

Gene-culture coevolution in the age of genomics

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The use of socially learned information (culture) is central to human adaptations. We investigate the hypothesis that the process of cultural evolution has played an active, leading role in the evolution of genes. Culture normally evolves more rapidly than genes, creating novel environments that expose genes to new selective pressures. Many human genes that have been shown to be under recent or current selection are changing as a result of new environments created by cultural innovations. Some changed in response to the development of agricultural subsistence systems in the Early and Middle Holocene. Alleles coding for adaptations to diets rich in plant starch (e.g., amylase copy number) and to epidemic diseases evolved as human populations expanded (e.g., sickle cell and *G6PD* deficiency alleles that provide protection against malaria). Large-scale scans using patterns of linkage disequilibrium to detect recent selection suggest that many more genes evolved in response to agriculture. Genetic change in response to the novel social environment of contemporary modern societies is also likely to be occurring. The functional effects of most of the alleles under selection during the last 10,000 years are currently unknown. Also unknown is the role of paleoenvironmental change in regulating the tempo of hominin evolution. Although the full extent of culture-driven gene-culture coevolution is thus far unknown for the deeper history of the human lineage, theory and some evidence suggest that such effects were profound. Genomic methods promise to have a major impact on our understanding of gene-culture coevolution over the span of hominin evolutionary history.

cultural evolution | human evolution | Pleistocene | recent selection

The human cultural system supports the cumulative evolution of complex adaptations to local, often ephemeral environments. Using elaborate technology and depending on large bodies of cultural knowledge about plants and animals, stone-age foragers spread to a much wider range of habitats than any other mammal, from the frigid tundra in the Arctic to the arid deserts of Australia. The Polynesian outrigger canoe and the Arctic kayak are examples of the astoundingly sophisticated cultural adaptations that people have used to occupy distant corners of the globe. The forms of social organizations observed in humans are more diverse than the rest of the primate order combined. Humans constitute one of the world's most impressive adaptive radiations. We have occupied virtually every habitat on earth by using technology and social organization to generate thousands of socioeconomic systems (1, 2).

Cultural Evolution and Gene-Culture Coevolution

Culture has many definitions, but for our purposes a useful one is all of the information that individuals acquire from others by a variety of social learning processes including teaching and imitation (3). Transmission fidelity is often sufficiently high for culture to act as an inheritance system (4). We commonly observe that the ideas, practices, skills, attitudes, norms, art styles, technology, ways of speaking, and other elements of culture change through time, but we also see that persistent traditions exist. The English of Shakespeare is plainly a recent ancestor of the language spoken in England today, but modern English speakers cannot fully appreciate his plays without some knowledge of the differences between Elizabethan and modern English. Culture is thus a system of descent with modification. The idea that culture is fundamentally a kind of inheritance system

that can be investigated using “population thinking” has been very productive. It led evolutionary theorists to model cultural evolutionary process by drawing tools and inspiration from fields as diverse as population genetics, epidemiology, ecology, game theory, and stochastic processes (3, 5).

Those familiar with genetic evolution may be aided by considering some of the similarities and differences between genetic and cultural evolution. Key differences include the nature of forces that act on cultural transmission, the observed patterns of transmission, and the relative rates of adaptation. Several of the forces that act on cultural variation to cause cultural evolutionary change include ones familiar to evolutionary biologists, such as random errors in teaching or acquiring items of culture (mutation), statistical effects in small populations (drift), and the effects on an individual's life chances as a consequence of using different cultural variants (natural selection). Other forces on cultural evolution are distinctive and derive from the fact that the acquirers of culture, even infants, are choice-making agents. People can to some extent pick and choose from among the different cultural variants they observe. Assuming their choices are not random, this creates a variety of bias forces that can be defined by how the choices are made (6). Humans also selectively transmit variants that they have learned to their offspring and to others. We call such psychological processes “decision-making forces.” Parent-offspring transmission dominates much (although not all) genetic transmission. In contrast, evidence on transmission patterns from a variety of sources indicates that individuals, including both children and adults, learn from a large, dynamic social network including parents, siblings, peers, and a wide range of others. The social learner uses biases that focus attention on those who tend to be same-sex, same-ethnicity, older, successful, prestigious, and available in order to accumulate a cultural repertoire from their social networks (7–9). Humans also generate new variants by nonrandom processes such as individual learning and creative thinking.

