

WAS HUMAN EVOLUTION DRIVEN BY PLEISTOCENE CLIMATE CHANGE?

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Modern humans are probably a product of social and anatomical preadaptations on the part of our Miocene australopithecine ancestors combined with the increasingly high amplitude, high frequency climate variation of the Pleistocene. The genus *Homo* first appeared in the early Pleistocene as ice age climates began to grip the earth. We hypothesize that this co-occurrence is causal. The human ability to adapt by cultural means is, in theory, an adaptation to highly variable environments because cultural evolution can better track rapidly changing environments than can genes. High resolution ice and sediment cores published in the early 1990s showed the last ice age was characterized by high amplitude millennial and submillennial scale variation, exactly the sort of variation mathematical models suggest should favor a costly capacity for culture. More recent cores suggest that over the last several 100 thousand year glacial cycles the amount of millennial scale variation has increased rather dramatically in parallel with increases in hominin brain size and sophistication of the artifacts they made.

Introduction

The evolution of the human species presents a hard problem for the science of evolution to solve. The evolution of our large brain and associated complex technology and large scale social organization was a spectacularly successful adaptation, at least in the late Pleistocene and Holocene. Yet vertebrates with generically rather similar nervous systems¹ and many other complex adaptations, like camera style eyes and internal skeletons, evolved 350 million years ago. One way to explain such a late evolution of the human adaptation is to assume that the evolution of complex features like the human brain is a very slow process. However, many modern studies of evolution suggest that it is actually quite fast on the geological time scale.² Another explanation is that the sorts of environments that might favor the human adaptation did not occur until quite recently, geologically speaking. The challenges of a highly variable environment might result insufficiently strong selection pressure to favor the sort of problem solving that would require a large brain. The Pleistocene environment with its high amplitude, rapid variation in climate is potentially the geologically unique environment that could favor our large brains. The argument in this paper is that the Pleistocene environment was indeed what selected for the human brain and the culture it produces.

Preadaptations and Human Uniqueness

The first part of the argument relies on the understanding of some unique preadaptations that explain how the evolution of human culture in the Pleistocene might be possible. Hill *et al.*³ stress bipedalism and the potential to cover larger geographical areas. Bipedalism is linked to the possibility to carry more objects with less cost and to develop hands specialized for tool use. The long apeline span opened up opportunities to learn to use tools to extract otherwise unavailable resources from the environment. These preadaptations in turn favored the evolution of a capacity to adapt to environmental variation using the cultural transmission of ever more complex technology. Human subsistence eventually came to depend upon toolkits so complex that no one individual could hope to reinvent more than a small fraction of them.⁴ Similarly, our australopithecine ancestors probably lived in fairly large groups, something like those of chimpanzees and bonobos. Our lineage was preadapted to evolve complex social insti-

¹ STRIEDTER, G. F. *Principles of Brain Evolution*. Sinauer, 2005.

² THOMPSON, J. N. *Relentless Evolution*. Chicago: University of Chicago Press, 2013.

³ HILL, K.; BARTON, M. & HURTADO, A. M. The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology*, 18:174-187, 2009.

⁴ BOYD, R.; RICHERSON, P. J. & HENRICH, J. The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences*, 108 (Supplement 2): 10.918-10.925, 2011. <http://www.pnas.org/content/108/suppl.2/10918.abstract>

- ⁵ BURKART, J. M.; HRDY, S. B. & VAN SCHAIK, C. P. cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, 18: 175-186, 2009.
- ⁶ MOFFETT, M. Human Identity and the Evolution of Societies. *Human Nature*, 24 (3):219-267, 2013. <http://dx.doi.org/10.1007/s12110-013-9170-3>
- ⁷ HENRICH, J. Demography and cultural evolution: Why adaptive cultural processes produced maladaptive losses in Tasmania. *American Antiquity*, 69(2):197-214, 2004. KLINE, M. A. & BOYD, R. Population size predicts technological complexity in Oceania. *Proceedings of the Royal Society B*, 277:2.559-2.564, 2010.
- ⁸ KLEIN, R. G. *The Human Career: Human Biological and Cultural Origins*. Chicago: University of Chicago, 2009.
- ⁹ BARRETT, H. C. A hierarchical model of the evolution of human brain specializations. *Proceedings of the National Academy of Sciences*, 109(Supplement 1): 10.7333-10.740. 2012. <http://www.pnas.org/content/109/suppl.1/10733.abstract>
- ¹⁰ READER, S. M. & LANDAU, K. N. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences USA*, 99:4.436-4.441, 2002.
- ¹¹ ZACHOS, J. et al. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292(5517): 686-693, 2001. <http://www.sciencemag.org/cgi/content/full/292/5517/686> e <http://www.sciencemag.org>
- ¹² JERISON, H. J. *Evolution of the Brain and Intelligence*. New York: Academic Press, 1973.
- ¹³ TENNIE, C.; CALL, J. & TOMASELLO, M. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Trans-*

