

Built for Speed: Pleistocene Climate Variation and the Origin of Human Culture

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Abstract. Recently, several authors have argued that the Pleistocene climatic fluctuations are responsible for the evolution of human anatomy and cognition. This hypothesis contrasts with the common idea that human language, tools, and culture represent a revolutionary breakthrough rather than a conventional adaptation to a particular ecological niche. Neither hypothesis is satisfactory. The “Pleistocene hypothesis”, as proposed, does not explain how Pleistocene fluctuations favor the particular adaptations that characterize humans. The alternative hypothesis does not explain what has prevented many animal lineages in the remote past from evolving a similar adaptive complex of tools, language and culture. Theoretical models of the cultural evolutionary process suggest some answers to these questions. Learning, including social learning, is rather generally a useful adaptation in variable environments. The progressive brain enlargement in many mammalian lineages during the last few million years suggests that climatic deterioration has had the general effect predicted by the Pleistocene hypothesis. Increased dependence on simple social learning was a preadaptation to the evolution of a capacity for complex traditions. The evolution of a costly capacity to acquire complex traditions is inhibited because, initially, complex traditions will be rare. Having the capacity to learn things that are far too complex to invent for oneself is not useful until traditions are common, but traditions cannot become complex before the capacity to acquire them is common. This problem may explain why many animals became more sophisticated learners in the Pleistocene, but why complex, cumulative cultural traditions are so rare. The history of our lineage must have included unique preadaptations that permitted us to evade the useless-when-rare problem.

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Introduction

The evolution of humans is a major event in the Earth's biotic history. Never before has a single species of organism so dominated the planet. Hunting and gathering people penetrated to nearly every habitable scrap of the Earth's surface by the end of the Pleistocene. Beginning about 10,000 years ago, food plant production, and its evolutionary sequelae, have made us a geochemical and geophysical force to be reckoned with.

Most accounts of human origins take this ecological dominance as a sign of a qualitatively new and superior form of adaptation and ask, what evolutionary breakthrough led to the unique human adaptive complex—tool making, language, complex social organization, and other aspects of culture.

More recently, behavioral ecologists (Smith and Winterhalder 1992) have pursued a different line of research. They argue that humans are just, as Foley (1987) put it, “another unique species.” According to the theory of evolution by natural selection, change results from adaptation to local environments. Scholars in this tradition are suspicious of granting human culture and its products special status. Rather than being a history of a breakthrough to a new adaptive plane, human evolution is more likely a history of adaptation to local environments that happens to have resulted in our current ecological dominance by accident.

Evolutionary psychology is an active research program. Several of the practitioners of this research program believe that much human behavioral variation is the evoked product of innate structure in the mind and minimize the role of cultural transmission (Thornhill, Tooby, and Cosmides, 1996; Pinker, 1997; in contrast see Nisbett and Cohen, 1996). They argue that we should be able to infer the cognitive adaptations ought to characterize human minds from the challenges of living as a hunter-gatherer in the Pleistocene. On this view, cognitive adaptation to the Pleistocene should take the form of many innate modular algorithms, each designed to solve a particular adaptive problem posed by occupying such a niche. Much variation in human behavior, on this view, results from the same innate modules expressed in different environments. In other words a substantial fraction of human behavior across space and time results from the contingent decisions made in the different environments.

Most social scientists imagine a much larger role for transmitted culture in explaining human behavioral diversity. According to this view, what most distinguishes human cognition from that of most other animals is our capacity to transmit large amounts of information culturally, by teaching and imitation. Sophisticated innate cognitive structures are certainly necessary make such transmission possible and to guide it in adaptive directions. However, these innate structures have the effect of setting up a rather general-purpose adaptive system, witness the ability of human populations, using a stunning diversity of culturally transmitted technologies and social institutions, to live practically anywhere on earth. Is there anything about Pleistocene

environments that would have favored the evolution of such an extra-genetic, general-purpose adaptive system?