Field evidence on adaptive rates shows that they can be much faster for cultural evolution compared with genetic evolution (1, 10). For example, when American sweet potatoes tolerant of cool weather became available to the peoples of Highland New Guinea, the new crop set off a population explosion and a spurt of parallel social and economic innovations in a number of Highland societies (11). Attractive gadgets, such as mobile phones, have been taken up avidly around the contemporary world, and many of them lead to important knock-on cultural changes. The upshot of the differences between cultural and genetic evolution is that cultural evolution is inherently faster than genetic evolution.

Converging lines of evidence from many disciplines indicate that our psychological capacities for cultural learning evolved as an

This paper results from the Arthur M. Sackler Colloquium of the National Academy of Sciences, “In the Light of Evolution IV: The Human Condition,” held December 10–12, 2009, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. The complete program and audio files of most presentations are available on the NAS Web site at www.nasonline.org/SACKLER_Human_Condition.

Author contributions: P.J.R., R.B., and J.H. designed research, performed research, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0914631107/DCSupplemental.

adaptation to temporally and spatially variable environments (12, 13). By adding bias forces and the transmitted effects of individual learning to random variation and natural selection, the cultural system can more rapidly track changing environments than can genes alone, albeit at some considerable cost in maintaining a large brain to support the cultural system (3, 14). Fast change also leads to large differences between neighboring societies, an important consideration for the evolution of human sociality (1). Even the most sophisticated social learners among other species, such as chimpanzees, are poor social learners compared with young children (15). Recently, empirical investigations of cultural transmission and evolution have become common (e.g., 7, 16–18) and much work in linguistics (19, 20), applied psychology (21), and many other social scientific and historical investigations give convincing evidence of cultural evolution.

Cultures create novel environments that lead to new pressures from natural or social selection on genes (1). [We include here the effects of niche construction (22) insofar as modifications of the environment are rooted in culturally transmitted technology or social institutions.] To some degree, human culture is like any system of phenotypic flexibility. It has evolved to respond to environmental variation, allowing genes to be spared natural selection. Many elements of the biology of complex organisms such as humans act as mechanisms of phenotypic flexibility (23). For example, many developmental processes have an element of random variation and selective retention. Nerve axons grow prolifically and are pruned if they do not find appropriate targets. Like other systems for the inheritance of acquired variation, culture can play an active role in evolution through what is known as the Baldwin effect (24, 25). Systems for phenotypic flexibility, if they are adaptive, will generate phenotypes that tolerate small environmental changes and small genetic departures from current optima. Near-selective optima, mechanisms of phenotypic flexibility, shelter near-optimal genetic variants from selection. But away from selective optima, phenotypic flexibility has the opposite effect. By making survival and reproduction possible in novel environments, a system of phenotypic flexibility can expose genes to selection. Thus, presumably, the anatomically modern human populations that left tropical Africa to invade temperate and periglacial environments in Eurasia adapted first to them using clothing, shelter, and fire, but later also evolved husky physiques and lighter skin pigmentation adapted to cold temperatures and low light (26).

Genes and culture resemble a symbiosis—two inheritance systems occupying the same physical body. The cultural partner can create complex adaptations rapidly compared with the genetic partner. As cultural adaptations became important, much could be gained from imitating a seemingly successful idea or practice. If people can judge what is successful, or who is successful, new adaptive variation can rapidly spread through an entire population, sometimes within one generation. This ability might have been particularly important in glacial climates that were extremely variable on timescales ranging from a generation to a few tens of generations. Theoretical models suggest that such variation should favor the evolution of a cognitively costly system of cultural adaptation (13). When variation has smaller amplitudes or longer timescales, selection causes genetic variation to track environmental changes at a lesser cost. When variation is strong at timescales of a generation or less, individual learning and other nontransmitted mechanisms for phenotypic flexibility will be favored by selection. The human genome and its associated biology provide a large brain, anatomic modifications for speech, and no doubt a large number of other genetically coded mechanisms that enable humans to host a fancy cultural system (3). At the same time, complex cultural systems will tend to adapt to genetically constrained cognitive capacities so as to be learnable and useful. Cultural adaptation to constrained cognition has recently been argued to be the case for language acquisition (27) and reading (28).

Coevolutionists debate whether cultural evolution was largely controlled by selection acting on genes or whether cultural evolution often played the leading role during human evolution. For example, Wilson (29) argues that epigenetic rules controlled cultural evolution until the latest Pleistocene or Holocene. In contrast, we have argued that cultural evolution has played a large role in shaping human genes. For example, group selection on cultural variation plausibly played a leading role in the evolution of genes underpinning our unusual social systems, including cooperative breeding and cooperation among distantly related individuals (1, 30). Theory suggests that variation between groups can more easily be created in the cultural than the genetic system, and this prediction has some empirical support (18). Did natural selection first create capacities for culture for noncultural reasons after which cultural evolution began, as Ayala (31) argues for systems of morality, or did culture commonly play leading roles in gene-culture coevolution, even in the evolution of the earliest hominins? Perhaps human nature itself is substantially a product of cultural evolution influencing human genetic evolution by a systematic, large-scale Baldwin effect.