tutions, perhaps beginning with cooperative child rearing. Culturally transmitted social institutions led to the evolution of extensive cooperation first with extended families and then with non-kin.⁵ Eventually, human societies became regulated by institutions so efficiently that we can cooperate with people who are only known to us by their social status, societies that Moffett⁶ calls “anonymous.” The simplification of culture apparent on isolated islands suggests that fairly large social networks are necessary to support culture of the complexity apparent in the late Pleistocene and Holocene.⁷ These preadaptations mostly evolved since the separation of the hominin lineage from that of the other apes (5-6 million years ago (mya)) but before the evolution of our genus 2-2.6mya.⁸ If our environment driven hypothesis is correct we must be able to point to environmental changes over the last 2.6 mya that might plausibly have favored the evolution of very large brains and the complex cultures they support.

Climate variation in the Pleistocene

The Pleistocene climate is potentially an important factor in the evolution of the very large human brain and also an important step in the development of a culture. Large brains support cognitive systems for contingent behavioral responses to variable environments using some combination of norms of reaction⁹, and open-ended innovation, individual learning, and social learning¹⁰. The Pleistocene ice ages are the culmination of an irregular trend toward cooler, drier and more variable climates over the course of the Cenozoic. Cooling was least marked at the equator but increased low latitude aridity led to deserts, grasslands, and arid woodlands with their extensive small-scale mosaicism.¹¹ A general trend toward larger brains occurred in many mammalian lineages during this period¹² although absent our critical preadaptations for tool use and sociality no other species appears to have evolved a capacity for the cumulative evolution of complex cultural adaptations¹³.

Our understanding of the Pleistocene environment derives from proxy data recovered from ice and ocean sediment cores, and other datable deposits. $\delta^{18}\text{O}$ and pollen grains are examples of these paleoclimate proxies.¹⁴ $\delta^{18}\text{O}$ is expressed as deviations from a standard sample in parts per thousand of the ratio of the main natural heavy isotope of oxygen to the most abundant isotope ^{16}O . $\delta^{18}\text{O}$ is sensitive mainly to the volume of ice in glaciers because a molecule

actions of the Royal Society B: Biological Sciences, 364 (1528):2.405-2.415, 2009. <http://rstb.royalsocietypublishing.org/content/364/1528/2405.abstract>

- ¹⁴ BRADLEY, R. S. *Paleoclimatology: Reconstructing Climates of the Quaternary*. Third Edition. New York: Academic Press, 2013.
- ¹⁵ OPDYKE, N. D. Mammalian migration and climate over the last seven million years. In: VRBA, E. S. et al. (Eds.). *Paleoclimate and Evolution, With Emphasis on Human Origins*. New Haven: Yale University Press, 1995.
- ¹⁶ KLEIN, E. & LACHIÈZE-RAY, M. *The Quest for Unity: The Adventure of Physics*. Oxford: Oxford University Press., 1999.
- KLEIN, R. G. *The Human Career: Human Biological and Cultural Origins*. Chicago: University of Chicago. 2009.

with an atom of the heavier isotope has a lower vapor pressure than the more common molecules with two lighter atoms. Hence, as ice volume increases the heavier atoms disproportionately remain in the oceans and the lighter ones are disproportionately distill into the atmosphere to be precipitated and stored in the polar ice sheets. Pollen grains rain out into lakes and coastal oceans providing a rough picture of the prevailing local vegetation which in turn is sensitive to paleoenvironment.

Glacial cycles are identified utilizing these proxies. Figure 1, depicts the development of glacial climates since the mid-Miocene. Our genus *Homo*, marking the beginnings of brain size increase and dependence on stone tools, evolved during a time when the climate changed from the domination of a 23 thousand year (ky) cycle to one dominated by a higher amplitude 41ky cycle. Nevertheless, this change, by itself, probably did not favor cultural evolution or the increase of brain size to support it. The variation presented in these cycles are rather slow to require costly adaptations for phenotypic flexibility. It could be accommodated by humans due to genetic changes and range shifts.