The deterioration of the Earth's climate during the Pleistocene ice age is a major event in the history of the planet's physical environment. Over the last 6 million years, the climate has gotten colder, drier, and more variable. Geology records several other glacial episodes, but the most recent prior one ended 250 million years ago, well before the age of the dinosaurs (Lamb, 1977:296). Theoretical models of cultural evolution suggest that social learning enhances ability to respond to temporal and spatial variations in the environment. Cultural evolution allows speedy tracking of a rapidly fluctuating environment because it supplements natural selection with learning and other psychological forces. The main hypothesis in this paper is that social learning is a specific mechanism by which mammals adapted to the Pleistocene climate deterioration. Many animal lineages seem to have taken advantage of the potential of simple forms of social learning. In many respects, human culture is nothing more than a straightforward adaptation to climatic deterioration. However, humans do differ from proto-cultural animals in having the ability to evolve complex, multi-part cultural traditions that must evolve cumulatively, normally over many generations. Technology and social organization furnish many examples of complex traditions that evolve by descent with modification like complex organic adaptations (albeit at a faster rate), whereas other animals have little or no ability to acquire complex traditions. Many aspects of human cognition probably evolved in parallel with the other recently encephalized mammalian lineages, but a complete explanation must deal with our unique dependence on complex traditions.

If the hypothesis here is correct, the central issues of human evolution are how the capacity for complex culture arose from simpler precursors and why our species is unique in possessing what appears to be a rather generally successful adaptation. The correlation between the deteriorating environment of the last few million years and brain size enlargement in mammals generally is strong. This pattern supports the theoretical argument that speed of evolution is the central adaptive advantage of social learning. However, it makes the central puzzle of humans more pointed. If many mammals possess the basic proto-cultural preadaptation for complex culture, why has only our species gone on to acquire the capacity for complex culture? Theoretical models suggest some reasons why the evolution of complex culture may be inhibited until some key preadaptation—more likely a succession of preadaptations—in addition to proto-culture occurs, finally resulting in the breakthrough to culture on the human scale of sophistication.

Reconstructing the evolution of any given lineage involves taking account of poorly understood historical contingencies, requiring some speculative leaps to produce an account of what happened. Nevertheless, explanations of particular historical trajectories are not inherently unscientific (Hull, 1992, Boyd and Richerson, 1992). Every speculation is a hypothesis to be tested, and, indeed, clever investigators often find a way to do so. Sparse data and the inherent unpredictability of evolutionary phenomena do limit, perhaps sharply limit, the detail to which reconstruction can aspire. However, we can reasonably hope to understand the general

processes that shaped our evolution in the face of these limitations. One test that any acceptable theory of human evolution must pass is a fit to the large-scale patterns of the paleontological and paleoenvironmental records. This chapter uses such data to test predictions stemming from the general evolutionary properties of systems of social learning and human culture.

Culture As An Adaptation To Variable Environments

Social Learning A Response to Variability Selection

Potts (1996:231–238) has argued that the fluctuating climates of the Plio-Pleistocene have imposed a regime of what he calls “variability selection” on the Earth’s biota. When environments vary, Potts argues, “genetic variations favor open programs of behavior that vary and extend the adaptive possibilities of the individual. These are conserved in the gene pool over time because of the inconsistency in the short-term effects of natural selection. Organisms eventually build up an inheritance system that enables them to buffer larger and larger disturbances in the factors governing survival and successful reproduction” (Potts, 1996: 237; see also Davies, et al., 1992). This is an interesting supposition, though lacking in detail about mechanisms. Social learning is a mechanism for adapting to variable environments that may increase dramatically under variability selection. Odling-Smee (this volume) traces out in some detail how the genetic and social transmission might coevolve under an extended regime of variability selection.

Testing this idea is a formidable challenge. Certainly not every lineage on the earth responded to the onset of glacial fluctuations by evolving social learning. Further, humans are the only species to respond to the ice age by evolving the very complex forms of social learning usually given the term “culture.” The unique importance of culture in humans is an embarrassment the hypothesis. How can an environmental event that affected the entire earth account for the evolution of one species’ peculiar adaptation? The skeptic might ask, if social learning is an adaptation to the Pleistocene, why aren’t many species capable of human-like feats of social learning? Is there any evidence that social learning has anything to do with climatic deterioration? How does social learning fit into a pattern of responses to variability selection if indeed this concept is useful?

