaptive beliefs and practices. For example, the tendency to imitate the prestigious, or those making credibility-enhancing displays of commitment, can lead to a "runaway" process analogous to sexual selection (10), and this may explain the cultural evolution of maladaptive cultural systems in which people risk life and limb to summit icy peaks or achieve spiritual perfection in celibate seclusion (61).

Culture Is Part of Human Biology and Has Profoundly Shaped Human Evolution

We have recounted two contrasting accounts of the nature and origins of human uniqueness. On the one hand, there is a widespread view is that people are like other mammals, just a lot smarter—in essence, we are brainy, hairless chimpanzees. We have a uniquely flexible cognitive system that lets us make causal inferences in a wide range of environments and use that information to create much better tools, and these differences have allowed us spread across the world, dominating the world's biota like no other creature. By contrast, we argue that individuals are not nearly smart enough to solve the myriad adaptive problems they face in any of their many habitats. Even experts lack a detailed causal understanding of the tools and techniques that permit them to survive. High-fidelity cultural learning allows human populations to solve these problems because it allows selective learning and the accumulation of small improvements over time. Of course, sophisticated, flexible cognition is important too. However, the degree of cognitive flexibility varies widely in nature—chimpanzees can solve problems that baffle monkeys, and monkeys are geniuses compared with opossums. Nonetheless, no species occupies as wide a range of habitats as *Homo sapiens*. In contrast, there is a sharp break between human cultural learning capacities and those of even our closest relatives. As a result, it is more apt to think of humans occupying a cultural niche than a cognitive niche.

The evolution of the psychological capacities that give rise to cumulative cultural evolution is one of the key events in our evolutionary history. The availability of large amounts of valuable cultural information would have favored the evolution of bigger brains equipped to acquire, store, organize, and retrieve cultural information, a fact that may explain the rapid increase in human encephalization over the last 500,000 y and the evolution of specialized cognitive abilities that emerge early in life, such as theory of mind, selective social referencing (45), overimitation (52), a functional understanding of artifacts (62), and the use of taxonomic inheritance and category-based induction for living kinds (63). The presence of culturally evolved techniques and products—such as fire, cooking, weapons, and tools—created new selection pressures acting on our bones, muscles, teeth, and guts (9).

Culture has opened up a vast range of evolutionary vistas not available to noncultural species. Nonetheless, culture is as much a part of human biology as our peculiar pelvis. This approach contrasts with the common view that culture and biology are in a tug-of-war for control of human behavior. This common view probably taps into a deep vein of Western thought, which itself may be the result of evolved cognitive biases (64), but it makes little sense. The ancestral condition in the human lineage is a psychology that does not permit cumulative cultural evolution. Despite earnest efforts, chimpanzees cannot be socialized to become humans and have little or no cumulative cultural evolution. Beginning early in human ontogeny, our psychology allows us to learn from others, powerfully and unconsciously motivates us to do so, and shapes the kind of traits that evolve. So it does not make sense to ask, does culture overcome biology? The right question to ask is, how do genetic and cultural inheritance interact to produce the observed patterns of human psychology and behavior (65)?

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