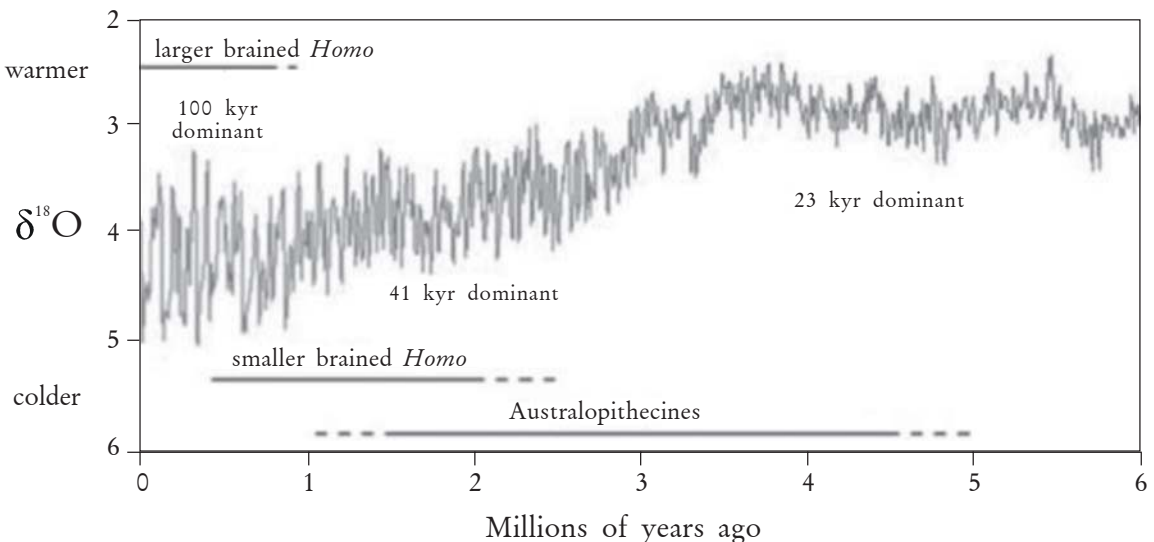


Figure 1: A composite marine core record of climate deterioration since the mid-Miocene. Periods during which different orbital quasi-cycles dominate the variation in $\delta^{18}\text{O}$ are indicated. The time lines for important groups of hominine taxa are indicated. The line for small-brained *Homo* includes *H. rudolfensis*, *erectus*, and *ergaster*. The line for large-brained *Homo* includes *H. heidelbergensis*, *neanderthalensis*, and *sapiens*. Redrawn from Opdyke¹⁵; Hominin time lines adapted from Klein & Lachièze-Ray¹⁶. See also deMenocal¹⁷.

¹⁷ deMENOCA, P. B. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters*, 220:3-24, 2004.

¹⁸ BOYD, R. & RICHERSON, P. J. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press, 1985.

¹⁹ DITLEVSEN, P. D.; SVENSMARK, H. & JOHNSEN, S. Contrasting atmospheric and climate dynamics of the last-glacial and Holocene periods. *Nature*, 379(29 February): 810-812, 1996.

²⁰ BOND, G. *et al.* Correlations between climate records from North Atlantic sediments and Greenland ice. *Nature*, 365 (9 September): 143-146, 1993.

Theoretical models¹⁸ suggest that individual learning and similar mechanisms of phenotypic flexibility are advantageous when environments are changing so rapidly in space or time that individuals' environments are only weakly correlated with that of their parents or cultural models. If environmental change is sufficiently slow, animals will adapt genetically or shift their ranges. A costly system of social learning is most adaptive under conditions of high amplitude variation at medium time scales. Small-scale fad and fashion changes occur on an annual time scale whereas major Holocene trends in social organization and technology have unfolded on the time scale of millennia. The coupling of individual learning and choice-making to an inheritance system based on imitation and teaching allows cultural adaptations evolve much more swiftly than is possible by the genetic system. The last glacial is notable for having much variation at millennial and submillennial time scales as seen in figure 2. Note how variable the climate was in the Pleistocene compared with the last 11,500 years of the Holocene. Paleoeological reconstruction is less well advanced than paleoclimate reconstruction. We do not yet have much information on conditions in the critical region of tropical Africa where so much hominin evolution occurred. Ambitious attempts to rectify this important data gap are under way.

