

Supporting Information

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SI Text

We first sketch the Plio-Pleistocene evolutionary events known from skeletons and artifacts and then conjecture about how genomic data might help resolve issues by the paleoanthropology of this period. Then we turn to the problems of the evolution of language and social organization. Events in the evolution of these two especially important features of gene-culture coevolution have been difficult to reconstruct because the skeletal and artifact data regarding them are so enigmatic. Here genomic data are likely to prove especially useful. The genome wide scans for genes under selection in the last few tens of thousands of years described in the main text are based on single nucleotide polymorphisms (SNPs) from a relatively limited sample of genomes. These data provide only a relatively low resolution picture of genetic variation. The 1000 Genomes Project is in the process of fully sequencing at least 1,000 genomes from 11 populations representing the major regions of the world (<http://www.1000genomes.org/page.php>). The cost of such full sequences will probably continue to fall. Over the next decade, a large representative sample of high-resolution sequences should be available. We can anticipate that the information in these sequences, together with advances in functional genomics, will offer great insights into the deep evolutionary history of our lineage.

Selection in the Late Pleistocene. To judge from paleoanthropological data, the period from ~250 kya to 50 kya was the time interval over which people became behaviorally modern. African populations had rather modern, but not completely modern, skeletons and large brains early in this period (1), but mostly made comparatively simple stone tools until about 40 kya. About this time, anatomically modern Africans dispersed from Africa to Eurasia. In western Eurasia and northern Africa, anatomically modern populations began making sophisticated Upper Paleolithic stone tools and art objects about 40,000 years ago. Ephemeral episodes of more sophisticated tool making do occur much earlier in Africa (2). The early, if ephemeral, occurrence of sophisticated stone tools at the same time period as large-brained early modern humans is consistent with behavioral modernization being toward the beginning of this period. If so, the fact that anatomically modern humans were confined for so long to Africa, usually making fairly simple stone tools, is puzzling. If people were capable of modern behavior, why did they so seldom exhibit it? Why was their dispersal out of Africa so late? Klein (3) suggests that a fortuitous mutation perhaps ~60 kya led to the final modernization of humans and to our movement out of Africa. An uptick in the millennial and submillennial scale climate variation after about 70 kya might have advantaged the more cultural hominins and led to a substantial bout of gene-culture coevolution. Or perhaps the explanation is entirely environmental and genes played little or no role. Simply increasing human population densities in some times and places could support the evolution of more complex technology (4, 5).

As mentioned in the main text, genomic studies have already revolutionized our understanding of our migration out of Africa, following the pioneering mitochondrial DNA phylogeny of Cann, Stoneking, and Wilson (6). By now it is clear that much of the genetic variation and genetic diversity in human populations is consistent with a spread out of Africa about 60–50 kya (7, 8). Examples of genes that very likely came under selection in this period include genes affecting skin pigmentation (9, 10). As with genes selected in the Holocene, different populations have reached parallel solutions to the same adaptive problem. The

genes that underlie the light skin adaptation to increase vitamin D photosynthesis in cold, low-sunlight environments are different in eastern and western Eurasia (11).

Ideally, genomic data will provide an accurate timescale for major evolutionary events, which can then be used in conjunction with paleoanthropological data to resolve some of the puzzles noted above. This quest for well-dated selection events will require more data and improved methods. The best tool for younger events, dates estimated from the long haplotypes associated with genes under selection, is nearly erased by recombination in this earlier period. The reduced diversity and excess of rare haplotypes in the regions flanking genes under selection in theory will lead to datable genomic events in this time period (12). An interesting example of another kind of data that might prove useful is the study of the evolution of human commensals and parasites. For example, the human body louse lives in clothing but feeds on the body. It evolved from the head louse, which lives in hair, 72 kya \pm 42 kya (13). Thus, clothing must have evolved fairly recently, perhaps associated with the out-of-Africa migration of anatomically modern humans to higher latitudes. Aside from the human genome itself, we wonder how much evolutionary history might be reconstructed from the diverse microflora that inhabit our digestive tract and skin (14).