The hypothesis that climatic variability drove the evolution of human culture derives from the study of theoretical models of the processes of cultural evolution. These models are meant to mimic several aspects of culture. They ask, under what environmental circumstances is a capacity for social learning an adaptive advantage? Like any other adaptation, social learning has costs and benefits, and selection will tend to reach a reliance on social learning that optimizes fitness. What is the basic shape of the adaptive tradeoffs for such systems? A common theme in the results of many models is that social learning is an effective adaptation to spatially and temporally variable environments (Boyd and Richerson, 1985). The models suggest that social learning should commonly arise as an adaptation to variable environments whenever there is an opportunity to learn from more experienced conspecifics.

Most of these models are so basic that they apply equally to simple systems of animal social learning based on stimulus or local enhancement (Galef, 1988) and to the sophisticated systems of imitation used by humans, and perhaps a few other animals, to create complex cultural traditions. Hence most of what follows uses terms like “social learning” and “culture” as if they were synonyms. The difference is important, however. Human culture based upon rather free imitation supports massive amounts of social learning. Although simple social learning seems to be very common, complex culture based on imitation is much rarer (Moore, 1996). Some of the models suggest why the evolution of complex culture may present a special problem. The issue of complex traditions is discussed explicitly at the end of the chapter.

Simple Models of Social Learning

One of the most important general features of systems of social learning is that they are systems for the inheritance of acquired variation. What individuals learn for themselves others can acquire by social learning. Our (Boyd and Richerson, 1985) models of this process set up the basic adaptive calculus for a system of inheritance of acquired variation. To learn for itself, an animal will have to expend time and energy in learning, incur some risks in trials that may be associated with large errors, and support the neurological machinery necessary to learn. Social learning can economize on the trial and error part of learning; if offspring learn from parents or other conspecifics, they can avoid repeating their mistakes. With social learning, it may also be possible to economize on neurological machinery. Individual learning does not need to be as powerful if most individuals can rely upon social learning most of the time, turning to individual learning only if something indicates that a behavior copied from an experienced conspecific is seriously awry. Or, an animal can use the same neurological machinery to maintain more behaviors to a higher standard of adaptation. Natural selection ought to “tune” capacities for individual and social learning to maximize fitness in the face of their costs and benefits. There is also the alternative of transmitting innate patterns of behavior and foregoing phenotypic flexibility to a greater or lesser degree.

Because a mechanism of phenotypic flexibility, learning, is coupled to a scheme for acquiring the results of such learning by others, a socially transmitted behavior evolves in response to the Lamarckian pressure of learning as well as the pressure of natural selection (on the socially transmitted variation). We label the Lamarckian effect “guided variation” because it acts as an adaptively non-random form of mutation. Guided variation, using innate decision rules, causes a population’s behavior to track environmental change in time or space more accurately than can genes that only respond to selection. In the human case, cultural rules, or mixed innate and socially acquired judgments, may act to guide variation for other behaviors. Thus, natural selection on genes can favor the evolution of a social learning system in appropriately variable environments.

Without any further argument, you can see the temptation to attribute the evolution of cultural systems to the onset of Pleistocene climatic deterioration. A pattern of increasing environmental variation is just the thing to give capacities for various amounts and kinds of social learning an

adaptive advantage over systems of individual learning and innate repertoires lacking the inheritance of acquired variation.

The rest of this section describes two of the models we have used to more rigorously test the logic of these intuitive claims. Readers who already find the intuition compelling and the description of models tedious may wish to skip the rest of this section. Be warned, however, that theorists have already uncovered a number of subtle dynamic problems in systems of social learning (e.g. Rogers, 1989, Boyd and Richerson, 1996). As in evolutionary biology, the intricacies of cultural evolution and gene-culture coevolution frequently defy intuition and verbal reasoning, motivating the use of formal mathematical models.

