Just How Special Are Humans?

with Eric Priest, Celia Deane-Drummond, Joseph Henrich, and Mary Meyers, "Introduction to Symposium on 'Just How Special Are Humans?'"; Eric Priest, "Human Uniqueness: Debates in Science and Theology"; Joseph Henrich, "How Culture Made Us Uniquely Human"; Agustín Fuentes, "Distinctively Human? Meaning-Making and World Shaping as Core Processes of the Human Niche"; Cristine Legare, "The Cumulative Quality of Culture Explains Human Uniqueness"; David Reich, "Human Uniqueness from a Biological Point of View"; Alan Mittleman, "'The Mystery of Human Uniqueness': Common Sense, Science, and Judaism"; Jan-Olav Henriksen, "Experiencing the World as the Evolved Image of God: Religion in the Context of Science"; Jennifer A. Herdt, "Responsible Agency: A Human Distinctive?"; Celia Deane-Drummond, "Tracing Distinctive Human Moral Emotions? The Contribution of a Theology of Gratitude"; and John Behr, "Nature Makes an Ascent from the Lower to the Higher: Gregory of Nyssa on Human Distinctiveness."

HUMAN UNIQUENESS FROM A BIOLOGICAL POINT OF VIEW

by David Reich

Abstract. This article seeks to provide some genetic perspectives on the question "Just How Special Are Humans—Really?" It begins with an introduction to how genetic variation can provide information about the past. It continues by discussing two ways in which genetic analyses has, on multiple occasions, shown that humans are less unique than we thought we are. We have a cognitive bias to toward thinking we are special. Our species has colonized an ecological niche not exploited by any other species on our earth, but how much of our adaptation to that niche is cultural rather than genetic?

Keywords: biology; cultural evolution; genetic evolution; human uniqueness

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To understand why genetics is able to shed light on the history of our species, it is necessary to understand how the genome—defined as the full set of genetic code each of us inherits from our parents—records information. James Watson, Francis Crick, Rosalind Franklin, and Maurice

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Wilkins showed in 1953 that the genome is written out in twin chains of about three billion chemical building blocks (six billion in all) that can be thought of as the letters of an alphabet: A (adenine), C (cytosine), T (thymine), and G (guanine) (Watson and Crick 1953). What we call a "gene" consists of tiny fragments of these chains, typically around a few thousand letters long, which are used as templates to assemble the proteins that do most of the work in cells. In between the genes is noncoding DNA, sometimes referred to as "junk" DNA.

Although the great majority of scientists are focused on the biological information that is contained within the genes, there are actually occasional differences between DNA sequences—about one every thousand letters or so—reflecting random errors in copying of genomes—mutations—that have occurred at some point in the past. It is these differences, occurring in both genes and in "junk," that geneticists study to learn about the past. Over the approximately 3 billion letters, we find typically around 3 million differences between unrelated genomes. The higher the density of differences separating two genomes on any segment, the longer it has been since the segments shared a common ancestor, and thus the density of differences provides a biological stopwatch, a record of how long it has been since key events occurred in the past (see Figure 1).

The first major application of genetics to the study of the past involved mitochondrial DNA. This is a tiny portion of the genome—only approximately 1/200,000th of it—which is passed down along the maternal line from mother to daughter to granddaughter. In 1987, Allan Wilson and his colleagues sequenced a few hundred letters of mitochondrial DNA from diverse people around the world. By comparing the mutations that were different among these sequences, he and his colleagues were able to reconstruct a family tree of maternal relationships. What they found is that the three deepest branches of the tree—the three branches that left the main trunk earliest—are only found today in people of sub-Saharan African ancestry, suggesting that the ancestors of modern humans lived in Africa. In contrast, all non-Africans today descend from a single late branch of the tree (Cann, Stoneking, and Wilson 1987). This finding became an important part of the evidence for the theory that modern humans descend from a primarily African ancestral population. Based on the rate at which mutations are known to accumulate, Wilson and his colleagues estimated that the most recent African ancestor of all the branches, "Mitochondrial Eve," lived around 160,000 years ago (Fu et al. 2013), although it is important to realize that like most genetic dates, this one is imprecise because of uncertainty about the true rate at which human mutations occur.