Complete sequences of Neandertal autosomal DNA promise to revolutionize our understanding of selection in the Late Pleistocene (15). Improvements in the database of fossil mitochondrial DNA sequences also promise much (16). Assuming that the ancestral *Homo heidelbergensis* population that gave rise to Neandertals and ourselves lived around 200–600 kya (17), and if there was no introgression of genes from Neandertals to anatomically modern humans (or that such introgression as did occur is detectable), then any genetic variants that we share with Neandertals (such as, possibly, the derived *FOXP2* variant) must have had its origin before the date of separation of the two species. Derived genes not shared with Neandertals are candidates to have evolved on the anatomically modern lineage. We might not want to discount the possibility of convergent evolution in the two species. Neandertals had brains as large as anatomically modern humans (3). By some accounts, Neandertals proved as capable of sophisticated culture as anatomical moderns. Just before we came into contact with them, and after the uptick in millennial and submillennial scale variation ~60 kya, Neandertals may have independently evolved the modern behaviors ascribed to the makers of the Upper Paleolithic industries of western Eurasian anatomical moderns (18, 19). Introgression between anatomically modern humans and Neandertals is a possibility (20), and what genes did introgress would be informative if they can be reliably detected, particularly if they generated parallel selective sweeps in the two species.

For this period, we have nothing like the unmistakable signature of cultural changes driving genetic changes that we see in the Holocene. If anything, genetically determined traits such as brain size seem to appear in the paleoanthropological record preceding, rather than following, the most conspicuous cultural changes. Perhaps the most interesting single question here is whether genes underlying modern behavior evolved early or late in this period. The durable artifacts tend to support a late interpretation, because a great number of traits that are most diagnostic of modern behavior, such as symbolic behaviors (art), develop rather late. If Neandertals did independently evolve modern behavior, then perhaps parallel or convergent genetic or cultural responses to increased climate variation can explain the

pattern. The capacity for modern behavior need not necessarily have been present in the last common ancestor. The skeletons of early anatomically modern humans are still very robust and nonmodern in other ways (1). The fossils and stone tools do not necessarily contradict the hypothesis that large-brained but archaic anatomical modern genes were coevolving in response to Middle Paleolithic cultural innovations. The combination of large brains and comparatively simple technology is a major puzzle nonetheless. How were our ancestors supporting such an energetically expensive organ unless by modern or near-modern behavior? Even the anatomically modern humans that left Africa and moved eastward to eastern Eurasia and Australia did so using relatively simple Middle Paleolithic toolkits (21). The most dramatically modern Upper Paleolithic industries rich in symbolic artifacts were seemingly confined to western Eurasia and northern Africa for tens of thousands of years after 40 kya.

The especially intense pattern of millennial and submillennial scale variation after 70 kya suggests that environmental conditions potentially played some role. We might imagine that the adaptive advantages of Middle Paleolithic stone tool traditions were sufficient to induce the evolution of very large brains in both anatomical moderns and Neandertals. Perhaps the achievement of ephemeral sophisticated industries in Africa before 70 kya, and later more permanently in western Eurasia, depended upon larger populations, leading to the ability to accumulate more innovations. Rather than a bottleneck around 70 kya as mitochondrial coalescence data suggest, perhaps human populations were chronically rare before 70,000 kya. Imagine that humans were competing in a rather crowded guild of top carnivore species: lions, leopards, cheetahs, and other large cats, hyenas, wild dogs, wolves, and bears. More variable environments, to which humans could adapt culturally, might have given our species a competitive advantage. An increase in millennial and submillennial scale climate variation might thus have led to the spread of moderns out of Africa, and to population densities high enough to lead to Upper Paleolithic and similar industries (22).