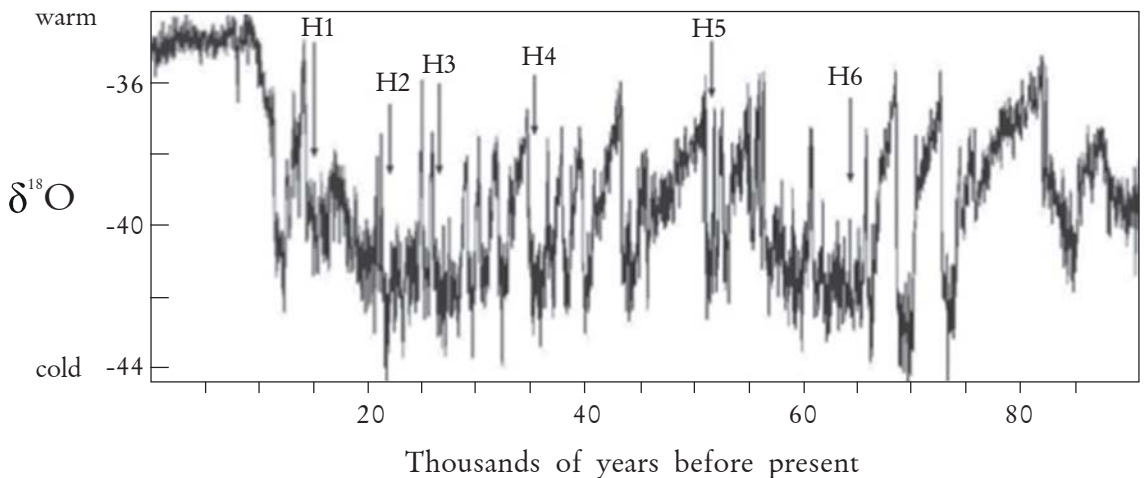


Figure 2: The Greenland ice paleotemperature proxy record. These data are filtered (averaged) using a 150 yr. low-pass filter so that variations on the time scale of 150 years and less are not portrayed. The Holocene is the little-varying last 11,000 years. The Heinrich events, when large volumes of ice-rafterd debris from the North American Glacier were deposited in the western North Atlantic, are noted as H1-H6. Redrafted after Ditlevsen, Svensmark & Johnsen¹⁹ and Bond *et al.*²⁰.

Implications for human evolution

The Pleistocene climate variation must have been a challenge in terms of survival for all species. Our critical preadaptations probably led to our uniquely large brain and the capacity for complex cumulative cultural traditions that this brain makes possible.²¹ Consequences of this period in the human history can be tracked also by the development of tool use and the repeated range expansion of hominins out of Africa.

The relationship between the earth's climate variation and human evolution is reflected in the increase of brain size in this period. Paleoclimatologists have begun to obtain high resolution records beyond the last glacial-interglacial cycle. A marine core from the eastern Atlantic off Iberia covering 4 100,000 year glacial-interglacial cycles²², and the EPICA Dome C ice core from Antarctica covering 8 glacial-interglacial cycles²³, are the longest high resolution cores to date. They trace how the millennial scale variability of climate evolved in the middle and late Pleistocene. In the figure 3, abrupt climate events depicted by these cores suggest a relation with events of increase in brain size.²⁴ As the number of abrupt changes in the cores increases, so does human brain size.

Brain size is significant because brains are expensive organs. In an adult, the brain consumes ~16% of total metabolism against 5% for mammals with average brain size.²⁵ Normally, small brains will be favored by natural selection. However, in complex or variable environments, big brains might be adaptive. Jerison's²⁶ fossil brain endocast data suggested that many mammalian lineages besides humans evolved larger brains rapidly in the Pleistocene, though the resolution of this record is far poorer than the Ash and Gallup one in figure 3. The hypothesis that human brain size increase was responding to the selective pressures exerted by increases in millennial and sub-millennial climate is thus supported by the available data. As the spatial and temporal resolution of the data continues to improve it will be tested ever more rigorously.

The more specific hypothesis here is that increasing human brain size supported increasingly complex cultural adaptations as climate variation increased. An alternative hypothesis is that big brains supported individual intelligence rather than the social intelligence born of passing good ideas on by cultural transmission coupled with marginal improvements by individuals. In the cultural scenario, individuals might not be much, if any, smarter at the individual

²¹ RICHERSON, P. J. & BOYD, R. Built for speed: Pleistocene climate variation and the origin of human culture. In: TONNEAU, F. & THOMPSON, N. S. (Eds.). *Perspectives in Ethology 13: Evolution, Culture, and Behavior*. Kluwer Academic/Plenum, 2000.