The finding of such a recent common ancestor was exciting because it refuted the "multiregional hypothesis," according to which modern humans living in each part of the world descend substantially from an early expansion of humans out of Africa (at least 1.8 million years ago) of *Homo*

erectus, a species that made crude stone tools and whose members had brains about a third the size of ours. The multiregional hypothesis implied that descendants of *H. erectus* evolved in parallel across Africa and Eurasia to give rise to present-day populations who live in the same places today. This scenario would imply that there would be mitochondrial DNA sequences among present-day people separated by more than a million years, the age of the dispersal of *H. erectus* and its descendants. However, the genetic data were impossible to reconcile with this. The fact that all people today share a common mitochondrial DNA ancestor five to ten times more recently showed that humans today largely descend from a later expansion from Africa.

Anthropological evidence pointed to a likely scenario for what occurred. The earliest known "anatomically-modern human" skeletons—defined as falling within the range of variation of all humans today with regard to having a globular brain case and other traits—date to between around 300,000 and 200,000 years ago and are all from Africa (Fleagle et al. 2008; Richter et al. 2017). Outside of Africa and the Near East, though, there is no convincing evidence of anatomically modern human skeletons older than 50,000 years. Archaeological evidence of stone tool types also points to a great change after 50,000 years ago, a period known to archaeologists of West Eurasia as the Upper Paleolithic, and to archaeologists of Africa as the Later Stone Age. After this time, the manufacture of stone tools became far more efficient and innovative, with changes in style every few thousand years compared with the glacial earlier pace of change. Humans in this period also began to leave behind far more artifacts that revealed their aesthetic and spiritual life: beads made of ostrich eggshells, polished stone bracelets, body paint made from red iron oxide, and the world's first representational art. The world's earliest known figurine is a roughly 40,000-year-old "lion-man" carved from a woolly mammoth tusk, found in Hohlenstein-Stadel in Germany. The 30,000-year-old drawings of pre-Ice Age beasts, found on the walls of Chauvet Cave in France, even today are recognizable as transcendent art.

The dramatic acceleration of change in the archaeological record after around 50,000 years ago is also reflected in population change. The Neanderthals, who had evolved in Europe by around 400,000 years ago and who are considered "archaic" in the sense that their body shape did not fall within modern day variation, went extinct in Europe between 45,000 and 39,000 years ago, within a few thousand years of the arrival of modern humans (Higham et al. 2014). Population turnovers also occurred elsewhere in Eurasia, as well as in southern Africa where there is evidence of abandonment of sites and the sudden appearance of Later Stone Age cultures.

The natural explanation for all these changes was the spread of an anatomically modern human population whose ancestors included

Mitochondrial Eve, who practiced a sophisticated new culture and largely replaced the people who lived in each place before.

The Hypothesis of a Genetic Switch

The finding that genetics could help to distinguish between competing hypotheses of human origins led in the 1980s and 1990s tKo exuberance about the power of the discipline to provide simple explanations. Some even wondered if genetics might be able to do more than provide a supporting line of evidence for the spread of modern humans from Africa and the Near East after around 50,000 years ago. Perhaps genes could also be the cause of that spread, providing a biological explanation for the quickening pace of change in the archaeological record evident after around 50,000 years ago.

The anthropologist best known for embracing the idea that a genetic change might explain how we came to be behaviorally distinct from our predecessors was Richard Klein. He put forward the idea that the Later Stone Age revolution of Africa and the Upper Paleolithic revolution of Eurasia, when recognizably modern human behavior burst into full flower after around 50,000 years ago, were driven by a genetic change—the rise in frequency of a single mutation of a gene affecting the biology of the brain, which permitted the manufacture of innovative tools and the development of complex behavior.

According to Klein's theory, the rise in frequency of this mutation primed humans for some enabling trait, such as the ability to use conceptual language. Klein thought that, prior to the occurrence of this mutation, humans were incapable of modern behaviors. Supporting Klein's notion are examples, among other species, of a small number of genetic changes that have affected major adaptations, such as the five changes that are sufficient to turn the tiny ears of the Mexican wild grass teosinte into the huge cobs of corn that we buy in the supermarket today (Doebley 2001).