Selection from the Late Pliocene to Middle Pleistocene. Events deeper in the evolution of hominins are naturally even more opaque. The interesting high-frequency part of the paleoclimate record is seriously deficient for this period. During the long period from about 2.6 to 1 million years ago, when the low-resolution record was dominated by the 41,000-year cycle, early members of our own genus *Homo* enter the fossil record, particularly *H. erectus* sensu lato. These populations had relatively modern postcrania and brain sizes relative to body sizes intermediate between Australopithecines (and living apes) and anatomically modern humans and Neandertals (23). Many, if not most, of the major genetic changes between humans and the rest of the apes probably occurred in this period, during the transitions from Australopithecines to *H. habilis* and from *H. habilis* to *H. erectus*. According to some interpretations, *H. erectus* had a rather modern physique and an enlarged brain relative to body size (24). Subsistence activities might have included a considerable ability to acquire meat and fat from hunting. For example, an important component of human hunting is the ability to run down large- and medium-sized game. Humans from *H. erectus* onward could probably run efficiently and sweat to keep our body temperature down during extended exercise. *H. erectus* hunters could thus probably have run medium-sized herbivore prey until they were exhausted or overheated or both, and then dispatched them with unsophisticated weapons (11, 25, 26). We can expect to find genes related to a large variety of specifically human traits to have evolved in this period, but in most cases we will have to entertain the hypotheses that they evolved earlier in Australopithecines or in post-*H. erectus* hominins.

Early *Homo* skeletal material is loosely associated with two successive tool traditions, the Oldowan and the Acheulean. *H.*

erectus spread out of Africa and into island southeast Asia, tolerating temperate climates and apparently crossing deep water, apparently some 1.7 mya (27). Some authorities emphasize the expedient simplicity of the Oldowan and early Acheulean industries. de la Torre and colleagues (28, 29) argue that a rather sophisticated appreciation of the properties of stone, and a fairly sophisticated approach to knapping, characterized these two industries. Sharon (30) presents evidence that Acheulean makers of large biface tools had efficient and culturally variable techniques for producing these signature artifacts. A recently published Acheulean campsite dating to 750 kya seems to have been fairly complex. It contained remains suggesting that *H. erectus* could exploit a wide variety of plant and animal resources, including fish and acorns, and that they controlled fire (31). Evidence for still-earlier use of fire is controversial (32). Interestingly, reports on living individuals with primary microcephaly (small brains but without organizational disruptions) indicate that they suffer only mild to moderate mental retardation (33). Perhaps these brains are a clue to the cognitive capabilities of *H. erectus*. *H. erectus*'s brain architecture and behavior might have been rather modern in many respects. Donald (34) suggests that *H. erectus* had advanced abilities to imitate motor patterns but still lacked speech. He reviews 19th-century data on deaf mutes as evidence that alinguistic people would be capable of imitating many if not most modern skills except ones directly dependent on language. Thus, culture-led gene-culture coevolution could have been an active process in this period. After 1 mya, the 100-ky cycle came to dominate the low-frequency component of the climate record. Early in this period, larger-brained hominins, often lumped into the taxon *H. heidelbergensis*, evolved in Africa and western Eurasia (35). Thus, there are hints, but at this point only bare hints, that changes in climate variation were increasing selection in favor of more sophisticated culture capacities. Some progress has been made on the representation of tool use in the brain (36). Many genes associated with the ability to make and use tools probably evolved during this long period.

Since the sequencing of the chimpanzee genome, a considerable amount of effort has gone into searching for the differences between the two species (37–40). Many candidates for genes that have come under selection have turned up in these comparisons. Some of the apparently most interesting genes, such as copy number in the gene *MGC8902*, have unknown function. The large *OR* family of genes (~1,000–1,400 loci) involved in odor perception has a very high percentage of nonfunctional genes in humans, although some specific genes seem to have undergone positive selection.

This pattern of loss of function of olfactory genes is related to the reduced area of olfactory epithelium and relatively small olfactory bulb in humans. Likely enough, the development of cooking and the use of cultural traditions to identify suitable food items reduced our dependence on olfaction. The beginning of cooking likely also caused major changes in human diets which should be reflected in the genome (32). Our Australopithecine ancestors were probably largely herbivorous. Early species of *Homo* were probably generalist omnivores with significant access to hunted and scavenged fat and meat (41). By Middle and Upper Paleolithic times, stable isotope analysis and zooarchaeological remains suggest that humans were highly carnivorous (42, 43). The expansion of brains in *Homo* was very likely tied to improved nutrition via hunting and cooking (44). Genes associated with dietary changes and brain-size increase should be correlated to each other and to patterns derived from paleoanthropology.