²² MARTRAT, B. *et al.* Four climate cycles of recurring deep and surface water destabilizations on the Iberian margin. *Science*, 317(5837): 502-507, 2007.

²³ LOULERGUE, L. *et al.* Orbital and millennial-scale features of atmospheric CH₄ over the past 800,000 years. *Nature*, 453(7193):383-386, 2008. <http://dx.doi.org/10.1038/nature06950> e http://www.nature.com/nature/journal/v453/n7193/supinfo/nature06950_S1.html

²⁴ RICHERSON, P. J. & BOYD, R. Rethinking paleo-anthropology: A world queerer than we supposed. In: HATFIELD, G. & PITTMAN, H. (Eds.). *Evolution of Mind, Brain, and Culture*. University of Pennsylvania Museum of Archaeology and Anthropology, 2013. p. 263-302.

²⁵ AIELLO, L. C. & WHEELER, P. The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, 36(2):199-221, 1995.

²⁶ JERISON, H. J. *Op. cit.*

²⁷ BOYD, R.; RICHERSON, P. J. & HENRICH, J. *Op. cit.*

²⁸ RICHERSON, P. J. & BOYD, R. Rethinking paleo-anthropology... *Op. cit.*

²⁹ MARTRAT, B. *et al. Op. cit.*

³⁰ LOULERGUE, L. *et al. Op. cit.*

³¹ ASH, J. & GALLUP, G. Paleoclimatic Variation and Brain Expansion during Human Evolution. *Human Nature*, 18(2):109-124, 2007. <http://dx.doi.org/10.1007/s12110-007-9015-z>

level than our marginally cultural Pliocene Australopithecine ancestors²⁷. (Note that, though opposed, these are not mutually exclusive hypotheses.) Understanding the challenges presented by living in the drier, more open environments of the Pleistocene is critical to testing this claim. Pleistocene environments were more dynamic, but also more productive of large game, than the closed canopy forests from Miocene. Richerson & Boyd²⁸ suggest three adaptive challenges that can be associated with this environment. The first one is how to take large herbivores and acquire other resources regularly in open spaces infested with many large carnivores that can easily outrun humans. Second is dealing with an uncertain environment with constant changes. Finally, the maintenance of a complex cultural system is a problem when populations are too small.