Klein's hypothesis came under intense criticism almost as soon as he suggested it, most notably from archaeologists Sally McBrearty and Alison Brooks, who showed that almost every trait that Klein considered to be a hallmark of distinctly modern human behavior was evident in African and Near Eastern archaeological record tens of thousands of years before the Upper Paleolithic and Later Stone Age transitions (McBrearty and Brooks 2000). But even if no single behavior was new, Klein had put his finger on something important. The intensification of evidence for modern human behavior after 50,000 years ago is undeniable and raises the question of whether biological change contributed to it.

One geneticist who came of age at this time of exuberance about the power of genetics to provide simple explanations for great mysteries was

Svante Pääbo. In 2002, Pääbo and his colleagues discovered two mutations in the gene *FOXP2* that seemed like they might be candidates for propelling the great changes that occurred after around 50,000 years ago. The previous year, medical geneticists had identified *FOXP2* as a gene that, when mutated, produces an extraordinary syndrome in which people have normal-range cognitive capabilities, but cannot use complex language, including most grammar (Lai et al. 2001). Pääbo and his colleagues showed that the protein produced by the gene has remained almost identical during the more than hundred million years of evolution separating chimpanzees and mice. However, two changes to the protein occurred just on the human lineage since separation from chimpanzee, suggesting that the gene had evolved much more rapidly on the human lineage (Enard et al. 2002). Later work by Pääbo and his colleagues found that engineered mice with the human versions of *FOXP2* are identical to regular mice in most respects, but squeak differently, consistent with the idea that these changes affect the formation of sounds (Enard et al. 2009). These two mutations at *FOXP2* cannot have contributed to the changes after 50,000 years ago, since Neanderthals shared them (Krause et al. 2007), but Pääbo and his colleagues later identified a third mutation that is found in almost all present-day humans and that affects when and in what cells *FOXP2* gets turned into protein. This change is absent in Neanderthals, and thus was a candidate for contributing to the evolution of modern humans after their separation from Neanderthals (Maricic et al. 2013).

Regardless of how important *FOXP2* itself is in modern human biology, Pääbo cites the search for the genetic basis for modern human behavior as the single most important justification for sequencing the genomes of archaic humans (Pääbo 2014). In 2010, he led the consortium that reported a draft whole-genome sequence from a Neanderthal, and that included a list of about one hundred thousand places in the genome where nearly all present-day humans carry genetic changes that are absent in Neanderthals. There are surely biologically important changes hiding in the list, but we are still only at the very beginning of the process of determining what they are, reflecting a more general problem that we are like kindergartners in our ability to read the genome. While we have learned to decode the individual words—as we know how the sequence of DNA letters gets turned into proteins—we still cannot parse the sentences. The sad truth is that it is possible to count on the fingers of two hands the examples like *FOXP2* of mutations that increased in frequency under the pressure of natural selection and whose functions we partly understand. In each of these cases, the insights only came from years of hand-to-hand combat with life's secrets by graduate students or postdoctoral scientists making engineered mice or fish, suggesting that it will take an evolutionary Manhattan Project to understand the function of each mutation that we have and Neanderthals do not. The Manhattan Project of human evolutionary biology is one to

which we as a species should commit ourselves. But even when it is carried out, I expect that the findings will be so complicated—with so many individual genetic changes contributing to the evolutionary changes that are critical to what makes humans distinctive—that few people will find the answer to be comprehensible. The scientific question is profoundly important, but my guess is that no intellectually elegant and emotionally satisfying molecular explanation for behavioral modernity will ever be found.

No Mutations Rose to Very High Frequency with the Advent of Modern Human Behavior

In 2011, an article by Heng Li and Richard Durbin showed that the idea that a single person's genome contains information about a multitude of ancestors was not just a theoretical possibility, but a reality (Li and Durbin 2011). To decipher the deep history of a population from a single person's DNA, Li and Durbin leveraged the fact that any single person actually carries not one but two genomes: one from their father and one from their mother. Thus, it is possible to count the number of mutations separating the genome a person receives from his or her mother and the genome the person receives from his or her father to determine when they shared a common ancestor at each location. By examining the range of dates when these ancestors lived—plotting the ages of one hundred thousand Adams and Eves—Li and Durbin established what the size the ancestral population had been at different times. In a small population, there is high chance that a pair of randomly chosen people will be siblings; in a large population, the chance is low. Thus, the times in the past when the population size was low can be identified based on the periods in the past when a disproportionate fraction of lineages have evidence of sharing common ancestors. Walt Whitman wrote, "Do I contradict myself? / Very well, then I contradict myself. / I am large, I contain multitudes" (Whitman 1855). Whitman could just as well have been talking about the Li and Durbin experiment—and its demonstration that a whole population history is contained within a single person as revealed by the multitude of ancestors whose histories are recorded within a single person's genome.