Evolution of Language and Social Organization. Language and social organization were probably closely related in the course of human evolution. Much of our use of language is related to social life, and it is reasonable to assume considerable parallelism in their evolution (45). They are both features that fossilize poorly. Inferences about their presence or absence are not easy to make.

For example, Philip Lieberman (46) has long argued from anatomical evidence regarding the shape of the vocal tract that the capacity to clearly articulate modern vowel systems only emerged around 50 kya. He nevertheless thinks that ancient species of *Homo* had some useful capacity for speech. Indeed, there is perhaps a consensus among evolutionists writing on language that it evolved by culture-led gene-culture coevolution over an extended portion of our evolutionary history (47). Nevertheless, dissenters on this point certainly exist. For example, Tattersall (48) argues that articulate language must have originated only 50 kya. He cites not only the anatomical evidence but also the late first finds of unambiguous symbolic artifacts such as art. Those who imagine that language arose by prolonged culture-led coevolution differ greatly in the details of their scenarios. For example, Pinker (49) argues that coevolution will lead to complex innate cognitive specializations for language. Kirby et al. (50) use simulations to illustrate how the basic features of language might be cultural adaptations to preexisting cognitive constraints on language learning. That is, language evolved to fit our brain, rather than the other way around (51). If cultural adaptation is sufficiently powerful, it might lead to little or no coevolutionary pressure on innate cognitive mechanisms. Tomasello (52) argues that language is a cultural construct and that most of the coevolved innate predispositions for language are shared with other cultural features. Although the involvement of the *FOXP2* gene in language evolution has turned out to be complex and controversial, the intense interest it has generated illustrates the questions we hope to answer with the help of genomic methods: What genes changed, when did they change, and what is the functional significance of the changes?

Many scenarios have been advanced in discussions of the evolution of social organization, although it has not received the same amount of attention as language. Lovejoy (53) argues that reduced canines in the possible ancestral hominid *Ardipithecus ramidus* indicate that this early species already exhibited reduced intrasexual antagonism and greater social adhesion on the part of both males and females. Hrdy (54) reviews a large body of evidence regarding the role of cooperative breeding (assistance to females with dependent offspring by others), concluding that cooperative breeding must have evolved in the hominid lineage before brain enlargement. The costly big brains and long juvenile

periods of great apes already strain the ability of mothers to rear such offspring. Despite having highly dependent infants needing to grow even larger brains, human interbirth intervals are shorter than those of great apes, something only possible with alloparental assistance. Burkart et al. (55) argue that cooperative breeding would have laid the initial basis for cooperative psychological predispositions in humans. Interesting progress has been made on the possible role of a vasopressin receptor gene polymorphism in human bonding (56). The comparative biology of human reproduction suggests that humans experience relatively low sperm competition, an indication of male investment in provisioning offspring rather than competing for mates (57, 58). Derived alleles for genes expressed in testes and sperm turn up in scans for evidence of selective differences between humans and chimpanzees (59).

However, much genetic change also appears to have happened in the Late Pleistocene and even in the Holocene according to data we have reviewed here and in the main text. Perhaps important innovations involving social predispositions occurred as late as 50 kya (3) or even in the Holocene (20). Once again, the evidence for just how far back in time the culture-led mode of gene-culture coevolution can be pushed is an open question to which evolutionary genomics will have much to contribute. As with language, not only is timing of important events uncertain but also the division of labor between genes and culture. We (60, 61) have suggested that humans' social psychology was fairly extensively remodeled by gene-culture coevolution. However, in ethnographically known societies, culturally transmitted norms and institutions do much heavy lifting. We do not anticipate finding that dramatic genetic changes were necessary to accompany the evolution of social complexity in the Holocene. The simpler societies known ethnographically rely heavily on norms and institutions to regulate social life, so no revolution in our innate psychology seems necessary to account for complex societies. Cosmides et al. (62) suggest that much more of the load is carried by content-rich cognitive adaptations than by transmitted culture. Functional and developmental genomics should eventually lay a foundation for understanding the roles of genes and culture in current behavior and in the past evolution of current behavioral capacities.

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