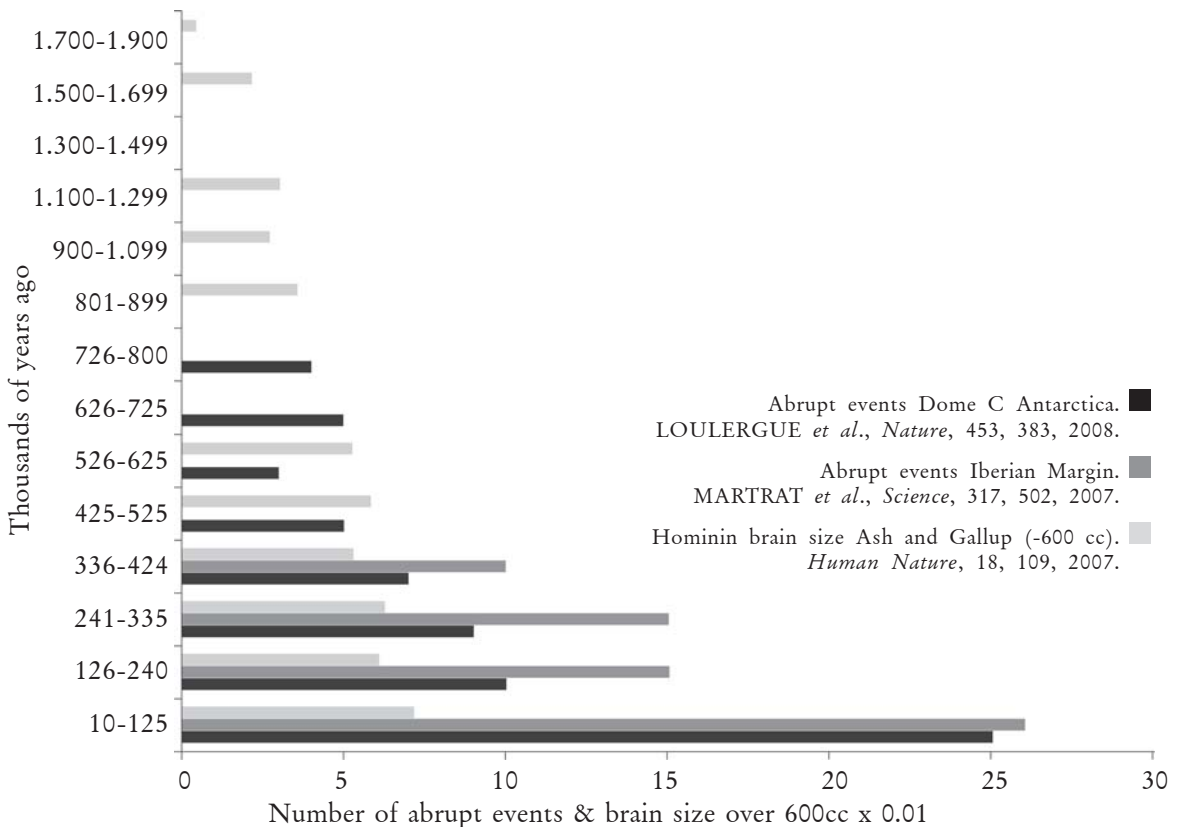


Figure 3: Number of abrupt events per glacial cycle and human brain size increase. Gray bars: sea-surface temperature in the Eastern Atlantic off Iberia. Martrat *et al.*²⁹. Black bars: Atmospheric methane concentration estimated from bubbles trapped in the EPICA Dome C ice core from Antarctica. Loulergue *et al.*³⁰. Number of abrupt events indicated by original authors in both cases. Open bars: Human brain size increase above ape baseline of 600 cc. Sample sizes per time bin range from two to twenty-seven. A single outlier in the 726-800 bin not plotted³¹.

³² AIELLO, L. C. & WHEELER, P. *Op. cit.*

³³ HILL, K.; BARTON, M. & HURTADO, A. M. *Op. cit.*

³⁴ ELTON, S.; BISHOP, L. C. & WOOD, B. Comparative context of Plio-Pleistocene hominin brain evolution. *Journal of Human Evolution*, 41:1-27, 2001.

³⁵ KLEIN, R. G. *Op. cit.*

³⁶ PERREAULT, C. The pace of cultural evolution. *PLoS ONE*, 7(9): e45150. 2012. <http://dx.doi.org/10.1371/journal.pone.0045150>

Game is a potential source of the protein and fat needed to grow and support a larger brain. As Aiello & Wheeler³² note, humans have apparently traded off the length of our gut (also expensive tissue). Short guts require energy dense foods. In addition to game, people often consume nutrient dense seeds and tubers that are unavailable to other herbivores. Gut size and brain size thus likely coevolved. Better technology led to more efficient hunting and gathering, which led to more nutrient dense diets, which permitted still larger brains and shorter guts. We have met this challenge through the emergence of the tool use that was in turn allowed through the emergence of bipedalism (discussed in the first section). Humans specialize in acquiring a suite of “extracted” resources that are largely unavailable to primate competitors.³³ Elton *et al.*³⁴ present data suggesting that early tool using hominins, but not the coexisting savanna dwelling ancestor of the gelada baboon, underwent cranial expansion in the early Pleistocene.

If tool use was an important proximate reason why large brains became progressively more important in the Pleistocene, then we should see a reasonably tight relationship between toolkit complexity and brain size. Klein’s³⁵ paleoanthropology textbook summarizes the evidence, which is depicted schematically in figure 4. Toolkit complexity does in fact follow roughly the same trajectory as brain size increases and increases in climate variation. Note that the rate of evolution of the toolkit appears to increase during the last 200,000 years, culminating in the Upper Paleolithic after 50 kya, when the diversity of the materials utilized to make tools, such as bones, ivory and shells, and their variety and sophistication more generally, reaches levels observed among living stone age people studied by ethnographers.

Dealing with the variable environment, the second challenge, is possible through our capacity of social learning. Currently, direct tests of this part of the cultural adaptation hypothesis are difficult due to the poor spatial and temporal resolution of the paleoecological and paleoanthropological records. We just don’t know in any comparative detail how humans and less cultural species responded to the increasing variability of the climate. This problem is widely recognized by both sets of specialists and work to improve the record is ongoing on many fronts. In the meantime, it is possible to estimate empirically rates of cultural evolution at different time scales using a large number of archaeological time series and compare them to rates of genetic evolution.³⁶ Cultural change occurs faster across