An unanticipated finding of the Li and Durbin study was its evidence that after the separation of non-African and African populations, there was an extended period in the shared history of non-Africans when populations were small, as reflected in evidence for many shared ancestors spread over tens of thousands of years (Li and Durbin 2011). A shared "founder event" among non-Africans—when a small number of ancestors gave rise to a large number of descendants today—was not a new idea. But prior to Li and Durbin's work, there was no good information about the duration of this event, and it seemed plausible that it could have transpired over just a few generations—for example, a small band of people crossing the

Sahara into North Africa, or from Africa into Asia. The Li and Durbin evidence of an extended period of small population size was also hard to square with the idea of an unstoppable human expansion of modern humans both within and outside Africa shortly after 50,000 years ago, suggesting that it may not have been a simple story of a dominant group running over all the populations it encountered as soon as it met them.

The newfound ability to take a whole-genome view of human biology—made possible by leaps in technology during the 2000s—allowed reconstruction of population history in far more detail than was previously possible, and in doing so revealed that the simple picture from mitochondrial DNA and the just-so stories about one or a few changes propelling the Upper Paleolithic and Later Stone Age transitions when recognizably modern human behavior become widespread were no longer tenable.

In 2016, Swapan Mallick in my laboratory and I led a study that used an adaptation of the Li and Durbin method (Schiffels and Durbin 2014) to compare populations from around the world to the earliest branching human population living today, the San Bushmen of southern Africa. Our study, like most other studies, found that the separation had begun by around 200,000 years ago and was mostly complete by more than 100,000 years ago. The evidence for this is that the density of mutations separating San genomes from non-San genomes is uniformly high, implying few if any shared ancestors between San and non-San in the last 100,000 years. "Pygmy" groups from Central African forests harbor ancestry that is arguably just as distinctive. Both findings conflict with the idea that a single mutation essential to distinctively modern human behavior occurred shortly before the Upper Paleolithic and Later Stone Age. A change in this time frame would be expected to be more common in some human populations today (those that descend from the population in which the mutation occurred) than others—which seems hard to reconcile with the fact that all people today are capable of mastering conceptual language and exhibiting the cultural innovation that is a hallmark of modern humans.

A second problem with the notion of a genetic trigger became apparent when my colleagues and I applied the Li and Durbin method to search for places where all genomes we analyzed shared a common ancestor in the period before the Upper Paleolithic and Later Stone Age. At *FOXP2*, the gene that seemed the best candidate as a trigger based on previous studies, we found that the common ancestor of everyone living today, the person in whom modern humanity's shared copy of *FOXP2* last occurred, lived more than a million years ago (Mallick et al. 2016). Expanding our analysis to the whole genome, we could not find any place—apart from mitochondrial DNA and the Y chromosome—where all people living today share a common ancestor less than about 400,000 years ago (Figure 1). This is a far longer time scale than the one required by Klein's