To test the logic of the claim that systems of social learning are adaptive in variable environments, we constructed very basic models of the individual/social learning process along the following lines: Suppose that the individual learning process is the primitive state. Virtually all animals show at least rudimentary abilities to learn. When animals like birds and mammals come to have extended maternal care, they have the opportunity to learn socially. The models assume that individuals have two sources of information, their own experience and the vicarious experience of individuals with whom they are in social contact. Using two different kinds of models, one based on quantitative characters (Boyd and Richerson, 1985: Ch. 4), and another based on discrete characters (Boyd and Richerson, 1989), we investigated how selection might optimize the relative dependence on the two sources of information.

In the discrete character model, organisms can express one of two behaviors (e.g. forage collectively or solitarily) and in two environments, (e.g. wet or dry). There is a fitness benefit for behaving correctly (forage collectively if environment dry, forage alone if wet). Individuals collect some more or less error-prone information about the state of the environment by individual learning. They can also opt to imitate another individual. The degree of dependence on social versus individual learning is controlled by a confidence-interval-like learning threshold, d , to be set by selection at an optimal point (Figure 1). While growing up, individuals gain some idea of the state of the environment. Because of the noisiness of the environment and the inevitable limitations of individuals' observational capabilities, their conclusions as to whether the environment is in the wet or dry state will not necessarily be correct. Even if the environment is dry on average, some individuals will experience an unusual run of rainy years. They are vulnerable to mistakenly deciding that the state of the environment is wet when it is really dry. The confidence parameter d tells us how heavily individuals weigh their noisy samples. If d is large, individuals look for quite definitive evidence that the environment really is in the wet or dry state, say entirely quite wet or quite dry during their formative years. If they do not see such evidence, and most will not if the evidence available to individuals comes from an environment with noisy variation, they imitate an experienced individual of the parental generation, such as their mother. If d is small, information from personal experience is virtually always deemed definitive, and learners depend almost entirely on their personal experience.

The potential advantage of social learning stems from the population level properties of the learning system. In a spatially or temporally varying world, some mixture learning and social learning is generally advantageous. In a noisy world, an evolving population is tending to integrate the experiences of many individuals. One can be saved from the perils of small number statistics by trusting a sample of the population over the noisy data from the environment. On the other hand, in a variable environment, the individuals one might learn from: (1) may have gotten caught in an environment switch, (2) might have migrated from nearby environment in the other state, carrying the wrong trait for their current environment, (3) might have unluckily gotten seemingly definitive information that the environment is in the state that it is not and switched to the wrong trait. If personal experience is sufficiently indicative of the state of the environment, it is liable to be the better guess. The optimal confidence rule (value of d) depends upon the nature of the environmental variation and the quality of the evidence available from personal experience. If the environment fluctuates sufficiently rapidly in time, or if the spatial habitat mosaic is sufficiently tight that individuals often migrate to a patch different from their parents, individuals should depend entirely on their own experience. In such a world, parental generation behavior is a useless guide, and there is nothing to do but to trust to the main chance of personal experience. As the statistical resemblance between parental generation and offspring generation increases, it is safer to depend upon social learning and demand ever more definitive personal evidence before breaking with tradition. In a world where the environment seldom really changes, but which is rather noisy from the individual perspective, a combination of natural selection and rather conservative reliance on own experience will result in a population in which most individuals are doing the right thing. Social learning becomes quite trustworthy (Figure 2).

The quantitative character model is similar in spirit and leads to a similar conclusion. It has one continuous character (frequency of foraging alone versus cooperatively) and a continuum of environments from wet to dry. In any given environment at any one point in time or space, there is an optimal mix of solitary and cooperative foraging. Bayesian considerations suggest that individuals should use a weighted average of social learning and own experience to determine how to behave. The optimal weighting parameter in this model behaves qualitatively just as d does in the discrete character model. When two models with rather different structure give the same result we have some confidence that the results are robust to differences of detail.