Gene-Culture Coevolution in Hominin History

Wood (32) provides an outline of human evolution. Studies of living apes (e.g., 33) suggest that culture has been at least a minor part of hominin capabilities since our last common ancestor with chimpanzees. Culture-led gene-culture coevolution thus potentially has a deep history in our lineage. Later, cultural evolution led to innovations in technology that, for example, made scavenging and hunting of meat productive. Ample meat and fat in diets, together with cooking, would have supported the evolution of larger, more expensive brains (34–37), leading to still-more sophisticated technology that eventually led to humans becoming specialized hunters of big game during the last couple of glacial cycles (38). After 11,500 years ago, as the highly variable climates of the last ice age gave way to the much less variable climates of the Holocene, plant resources began to be exploited intensively in many parts of the world. Agriculture progressively became the dominant subsistence system in most parts of the world (39). At the same time, human social organization was revolutionized. Evidence reviewed below shows that agricultural subsistence led to many genetic changes, but evidence regarding older episodes of coevolution is still scanty.

The idea that cultural variation fell under group selection at the scale of tribes is a modernization of a hypothesis first proposed by Darwin in the *Descent of Man* (40). Our last common ancestor with the other apes presumably had a social system based on dominance, with no provisioning of offspring beyond mother's milk. Cooperative breeding seems to have been essential to provide food supplements to mothers and juveniles to support the expansion of brains (41). In anatomically modern humans, at least to judge by well-studied ethnographic examples, adult male hunters produced a large surplus of meat and fat that was channeled to women and children (36, 42). To reduce the risk of big-game hunting, males cooperated in band-sized units including several good hunters. Bands were flexible units within a larger ethnolinguistic tribe from which bands drew members, partly but not entirely along kinship lines. As populations increased with the evolution of plant-intensive foraging and agriculture, population densities increased and social sophistication increased still further, leading to formal political systems (advanced chiefdoms and small states) by the Middle Holocene and to large states and empires in the classical period (43). Somewhere along this trajectory of increasing social sophistication, humans developed a social psychology organized around culturally acquired social rules (“norms” to psychologists, “institutions” to sociologists) (44). People came to take on social identities that tied them emotionally to their social groups (45). We became exquisitely sensitive to social boundaries symbolically marked by language,

dress, ritual, and other stylistic differences between “us” and “them” (ref. 8, chap. 9, 4647–48).

The paleoanthropological record is seriously deficient, as fossil records always are. Many forms of technology are very rarely preserved, including those made of wood, organic fibers, and leather. Usage wear on stone tools suggests that they were often used to make such products. Very rare finds, such as three aerodynamically sophisticated wooden javelins from an anaerobic deposit in Germany dating to 400 kya (49), suggest that relying entirely on stone artifacts to deduce the technical sophistication of archaic humans is potentially misleading. Inferring the sizes of human populations from the paleoanthropological record is also difficult. Demography is important because cumulative cultural sophistication advances further and faster in large interconnected than in small isolated populations (50, 51). Thus, human populations with identical spectra of individual cognitive ability can produce sophisticated or simple tools, depending upon effective population size. Exogenous controls on human populations from climate and competition with other species may be important. For example, in southern Africa between 70 and 80 kya, two short episodes with more sophisticated artifacts punctuate a long record with the less sophisticated Middle Paleolithic artifacts, perhaps because of population boom-and-bust events (52, 53). Immediately after anatomically modern humans left Africa, most populations seem to have been making Middle Paleolithic artifacts but, a short time later, the Upper Paleolithic peoples of western Eurasia made sophisticated tools and produced a large corpus of art (54) of a complexity only observed in some of the most complex ethnographically and historically known foraging populations.