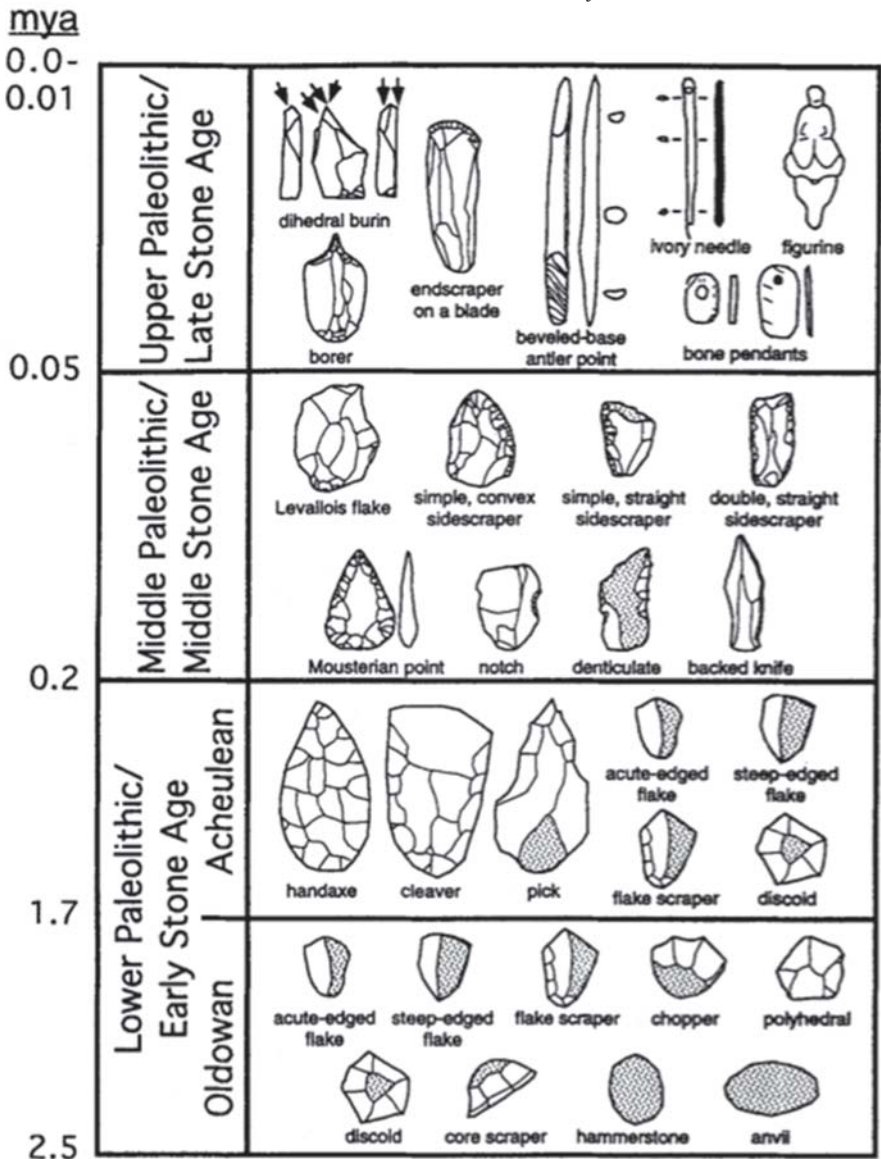


Figure 4: Stone tools increased in complexity during the Pleistocene. The rate of increase in complexity increased in the last 200,000 years and bone, antler, and ivory tools became common after 50,000 years ago. From Klein³⁷.

the most of the range of time scales resolved by the archaeological data. Interestingly, they do converge at the very shortest time scales estimated from microbial populations. Human fads and fashions evolve on annual time scales, much as flu viruses do. Thus we can imagine that when the environments of the last ice age depicted in figure 2 underwent their extremely abrupt changes (often nearly instantaneous within the limits of resolution of the cores, a few years to a few decades), humans could rapidly construct revised adaptations by using individual learning to discover better practices and trading various individual discoveries

³⁷ KLEIN, R. G. *Op. cit.*

on a short time scale over large areas by social learning. Thus no one individual would have to bear more than a small fraction of the cost of individual learning and yet complex new adaptations could evolve quickly.

³⁸ HENRICH, J. *Op. cit.*

The third challenge is the maintenance of complex cultures as a foundation for rapid innovation. In very small populations, stone age toolkits tend to simplify.³⁸ Parts of toolkits that might be re-purposed and recombined for new

tasks tend to disappear. This phenomenon may explain some of the subtleties of the relationship between brain size and toolkit complexity. Both anatomically Modern People and Neandertals usually made Middle Paleolithic tools before 50 kya, although Southern Africa appears to have short-lived regional exceptions to this generalization.³⁹ Perhaps temporary increases in population before 50 kya and more permanent ones after 50 kya allowed toolkit complexity to progressively accumulate.