Models focused on learning and social learning alone neglect the possibility that using genes instead of social transmission to transmit the population's "memory" to the next generation will restrict the range of environments in which social learning is favored. We (1985: Chap. 4) used the quantitative model to run a sort of mathematical tournament comparing the fitness advantages of using a conventional genes-plus-individual learning to a Lamarckian system of social learning plus individual learning. Suppose that there is some cost to being able to learn socially. Under what circumstances might there be a fitness advantage to adding social learning to the standard system where genes represent the wisdom of evolutionary history and individual learning bears the sole weight of running up the phenotypic fine tuning? The analysis varied the degree of fluctuation of the environment and the autocorrelation of the variation. Autocorrelation measures the pattern in the environmental variation as the value correlation between the

environments of older social models and younger naïve learners. If the variation is not autocorrelated at all, a statistical relationship between the environments of potential social learners and experienced individuals they might learn from is absent. If the autocorrelation is very high, pace of environmental change is very slow. Even though the environment may change a lot in the long run, the change from generation to generation is quite modest if autocorrelation is high.

A typical example of the results is shown in figure 3. The social learning system is a potential advantage over a wide range of conditions. The advantage of social learning is especially large when the environmental variance (V_H) is high and the degree of autocorrelation is high, but not too high. Under the parameter values chosen for illustration at least, the optimal dependence on social learning is often fairly high, on the order a 75% dependence on social models and a 25% dependence on individual learning. At very high autocorrelations, environments become so slowly changing that genes can track perfectly well, and the advantage of social learning disappears. The model suggests that social learning should be common, at least among social species living in variable environments.

We studied several other models in which the rules of social learning are more sophisticated than the copying of a random member of the population (Boyd and Richerson, 1985: Chaps. 5-7). For example, a socially learning individual might use several adults as models. If they exhibit two or more behaviors, the social learner might try each out and retain the one most often rewarded. Most behaviors current in a population are probably better than the trials that individual learners can attempt on their own. Plagiarism is easier than originality. Gathering a number of plausible initial guesses about the right behavior and using one's own experience to choose the best among them has advantages similar to the guided variation process discussed above. We call the series of forces on cultural evolution that result from non-random social learning "biased transmission."

Humans and some other animals also use cultural systems to evolve symbolically marked boundaries between sub-populations. This subdivision permits adaptive specializations to narrow niches to evolve rapidly. Much like speciation isolates ancestral populations by shutting off gene flow between them, culturally isolated groups reduce the flow of extraneous ideas from other environments so that their local adaptations can be perfected. Ethnic groups are a common example. Often, such groups are specialized to exploit particular habitats or economic roles (Barth, 1969). Models show that cultural badges—different language, dress, religious practices—can evolve to erect barriers to the free flow of ideas in spatially heterogeneous environments (Boyd and Richerson, 1987). (This is not the only evolutionary consequence of symbolic cultural badges, see Boyd and Richerson, 1985: Ch. 8.) Ethnic groups thus form the cultural analogs of reproductively isolated species. The main difference is that the barriers are much more permeable and the rate of evolution of culture is much higher than that of genes. Human cultural niche shifting is faster than that of animals that adapt mainly by organic evolution. Using this “pseudo-speciation” mechanism, late Pleistocene humans developed such a diverse array of subsistence economies that our species spread to the ends of the habitable earth

(Bettinger, 1991:203-5). Humans may not be the only species that uses this mechanism. Many birds learn their songs by imitating adults, creating local song traditions. Females may prefer to mate with males that sing the songs their fathers sang, potentially allowing the frequency of locally adapted genes to increase by restricting gene flow between groups (Nottebohm, 1975). Toothed whale vocalization dialects lead to similar population subdivisions according to Whitehead (1998).

The adaptationist account of non-human social learning is far from fully tested. An alternative hypothesis is that social learning is merely a byproduct of individual learning that has not come under selection for its improvement. Social learning may even be parasitical. Rogers (1989, see also Boyd and Richerson, 1995) constructed a model in which a social learning genotype could invade a population of individual learners. Initially, social learning is favored because social learners avoid the cost of individual learning and because they almost always imitate an individual learner. Thus, rare social learners get, on average, as adaptive a trait as they would get learning for themselves at less cost. However, as social learning increases in frequency, many social learners will acquire their behavior from another social learner. As the amount of individual learning goes down, the population as a whole will track changing environments less well. The social learners increase until their fitness falls to that of individual learners. Social learning in this case is not adaptive in the sense that it doesn't, in the end, raise the fitness of the individuals that do it. The reason that social learning is adaptive in our models is that individuals in their model use a strategy that mixes individual and social learning such that social learning makes individual learning cheaper and more accurate. Lefebvre (in press) discusses the tendency of flock living birds to scrounge off the food-finding behavior of skilled flock members, acquiring new food strategies by social learning without any apparent efforts to learn individually. The fitness consequences of social learning are yet to be measured in any species. Cases fitting Rogers' model are likely to turn up, and may be common.