Thus, the four most obvious indices of human cognitive complexity, brain size, ability to colonize a wide range of environments, stone tool complexity, and artistic productions, are only very imperfectly correlated, for reasons that remain enigmatic. Inferences about past behavior and social organization are necessarily based on slim evidence. Some authors argue that even quite ancient hominins had modern behavior (55). For example, Lovejoy suggests that the reduced canines of *Ardipithecus ramidus*, a form thought to be close to the last common ancestor with the other apes, indicate important social innovations very early in our lineage (56). At the other extreme, Klein (ref. 57, pp. 652–653) argues that at least one major social or cognitive modernization must have precipitated the exodus of anatomically modern humans out of Africa quite late in our evolutionary history. Both of these claims are controversial. Although the hypothesis that fast cultural evolution should have driven the gene-culture coevolutionary process is plausible on theoretical grounds, the fact is that the large brain of anatomically modern humans *predates* the Upper Paleolithic cultural system by perhaps 150 kya. Perhaps chronically low population densities prevented the cumulative cultural evolution of highly complex tools and symbolic behavior that characterize the Upper Paleolithic and Later Stone Age (51). Favorable circumstances that allowed more substantial populations, particularly in western Eurasia after 40 kya and more generally in the Holocene, may have allowed anatomically modern humans to create highly elaborated cultures much along the line of Ayala's (31) hypothesis about morality. Our hypothesis that culture was generally the leading rather than the lagging variable in the coevolutionary system may not always (or ever) be correct, even late in hominin evolution. Genomic data promise to have a large impact by shedding light on questions that are difficult to resolve with traditional methods.

New Genomic Tools

Whereas paleoanthropologists will make slow progress in solving the many riddles hinted at in the preceding section, the genomics revolution, made possible by the rapidly falling cost of se-

quencing genomes, is providing important new tools. These methods promise two important contributions. First, they already help us to better understand paleodemography (58). Second, genomic methods can be used to estimate where and when selection has occurred in the human genome.

Mitochondria and autosomal lineage coalescence times record some evidence of past genetic bottlenecks. When population sizes are small, genetic diversity is lost by drift. If a population increases suddenly, as the hominin population did when anatomically modern humans expanded out of Africa, then a larger number of genes will have coalescence times indicating the time when the human population became large enough to sustain higher diversity. Coalescence times are older for autosomes than for mitochondria or Y chromosomes in part because the effective population size for diploid autosomes is four times the size of the population of maternally transmitted haploid mitochondria or paternally transmitted Y chromosomes (59).

Studies of the mitochondrial and autosomal genomes have given an interesting picture of the demographic expansion out of Africa. A succession of population bottlenecks caused decreasing genetic diversity farther away from our ancestral African homeland (60–64). The populations most distant from one another, measured by the length of the most likely migration path from Africa, are most distant from one another genetically. Thus, the picture of the genetic architecture of human populations derived from molecular methods bears a strong resemblance to that derived from classical human genetics (65). Africans maintain the most genetic diversity, and the most distant migrants out of Africa retain the least due to successive bottlenecks. Selective sweeps and genetic drift have similar effects on the genome, so the most efficient estimation methods for dating selective sweeps are those which use selectively neutral variation to estimate population sizes and control for the effects of drift. The effects of selection on potentially nonneutral variation are then apparent as departures from expectations based on a neutral model (66, 67). To this point, limitations in the size and nature of the samples of sequenced human DNA do not allow high confidence in either the population or selection reconstructions. The continuing fall in the costs of sequencing will increase sample sizes and coverage, and statistical methods will most likely continue to improve as well.

Sabeti et al. (68) review the methods for detecting the action of selection on the genome on various timescales. On the longest timescales, selection is evidenced by functionally significant differences between species. For example, the *FOXP2* gene has two functionally significant differences between humans and chimpanzees. Preliminary sequences of Neandertal DNA suggest that we share these two changes with that species, thus placing the evolution of these changes before the separation of the two species several hundred thousand years ago (but see a discussion of problems with this interpretation below). Selective changes will show an excess of changes at sites that change amino acids of proteins compared with synonymous sites that do not. At shorter timescales, less than ~250 kya, positive selection leaves a signature of reduced diversity in genes linked to the target of the selective sweep due to hitchhiking. Mutation and drift eventually restore this diversity, but in the meantime an excess of rare alleles in the linked region provides an estimate of the timing of the selective sweep. At time scales < ~80 kya, the linked region will contain an excess of derived alleles that have hitchhiked to high frequency along with the allele that was the target of selection. As human populations left Africa and became exposed to divergent selection in different environments and cultures, different alleles will be swept to high frequency in different populations (< ~60 kya). Even if selection pressures are the same in different populations, and an allele with the same function is selected in different populations, the alleles in the different populations are likely to contain neutral differences in

sequence. The *LCT* regulatory gene down-regulates the secretion of lactase postweaning in most human populations. In western Eurasian and African dairying populations the gene is rendered nonfunctional, so that adults continue to secrete lactase and to benefit from lactose. Sequencing of the adult secretion variants of *LCT* from western Eurasia and Africa revealed that they were dysfunctional in different ways (69). Finally, at time scales < ~30 kya, the linked hitchhiking region around the selected allele will not have been subject to recombination for a time-dependent length of sequence. The whole haplotype will be monomorphic for a certain distance. Thus, the *LCT* gene, which evolved after the evolution of dairying ~5,000 years ago, is associated with a long monomorphic haplotype. Recombination reduces linkage disequilibrium around the selected allele over time, providing a rough estimate of the time of the sweep.