Expansion of the human population outside Africa may also be a result of this development. Atkinson, Gray & Drummond⁴⁰ used mtDNA to track the size of human population in 8 regions of the globe across the time. They conclude that the first expansion occurred around 52kya to Southern Asia. Not long after, the expansion reaches Northern and Central Asia (~49 kya), Europe (~42 kya) and Middle East (~40 kya). The last expansion, matching with the last glacial maximum (~20 kya), seems to occur to the Americas (~18 kya). The period 60-10 kya have been the most variable detected in the high resolution climate record. Perhaps humans did not so much get smarter around 50 kya as become numerous enough to evolve and sustain more complex toolkits than before. The population increase in turn might have resulted from humans being more effective competitors for the top carnivore niche in a highly variable environment where cultural adaptations were especially useful to track those fluctuations. Using cultural strategies to exploit extracted resources might tell a similar story.

Conclusion: Macroevolutionary explanations

To explain large scale evolutionary trends and events, such as we described here, the commonest, often tacit, hypotheses proposed are *internalist*. In this approach, brain size increase would be taken to happen at slow rates, limited by complex relations between genotypes and phenotypes. Many specific mutations and recombinations would have needed to occur and be tested by selection to get on the brain that we have today. A long time is thus required to evolve a structure complex as our brain. We think that this internalist argument is wrong.⁴¹ Our brain size more than doubled in two million years and to judge from responses to artificial selection strong selection could accomplish such an increase in an even shorter period of time. What internal preconditions selection did probably require

³⁹ JACOBS, Z. *et al.* Ages for the Middle Stone Age of Southern Africa: Implications for human behavior and dispersal. *Science*, 322:733-735, 2008.

⁴⁰ ATKINSON, Q. D.; GRAY, R. D. & DRUMMOND, A. J. mtDNA variation predicts population size in humans and reveals a major southern Asian chapter in human prehistory. *Molecular Biology and Evolution*, 25(2):468-474, 2008.

⁴¹ RICHERSON, P. J. & BOYD, R. Rethinking paleo-anthropology... *Op. cit.*

for human culture to evolve were the anatomical and social preadaptations for tool use and cooperation furnished by our bipedal ape ancestors. The australopiths had upright posture for millions of years before the first stone tools appear during the climate deterioration of the late Pliocene, suggesting that the preadaptations alone were not sufficient to favor a highly cultural adaptation.

The externalist sort of hypotheses seek a large environmental change to explain big evolutionary events. The onset of the Pleistocene climate variation 2.6 mya set in motion evolution in many lineages and reorganized the earth's biomes repeatedly by range changes. These changes are certainly candidates to do explanatory work in human evolution. Some paleobiologists have long argued that natural selection is a powerful force on the geological time scale.⁴² So the idea that selection for increasingly sophisticated social learning could track ongoing increases in millennial and submillennial scale climate variation with relatively short lags is not farfetched. Internalist and externalist are competing but not mutually exclusive hypotheses. We have developed a strongly externalist hypothesis here in part because we think that such hypotheses are too-often neglected in the study of human evolution. But we also appeal to internalist ideas of preadaptation to account for why only our lineage responded climate variation with adaptation by complex cumulative culture.

We hope to have convinced the reader that externalist hypotheses are generally important in macroevolutionary explanation. Microevolutionists certainly typically find that the organisms they study are responding to ongoing environmental changes.⁴³ Such studies suggest to authors like Walker and Valentine that internal limitations on organic evolution can exert themselves only on relatively small time scales. On the other hand, failures of complete convergence of plant and animal form in the various biogeographic realms suggest that historical contingency and hence internal limitations of some kind exist on long time scales. Only creatures in our lineage came to have such a large dependence on cultural adaptations. The question of what regulates the tempo and mode of evolution is an old but still an open one. The evolution of the hominins and the environments we evolved in is the focus of an unusual amount of attention and yet the macroevolutionary issues are mostly neglected.

⁴² WALKER, T. D. & VALENTINE, J. W. Equilibrium models of evolutionary species diversity and the number of empty niches. *American Naturalist*, 124:887-899, 1984.

⁴³ THOMPSON, J. N. *Op. cit.*

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