The theoretical models thus provide only tentative “in principle” support for the hypothesis that a capacity for social learning is likely to be favored by variability selection. Do the paleoenvironmental and paleontological records give any empirical support to the hypothesis?

Pleistocene Climate Deterioration

The first element of the empirical test of the hypothesis is whether the Earth's climate has imposed a regime of variability selection on humans and other lineages using social learning as a means of adaptation. The critical period for the evolution of human brains and origin of complex culture is the late Pliocene and Pleistocene geological epochs (hereafter “Pleistocene” for short), about the last 3 million years (Klein, 1999). As we will see in the next section, many mammalian lineages probably evolved more sophisticated capacities for learning and social learning during the same period. Do climates of the recent geological past exhibit a pattern of increased variability with patterns of autocorrelation that might favor the evolution of capacities for social learning in accord with the predictions of the models?

Using a variety of proxy measures of past temperature, rainfall, ice volume, and the like, mostly from cores of ocean sediments, lake sediments, and ice caps, paleoclimatologists have constructed an increasingly detailed picture of climate deterioration over the last few million years, culminating in the Pleistocene ice ages (Bradley, 1999). The trend of deteriorating climates began in the mid-Miocene, about 14 million years ago. By the Pleistocene, the Earth's temperature had dropped several degrees and the amplitude of climate variation increased nearly 10 fold (Figure 4). The earliest fossils of our genus, *Homo*, and the first stone tools appear about 2.5 million years ago, at the end of the late Pliocene deterioration episode when the climate underwent a marked cooling and increase in the amplitude of fluctuations. The onset of the classic expansions and contractions of Northern Hemisphere continental ice sheets began in the middle Pleistocene about 900,000 years ago. Minimum temperatures at the height of glaciations became colder still and the amplitude of fluctuations increased still further. The final modernization of human anatomy and many aspects of culture occurred in the last 100,000 years. The origins of agriculture, and complex, literate societies date only to the last few thousand years, following a dramatic Holocene amelioration of the climate (Figure 5).

Pleistocene environments varied greatly in complex ways that presented organisms with major adaptive challenges. Many environmental variables were entrained in the Pleistocene glacial fluctuations. For example, glacial environments were not only colder but drier and had lower CO₂ content (deMenocal, 1995, Raynaud et. al., 1993). Thus, during glacials overall plant productivity was lower, but a higher percentage of plant communities were tundra, shrub desert, and steppe, which favor large herbivores. Ocean currents shifted dramatically (Lehman, 1993). The causes of the Pleistocene climate deterioration are not well understood. They are probably the result of basic geological processes, such as the isolation of the Antarctic continent from warm ocean currents by circum-Antarctic currents flowing through the gap created by continental drift between Antarctica and South America (Partridge, et al., 1995).

As time series analysts say, the climate record of the past few million years is highly *non-stationary*. Not only does the climate vary, but also the statistics that describe the variation—the mean, variance and patterns of autocorrelation—change with time. The amplitude of fluctuations in temperature (and many other climate variables) increased as mean temperature dropped, as figure 4 shows. The pattern of fluctuation in climate is very complex. Much of the variation seems to arise from an enhanced sensitivity to radiation changes caused by periodic variations in the Earth's orbit and its orientation with respect to the sun. The radiation income in high northern latitudes has a 20% range of variation due to these effects (Milankovitch, 1941, Broecker and Denton, 1990). The eccentricity of the Earth's orbit varies on a 95,800 year time scale, the inclination of its axis with a periodicity of 41,000 years, and the precession of the equinoxes with a periodicity of 21,700 years. As the deterioration has proceeded, different cycles have dominated the pattern, causing different patterns of autocorrelation. The 21,700 year cycle dominated during most of the Pliocene, the 41,000 year cycle between about 3 and 1 million years ago, and the 95,800 year cycle from 1 million years ago to the present (de Menocal and Bloemendal, 1995). These shifts in dominant frequency correspond to the step-like increases in amplitude of the fluctuations illustrated in figure 4.