Akey (70) has reviewed the promise and pitfalls of DNA sequence methods based on 21 genome-wide scans for alleles under selection. To assess the reliability of these methods, Akey compared eight genome-wide scan studies using the Hapmap and Perlgen databases. The eight studies reported a total of 5,110 distinct regions under selection, but only 14.1% were identified in two or more studies and 2.5% in four or more. Nevertheless, he finds grounds for cautious optimism. First, many of the genes that occur in multiple studies have already been firmly identified as under selection, such as the *LCT* gene. Second, many of the genes under selection exhibit geographical differences. Because humans have recently spread from a tropical African homeland to the rest of the world, it is plausible that many genes have experienced divergent selection in the last 60,000 years. Evolution during this period is relatively easy to detect and many alleles under recent selection should be adaptations to the new local environments into which humans were dispersing. Significant issues remain. Some reflect the small and possibly nonrepresentative sample of genomes available for study. This defect will be remedied fairly rapidly. Statistical methods for detecting selection are also likely to improve dramatically (71). A deeper difficulty is the lack of understanding from genomics alone about the phenotypic effects of the genes that selection has targeted. In the case of genes with strong and direct phenotypic effects, such as *LCT*, *HBB* (the sickle cell gene), other genes coding for resistance to malarial, skin pigmentation genes, and a few others, a functional understanding of the genes preceded genomic analysis, which has added only wrinkles to the classic stories. Presumably, many of the genes under selection are quantitative trait loci in which selection for a given phenotype will exert weak selection at many loci. Functional annotations for genes that are transcribed into proteins give only general hints about the function of the particular alleles that have been selected in the human lineage. We do not seem to have any substitute for functional studies targeted on sequences that have apparently undergone recent selection to understand why they might have come under selection. To advance rapidly on a broad front will require the same sorts of high-throughput methods that have revolutionized genomics also be applied to the expression of genes during development, on the model of ChIP-on-chip technology, which is still in its infancy as far as vertebrate epigenomics is concerned.

Studies of the *FOXP2* gene provide a cautionary tale, exemplifying our still-primitive understanding of the connection between genotypes and phenotypes (72, 73). This gene, coding for a regulatory protein, has apparently been under strong selection since the last common ancestor with the other apes. Two amino acid substitutions have taken place in the hominin lineage. Early reports from a study of language deficits in a family with a rare *FOXP2* mutant suggested to some that it is a grammar gene. However, it turns out to be a highly conserved gene that is expressed in a wide variety of tissues during vertebrate development. In the brain, a ChIP study shows that it down-regulates

CNTNAP2, the gene encoding contactin-associated protein-like 2, a member of the neurexin superfamily. This gene is involved with cell recognition and cell adhesion, playing a role in nervous system development, including in the human frontal cortex during mid-development. Hence, it is expressed in tissues that may well relate to language abilities. However, other studies identified several hundred other potential targets of *FOXP2* as though it plays a role in many regulatory circuits during development.

The timing of the evolution of the common human *FOXP2* allele has also proven perplexing. The region near the substitutions in the derived human gene contains a high frequency of derived neutral variants that have not been disrupted by recombination, suggesting that the second of the two human substitutions on the gene must have taken place in the last 130 kya (73). On the other hand, Krause et al. (74) sequenced Neanderthal DNA and recovered the same genotype as modern humans, implying that the modern human allele evolved more than 300 kya. Several hypotheses have been proposed to explain this puzzle. They include (i) laboratory artifacts, (ii) introgression between Neanderthals and anatomically modern humans (75), and (iii) the possibility that the two amino acid substitutions are ancient, and that the linkage disequilibrium observed in modern humans arose from recent selection on a nearby gene rather than on *FOXP2* itself (73, 76). Thus, although the promise of genomics and related high-throughput techniques to study human evolution is high, human biology, evolutionary history, and extant population structure are all intimidatingly complex. Not every problem will be quickly solved, and many analytical improvements are needed.