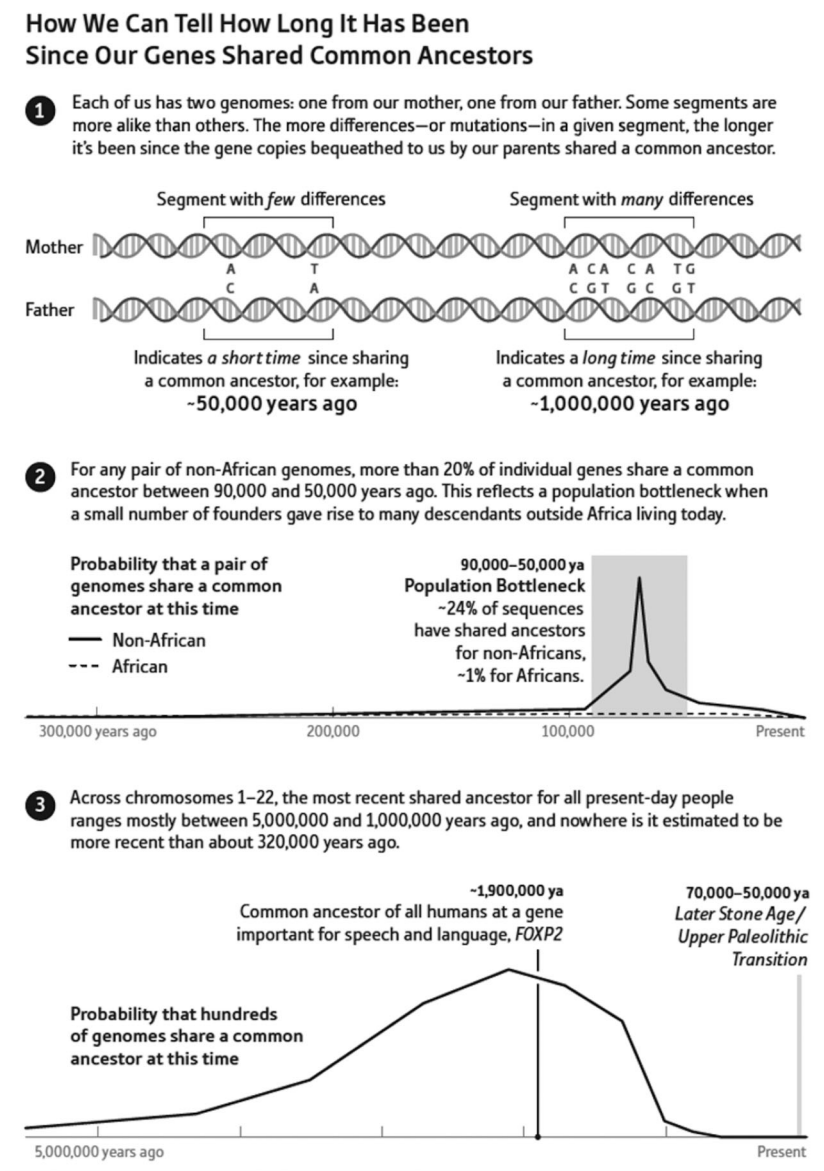

Figure 1. How we can tell how long it has been since our genes shared common ancestors.

hypothesis. If Klein was right, it would be expected that there would be places in the genome—beyond the mitochondrial DNA and the Y chromosome—where almost everyone shares a common ancestor within the last hundred thousand years. But these in fact do not seem to exist. Our

results do not completely rule out the hypothesis of a single critical genetic change. There is a small fraction of the genome that contains complicated sequences that are difficult to study and that were not included in our survey. But the key change, if it exists, is running out of places to hide. The timescale of human genetic innovation and human population differentiation is also far longer than mitochondrial DNA and other genetic data suggested prior to the genome revolution. If we are going to try to search the genome for clues to what makes modern humans distinctive, it is likely that we cannot look to explanations involving one or a few changes.

The whole-genome approaches that became possible after the technological revolution of the 2000s also soon made it clear that natural selection was not likely to take the simple form of changes in a small number of genes, as Klein had imagined. When the first whole-genome datasets were published, many geneticists (I included) developed methods that scoured the genome for mutations that were affected by natural selection (Sabeti et al. 2002; Voight et al. 2006). We were searching for the "low-hanging fruit"—instances in which natural selection had operated strongly on a few mutations. Examples of such low-hanging fruit include the mutation allowing people to digest cow's milk into adulthood or mutations that cause darkening or lightening skin color to adapt to local climates, or mutations that bequeath resistance to the infectious disease malaria by modifying the sequence of the components of the protein hemoglobin. As a community, we have been successful in identifying selection on mutations like these because they have risen rapidly from low to high frequency, resulting in a large number of people today sharing a recent ancestor or striking differences in mutation frequency between two otherwise similar populations. Events like these leave great scars on patterns of genome variation that can be detected without too much trouble.