The External Selective Environment

The role of culture in adapting to temporal and spatial environmental variability has long been an important theme in gene-culture coevolution theory (77–79). Environmental change over the course of hominin evolution has been substantial. Climate variation correlated with variations in Earth's orbit has progressively increased and shifted from the dominance of the 23-kyr (precession) cycle in the Miocene and Early Pliocene to the dominance of the 41-kyr (tilt) cycle from the Middle Pliocene through the Early Pleistocene, and finally to the dominance of the 100-kyr cycle (eccentricity) during the Middle and Late Pleistocene. The Middle Pliocene shift roughly correlates with the appearance of our genus, *Homo*, and the evolution of progressively larger-brained and technically more sophisticated humans occurs after the mid-Pleistocene shift (80). Variation on the orbital timescales (900+ human generations) probably has little direct impact on the gene-culture system. The higher-frequency components of climate variation, which are perhaps correlated with the lower-frequency orbital scale fluctuations, are likely to be much more important. High-resolution ice cores from Greenland first revealed that high-frequency, high-amplitude submillennial and millennial variation (1–100 human generations) occurred during the last ice age (81). Long high-resolution ocean cores suggest that the tempo of this variation has increased over the last four cycles (82). High-resolution paleoclimate data for the whole course of hominin evolution would be very interesting but do not yet exist.

The models of gene-culture coevolution described above, which predate the high-resolution paleoclimate data, suggest that a cognitive capacity to support a costly system for cultural transmission and evolution is favored by just such high-amplitude millennial and submillennial scale variations as occurred during at least the last four glacial cycles. Without such variation, genes and nontransmitted phenotypic flexibility are sufficient to allow a population to adapt to variation (ref. 3, pp. 125–131, 79) without the need for the faster-tracking but expensive cultural system. The paleoclimate data, as they currently stand, are consistent with the hypothesis that the evolution of human cul-

ture has been in response to increasing environmental variation over time. We know that brain-size increase is not unique to humans. Many mammalian lineages show increased brain size in the last couple of million years (83). Increases in mammalian brain size averaged over many lineages might be taken as a paleoclimate index of the amount of high-frequency environmental variation, on the grounds that costly nervous tissue would not evolve unless useful for adapting to high-frequency environmental change by individual learning and simpler forms of social learning (34, 84, 85).

Current Evidence and Problems to Solve

In this section, we outline the still-modest evidence that cultured gene-culture coevolution has been the dominant mode of human evolution, perhaps reaching back to the divergence of hominins from our last common ancestor with the other apes. The modest culture of chimpanzees and many other organisms (86–88) might also induce important gene-culture coevolution by a cultural Baldwin effect.

The best evidence about gene-culture coevolution comes from the present and immediate past (89). Estimating the current strength and direction of selection is a classic topic in evolutionary biology (90), and social scientists have conducted similar studies (91, 92). The environmental, genetic, and cultural data are rather good for the last 10 millennia. However, some of the most interesting questions come from deeper history, where all three kinds of investigations meet limits. Ancient ecosystems and their variation are hard to reconstruct (93), evidence of distant past selection is less precise than for recent selection, and the number of fossils and artifacts discovered and their condition declines with time (e.g., 94). The hope is that evolutionary genomics and related functional studies will provide a powerful third source of data to complement paleoenvironmental and paleoanthropological data. The way forward will be to make optimal use of all three forms of data, each with inevitable limitations, in evaluating hypotheses about our evolution.

Current Selection. Most but not all contemporary human populations have experienced rapid and dramatic cultural change in recent times due to economic development and the globalization of culture. Diseases and domesticates from all around the world have been introduced to climatically compatible regions. Large populations of mixed-race people have emerged. Many populations have reduced exposure to infectious diseases. Some populations have become so wealthy that consumption of food leads to diseases of nutritional excess rather than diseases of nutritional deficiency. In the past two centuries, beginning in Europe, an increasing number of societies have become highly urbanized. Kin have become less important in social networks in urban societies, leading to a host of fitness-related changes including demographic transitions and increasing tolerance for lifestyles that do not result in reproduction (95). Kin-dense social networks arguably support norms that encourage reproduction in a society because kin selection will have favored kin taking more interest in the reproduction of kin than in the reproduction of nonkin friends.

These changes all seem likely to generate measurable selection on genes. Some of these genetic changes are likely to result from relaxed selection, for example due to the reduced importance of infectious disease and nutritional deficiency in many populations. Some are likely to result from positive selection for resistance to new environments. For example, modern urban environments are often hygienically cleaned, apparently leading to the IgE component of the immune system to respond to inappropriate targets such as one's own tissue or harmless pollens (96, 97). Some of these diseases, like asthma, have appreciable death rates among children and young adults. A number of genes that might be targets of selection are known to be involved in asthma.

Some of the complexities of gene-culture coevolution can be illustrated by the impact of the demographic transition on genetic and cultural evolution. Whereas most of us celebrate the modern steep drop in fertility from the point of view of moderating anthropogenic climate change and similar problems, the first-order effect of natural selection is to favor the efficient conversion of resources into offspring. Thus, we might expect to see current selection favoring more pronatalist behavior in postdemographic transition societies. On the genetic side, a study of the heritability of fertility in Danish twins showed that the heritability of fertility was negligible in predemographic transition times but has become appreciable in later cohorts (98, 99). Formerly, pronatalist culture, which must have been the norm in most times and places throughout our evolutionary history, would have effectively encouraged most people to reproduce efficiently, despite minor genetic variation that might have led some people not to reproduce. A drastic fall in average fertility has likely caused variation that was once neutral, or nearly so, to have a much stronger effect on phenotypes. Two studies report that life-history characteristics are currently responding to selection (100, 101). Women seem to be under selection to enter menarche earlier, have earlier first births, and to reach menopause later. They seem to sacrifice height in the process of earlier reproduction. As to mechanism, earlier first births may simply result from earlier menarche, exposing more impulsive teenagers to risk of pregnancy.

Stearns and coauthors used the Framingham Heart Study to estimate the effects on lifetime reproductive success of traits measured in that study (102). Together with estimates of heritabilities of traits, they estimated selection strength on these traits. Women are under measurable selection for shorter but heavier bodies, earlier reproduction but also delayed menopause, as in the studies described just above, and lower blood pressure and lower cholesterol. The latter two traits suggest selection to adapt to the sedentary lifestyles and rich diets in the contemporary developed world.

Culture is also under selection to increase birth rates. Some subcultures, such as Old Order Anabaptists, have proven quite resistant to cultural modernization and have continued to reproduce at natural fertility levels (~7 children per woman). Anabaptist populations are apparently growing very rapidly (103, 104). Hout et al. (92) estimated the selective effects of other religious beliefs. The main effect in the United States seems to be that religious people have about twice as many children as the unchurched; differences among many denominations are otherwise modest. At the global level, religion is currently spreading faster than secularism because religious people are having more children (105). Sociologists of religion have argued that early Christianity spread in part by demographic increase in the Roman Empire because of its pronatalist proscriptions and prescriptions (106).

Selection in the Holocene. About 11,500 years ago the climate stabilized, beginning the current relatively invariant, warm, and wet interglacial. Over the next few thousand years, most human populations adopted some form of agricultural subsistence (39). Late Pleistocene humans appear to have depended disproportionately on game animals for subsistence (107). Thus, switching to a diet rich in plant carbohydrates confronted people with dietary challenges (108). Plant-rich diets also meant that human numbers could increase, leading to the acquisition of new epidemic diseases, often from domestic animals (109). Dense populations also led to the cultural evolution of new forms of social organization to replace the smaller-scale egalitarian societies that typify many hunter-gathers. Large social systems arose with hierarchically organized authority and an elaborate division of labor.

The evidence suggests that many new genes came under selection in the Early and Middle Holocene (110). Some of these

are familiar human polymorphisms already discussed, such as the *HBB* sickle cell gene, the *G6PD* malaria protection gene, and the *LCT* adult lactose secretion gene. Other interesting genes include amylase copy-number polymorphisms. Populations with a recent history of diets rich in starch have more copies of the gene coding for amylase (111). The functional annotations of genes identified in large-scale scans (e.g., 68) flag many as potentially of significance in disease resistance or dietary adaptations. As the vast task of identifying the functions of many genes proceeds, we anticipate many similar cases to emerge (112–114).

The category that will be controversial is genes related to behavior. The transformation of human social systems in the Holocene is every bit as dramatic as the transition in diet and disease exposure. Should we expect that many genes adapted to more complex and more hierarchical societies have arisen in the Holocene? Cochran and Harpending (115) have suggested that the Ashkenazi Jews have high intelligence, and a concentration of genetic diseases with neurological symptoms, due to their Medieval specialization in the businesses of banking and long-distance trade, and later in various managerial occupations. These jobs, emphasizing intellectual skills, generated selection for high IQ. Jews of that time were also relatively genetically isolated. Some of these genes are perhaps overdominant, leading to neurological pathologies when homozygous. One might imagine that the human division of labor is extensively supported by genetic specializations favoring different occupations. As cultures developed a larger number of economic and social roles, human genetic diversity might have increased to diversify human capabilities and inclinations. The honeybee division of labor is supported by queens mating multiply and so diversifying the genes of workers, whose differing genotypes are better at different tasks (116). This hypothesis suggests that genes controlling such things as personality should be more variable in populations that have long had a history of an extensive division of labor.