Cognitive and Behavioral Evolution Is Likely Polygenic, and Driven by Cultural Evolution

Excitement about this bonanza was tempered by work led by Molly Przeworski, who studied the types of patterns that natural selection is likely to leave on the genome as a whole. A 2006 study by Przeworski and her colleagues showed that genome scans of present-day human genetic variation will miss most instances of natural selection because they simply will not have the statistical power needed to detect it, and that scans of this type will also have more power to detect some types of selection than others (Teshima, Coop, and Przeworski 2006). A study led by Przeworski in 2011 then showed that only a small fraction of natural selection in the genome, probably less than 10%, has acted upon new advantageous mutations that had not previously been present in the population (Hernandez et al. 2011).

So what has been the dominant mode of natural selection in humans if not selection on newly arising single mutation changes that then rocket up to high frequency?

A potential clue to understanding what is going on comes from "genome-wide association studies," which since 2005 have collected genome-wide data from millions of people with a variety of measured traits, thereby identifying more than ten thousand individual mutations that occur at significantly elevated frequency in people with particular traits. The value of genome-wide association studies for understanding human health and disease has been contentious because the specific mutation changes that these studies have identified typically have such small effects that the results of these studies are hardly useful for predicting who gets a disease and who does not (Goldstein 2009). But what is almost universally overlooked is that genome-wide association studies have provided a powerful resource for investigating human evolutionary change over time. By testing if the mutations identified by genome-wide association studies as affecting particular biological traits have all tended to shift in frequency in the same direction, we can obtain evidence of natural selection for specific biological traits.

One of the most interesting examples of this type of selection that has already been identified was demonstrated in a study of Icelanders. By compiling the information on the number of years of education for over 400,000 people of European ancestry whose genomes have been surveyed in the course of various disease studies, Daniel Benjamin and colleagues identified 74 mutations, each of which has overwhelming evidence of being more common in people with more years of education than in people with fewer years even after controlling for possibly confounding factors in the analysis such as socioeconomic status (Okbay et al. 2016). An updated version of this study analyzing about 3 million people has identified 3,952 mutations that independently affect this trait (Okbay et al. 2022). When a specific genetic mutation is found to influence a behavioral measurement, it is important to be clear that it could do so through indirect social mechanisms. For example, a mutation that modulates skin color, or a Y chromosome causing a person to be male, might affect the way people with this trait are treated by others. But nongenetic factors cannot fully explain the results of the Benjamin study, as the genes harboring these 74 mutations tend to be involved in neurological development—that is, these genes are disproportionately active in the developing brains of fetuses compared with sets of genes found in studies of other traits like height, as expected for mutations that really do affect behavior (Okbay et al. 2016). Using the numbers from Benjamin and his colleagues' study, the probability of completing 12 years of education could be as high as 92% for the people with the highest genetically predicted chance of completion

compared with 46% for the lowest, suggesting that genetics can be made highly predictive.

How do these 74 mutations modulate educational attainment? The obvious guess is that they have a direct effect on academic abilities, but that is probably wrong. A study of more than 100,000 Icelanders showed that these mutations also reduce the age at which a woman has her first child, and that this is a more powerful effect than the one on the number of years of education. It is therefore likely that these mutations exert their effect indirectly, by nudging people to have children at a younger age, which in turn increases the probability they will leave school (Kong et al. 2017). This shows that, when we discover biological difference governing behavior, it may not be working in the way we would naively assume.

Average differences across populations in the frequencies of the mutations that affect educational attainment have not yet been identified. But older people in Iceland have a measurably higher predicted number of years of education than the youngest, which can only be explained by natural selection for people who had children at a younger age over the last century (Kong et al. 2017). Given that the genetic underpinnings of this trait have measurably changed over time under the pressure of natural selection, it seems highly likely that the trait differs across populations too. No one knows how these 74 mutations affect behavior in people of non-European ancestries, or in differently structured social systems. That said, it seems likely that if these mutations have an effect on behavior in one population they will have an effect in others too, even if the effects differ by social context. And educational attainment as a trait is likely to only be the tip of an iceberg of behavioral traits affected by genetics. The Benjamin study was joined by additional studies finding genetic predictors of behavioral traits (Lo et al. 2017; Davies et al. 2016; Sniekers et al. 2017), one of which was a study of more than 70,000 people that found mutations in more than 50 genes that were significantly predictive of performance on intelligence tests (Sniekers et al. 2017).

Studies like these will make it possible to explore whether the shift to behavioral modernity among our ancestors was driven by natural selection. This means that there is new hope for providing genetic insight into the mystery that puzzled Klein—the great change in human behavior suggested by the archaeological records of the Upper Paleolithic and Later Stone Age. But even if genetics, through coordinated natural selection on many mutations simultaneously, did enable new cognitive capacities, this is a very different scenario from Klein's idea of a genetic switch. Genes in this scenario are not a creative force abruptly enabling modern human behavior, but instead are responsive to pressures imposed by changing conditions. In this new scenario, it is not the case that the human population was "mutation-limited"—not able to adapt because no one carried a mutation

that allows a biological capacity not previously present. Instead, the genetic underpinnings for the striking advances in human behavior and capacities that occurred during the Upper Paleolithic and Later Stone Ages were not particularly mysterious, and many alternative combinations of mutations could have combined to produce the same effects. In other words, the mutations necessary to facilitate modern human behavior were probably already in place, and could well have all increased in frequency together in response to cultural innovations (such as the development of conceptual language) or new environmental conditions, which in turn would have enabled further changes in lifestyle and innovation, in a self-reinforcing cycle.

Perhaps it is true that increases in the frequency of mutations were important in allowing modern humans to match their biology to new lifestyles during the Upper Paleolithic and Later Stone Age transitions. But it is unlikely that the first occurrence of these mutations caused the great changes that occurred. If we search for answers in a small number of mutations that arose shortly before the time of the Upper Paleolithic and Later Stone Age transitions, we are unlikely to find magic-bullet explanations for human uniqueness.

Modern and Archaic Humans Regularly Interbred—Unexpected for Biological Uniqueness

Today, the particular subgroup of humans to which we belong—modern humans—is alone on our planet. We outcompeted or exterminated other humans, mostly during the period, after around 50,000 years ago, when modern humans expanded throughout Eurasia and when major movements of humans likely happened within Africa too. Today, our closest living relatives are the African apes: the chimpanzees, bonobos, and gorillas, all incapable of making sophisticated tools or using conceptual language. But until around 40,000 years ago, the world was inhabited by multiple groups of archaic humans, who differed from us physically but walked upright and shared many of our capabilities. The question that the archaeological record cannot answer—but the DNA record can—is how those archaic people were related to us.

For no archaic group has the answer to this question seemed more urgent than for the Neanderthals. In Europe after 400,000 years ago, the landscape was dominated by these large-bodied people with brains slightly bigger on average than those of modern humans. The specimen that gave its name to Neanderthals was found in 1856 by miners in a limestone quarry in the Neander valley (the German word for valley is "Tal"). For years, debate raged over whether these remains came from a deformed human, a human ancestor, or a human lineage deeply divergent from our own. Neanderthals became the first archaic humans to be recognized by

science. In *The Descent of Man*, Charles Darwin argued that humans are like other animals in being the products of evolution (Darwin 1871). Although Darwin himself did not recognize their significance, Neanderthals were eventually recognized to be from a population more closely related to modern humans than to living apes, providing evidence for Darwin's theory that such populations must have existed in the past.

Over the next century and a half, there were discoveries of many additional Neanderthal skeletons as well as their stone tools. These studies revealed that Neanderthals had first evolved in Europe from even more archaic humans who had spread out of Africa half a million years ago or more. In popular culture, the Neanderthals garnered a reputation as stupid and beastly—much more different from us than they in fact were. Neanderthals' primitive reputation was fueled in large part by the slouched reconstruction of the Neanderthal skeleton from La Chapelle-Aux-Saints made in 1911 by Pierre Marcellin Boule. But from all the evidence we have, Neanderthals living before around one hundred thousand years ago were behaviorally just as sophisticated as our own ancestors—anatomically modern humans—who lived in Africa at the same time as the Neanderthals lived in Eurasia (McDougall, Brown, and Fleagle 2005). Both Neanderthals and anatomically modern humans made stone tools using a technique that has become known as Levallois, which is just as complex in terms of the cognitive skills and dexterity needed to practice it as the Upper Paleolithic and Later Stone Age tool-making techniques that emerged among modern humans after around 50,000 years ago. In this technique, flakes are struck off carefully prepared rock cores that look nothing like the resulting tools, so that crafts-people must hold in their minds an image of what the finished tool will look like and execute the complex steps by which the stone must be prepared to achieve that goal. Other evidence for the cognitive sophistication of Neanderthals comes from the evidence that they cared for their sick and elderly. An excavation at Shanidar Cave in Iraq has revealed nine skeletons, all apparently deliberately buried, one of which had no teeth, suggesting that friends and family had chewed his meat for him (Solecki 1971). The Neanderthals also had an appreciation of symbolism, as revealed by jewelry made of eagle talons found at Krapina Cave in Croatia and dating to about 130,000 years ago (Radovcic et al. 2015), and stone circles built deep inside Bruniquel Cave in France and dating to around 176,000 years ago (Jaubert et al. 2016).