On the other hand, culture is a tremendous force for generating behavioral variation independently of genetic variation. Thus, human genetic variation for behavioral traits may be large because cultural variation shelters much genetic variation from selection. Literacy rates in societies with good education systems can approach 100% despite the fact that reading is not something human brains evolved to do. Rather, cultures evolved writing systems that take advantage of parts of the brain evolved to do quite different things (28). Cultures find ways to finesse disabilities so that the blind and dyslexic can learn to read. The idea that traits with high heritabilities such as IQ are unaffected by the cultural environment is falsified by the rapid secular increase in IQ in many developed countries during the 20th century (117), and by the fact that IQ is much less heritable among populations with lower socioeconomic status (118). Likewise, IQ is correlated across countries with stage of modernization (119). The amount and quality of education seem to explain most of the variation in IQ between groups and over time within groups (120). Botticini and Eckstein (121) argue that a tradition of education and literacy accounts for Jews entering jobs requiring high intellectual skills. Of course, this hypothesis and Cochran and Harpending's are not mutually exclusive. *To what extent* are the genes that underlie behavioral variation in humans evolving mostly by drift and mutation because they are protected from selection by culture, and *to what extent* have they been under frequency-dependent selection to support the division of labor in complex societies?

Selection in the Plio-Pleistocene. Humans emerged from the Late Pleistocene with a highly advanced capacity for culture and promptly evolved agricultural subsistence systems that radically altered human environments. The strong coevolutionary impact of cultural changes on genes in the Holocene is not surprising. But how far back into hominin history was this mode of coevolution important? Theory points to the speed of cultural evolution compared with genetic evolution. Even rudimentary culture capacities could support appreciable amounts of culture-driven gene-culture coevolution. This idea is difficult to test in humans given the limitations of the current record mentioned in the introduction to this section. Certain aspects of the record are now reasonably well understood, namely skeletons and stone tools. Genomic clocks can potentially be calibrated by matching the evolution of genes directly affecting skeletons and abilities to make stone tools to the paleoanthropological record. If genomic analysis can provide at least rough dates for when traits and capacities that are more poorly represented in the paleoanthropological record evolved, it will provide an important new source of information about how the coevolutionary process works. The logic of the argument can be illustrated by the refutation of an early coevolutionary hypothesis proposed by Sherwood Washburn (122). Washburn speculated that a coevolutionary process was set up by the development of traditions of making simple stone tools. The use of tools created environments that favored the specialization of hands for toolmaking, leading toward upright posture. As hands became more specialized for toolmaking, selection would favor larger brains, including improved manual dexterity in fine manipulations, that would underpin more complex tool traditions. This hypothesis is not correct, at least not in the simple form that Washburn proposed. Australopithecines were bipedal for several million years without any evidence of brain-size increase or tool use. Many plausible scenarios about human evolution in the Plio-Pleistocene have been advanced. Most of these are hard to test using skeletal and stone tool evidence alone. In *SI Text*, we illustrate how genomic data might help improve our understanding of hominin evolution in the Plio-Pleistocene.

Conclusions

Genomics has already made quite substantial contributions to our understanding of human evolution, beginning with the use of mitochondrial DNA variation to understand the timing of events in recent human evolution and to provide a window into human paleodemography, including past population sizes and migration patterns. The use of linkage disequilibrium to identify genes under recent selection suggests a massive Holocene wave of genetic change initiated by the cultural evolution of agricultural subsistence. Even here, our lack of knowledge of the functional significance of most of the alleles that have been under selection hides most of the details from us. As regards Plio-Pleistocene gene-culture coevolution, we are still at the very beginning of an understanding. In addition to a poor understanding of gene function, it is not clear how much information gene sequences contain about the timing of their selective history. Tools besides simple linkage disequilibrium suitable for deeper time will be required if genomics is to make a major contribution to resolving the many puzzles of the paleoanthropological record. We expect continued rapid progress.

ACKNOWLEDGMENTS. Many thanks to Francisco Ayala and John Avise for organizing such an interesting conference and to our fellow presenters for enlightening papers and discussions.

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