There is hard scientific evidence that modern humans and Neanderthals met. The most direct is from Western Europe, where Neanderthals disappeared between 41,000 and 39,000 years ago (Higham et al. 2014). The arrival of humans there seems to have been at least a few thousand years earlier: at Fumane in southern Italy around 44,000 years ago, Neanderthal-type stone tools gave way to ones typical of modern humans (Higham et al. 2010). In southwestern Europe, tools typical of modern humans, made

in a style called Châtelperronian, have been found amidst Neanderthal remains that date to between 44,000 and 39,000 years ago, suggesting that Neanderthals may have imitated modern human tool-making, or that the two groups traded tools or materials. Not all archaeologists accept this interpretation, though, and there is ongoing debate about whether Châtelperronian artifacts were made by Neanderthals or modern humans (Higham et al. 2010; Bar-Yosef and Bordes 2010).

Genetic studies have shown that Neanderthals and modern humans interbred as behaviorally modern humans spread out of Africa and the Near East between 70,000 and 50,000 years ago, and that almost all non-Africans today have inherited about 2% of their DNA from Neanderthals (Green et al. 2010). Further studies documented the existence of another group to archaic humans that lived in Asia at the same time as modern humans expanded there, the Denisovans (Reich et al. 2010). The Denisovans, too, interbred with modern humans spreading out of Africa and the Near East, contributing 3–5% of the ancestry of present-day indigenous people from New Guinea and Australia, and something like 0.2% of the ancestry of present-day people from East and South Asia.

When our collaborative team discovered the Denisovans, we had a heated debate about what to call the new population and decided to use a generic non-Latin name, "Denisovans," after the cave where they were first discovered, in the same way that Neanderthals are named after the Neander valley in Germany. This decision distressed some of our colleagues, who lobbied for a new species name—perhaps *Homo altaiensis*, after the mountains where Denisova Cave is located. *H. altaiensis* is now used in a museum exhibit in Novosibirsk, Russia, about the discovery at Denisova. We geneticists, however, were reluctant to use a species name. There has long been contention as to whether Neanderthals constitute a species separate from modern humans. The designation of a group as a species separate from another is often based on the supposition that the two cannot successfully interbreed—Ernst Mayr's 'Biological Species Concept (Mayr 1942)—but we know that both Neanderthals and Denisovans successfully interbred with modern humans. Some experts designate Neanderthals as a distinct species of the genus *Homo* (*Homo neanderthalensis*); others as a subgroup of modern humans (*Homo sapiens neanderthalensis*). The evidence for interbreeding indicates that despite what some morphologists think of as highly distinctive physical features specific to the human lineage, in fact archaic and modern humans may not be distinctive enough to meet the biological definitions of distinct species.

The evidence of the last few years has only made the evidence of archaic-modern human interbreeding clearer. Several individuals who were buried ~45,000 years ago at Bacho Kiro Cave in Bulgaria (Hajdinjak et al. 2021), and an individual who was buried ~40,000 years ago at Oase Cave in

Romania (Fu et al. 2015), were all genetically found to be mixtures of modern and archaic humans a few generations before they lived. It seems that when modern and archaic humans lived near each other, they mixed regularly, and recognized each other as similar.

Conclusions

This article has discussed two examples of how humans are less biologically unique than we might at first imagine. One example is the absence of evidence for genetic mutations that rose to high frequency when modern human behavior became strongly evident in the archaeologically record. A second example is the evidence of widespread interbreeding between archaic and modern humans. Paradoxically, genetic data are showing that there may be no reductionist genetic answers to what makes our species unique.

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