More significant for the ecological processes that drive evolution, the rather stately fluctuations on the time scale of the orbital cycles have a great deal of rapid, noisy fluctuation superimposed on them. On the time scale of 10s of thousands of years, the environment is probably so highly autocorrelated on the generation-by-generation time scale that organic evolution and migration can track changes well enough. For the last 120,000 years, data from ice cores taken from the deep ice sheets of Greenland and Antarctica document a great deal of variation on much shorter time scales (GRIP, 1993; Lehman, 1993), as can be seen in figure 5. The time resolution in these cores is as high as a decade even deep in the cores. Even when the climate is in the grip of the ice, there were brief excursions of about a thousand years' duration in which the climate reached near interglacial warmth. The largest of these warm spikes caused mass wastage of the continental glaciers, detected as layers of coarse iceberg-rafted erosion debris in ocean sediment cores (Lehman, 1993). Data from the upper part of the Greenland ice cores shows that the last maximum was considerably more variable than the last 10,000 years on time scales of a few years, the minimum that can be resolved due to diffusion mixing the cores. Presumably, the greater variability extends right down to the degree of variation between years (Ditlevsen, et al., 1996). Geophysicists expect a “cascade” of variance from large scale, low frequency, fluctuations to shorter time scales from general principles. Thus increase in variance at low frequencies tends to increase variation at higher frequencies as well. The Pleistocene climate appears to have ample variance at many different time scales to drive selection for mechanisms to adapt to it. No matter what generation length we consider, much variation is likely to have existed with degrees of autocorrelation that would favor social learning.

The causes of the high frequency variation in the Greenland ice data are uncertain, but most likely involve interactions of ice, atmosphere, and ocean current dynamics that are thrown out of equilibrium by the longer time scale processes and by the unstable dynamics of ice sheets (Broecker et al., 1985, Manabe and Stouffer, 1995, Cane, 1998). The last Interglacial (65,000-130,000 years before present) may also have been highly variable on the short time scales, as it seems to be the case in figure 5. Interpretation of the deeper portions of the Greenland ice cores is controversial because of the possibility that ice from colder and warmer periods has been folded by ice movement to create false fluctuations (Grootes, et al., 1993). Nevertheless, many lower-resolution records of the last interglacial also suggest that it was frequently punctuated by episodes of near-glacial cold (e.g. Lamb 1977: 333). Significant stretches of warm, moist, relatively invariant climate were probably quite unusual in the Pleistocene. A recent long core from Antarctica shows that the previous 3 interglacials were spikes of warmth compared to the 11,000 year long plateau of the Holocene (Petit et al., 1999). The possibility that our current climate system might be easily tipped into a regime of much greater variability by relatively weak forcing is cause for considerable worry regarding human caused increases in carbon dioxide and other greenhouse gasses (Broecker, 1997).

The current picture of the high frequency variation of the Pleistocene climate system is incomplete. It is a reasonable inference that pre-Pleistocene climates were much like the last 11,000 years, and that this tranquil period is unusual for the Pleistocene. It is a reasonable

inference that the extreme climate variations at the generation-to-generation time scales that are recorded in the ice cores dating to the last glacial are typical of the whole Pleistocene but not of earlier Epochs. If it is true that cognitive evolution is caused by climate variation we can use the evidence of increases in cognitive sophistication described below to make predictions about past climates. These predictions will be tested. Paleoclimatic records are far from fully exploited. For example, the African Great Lakes, especially Lake Tanganyika, sediment columns several million years old that have yet to be cored. Sediments from lakes or ocean basins with anoxic bottom water are barren of invertebrates that stir ordinary sediments and hence can have records as good as ice cores, but with less distortion and mixing with depth (Behl and Kennett, 1996).

Brain Size Evolution in the Pleistocene

Mammals show clear signs of responding to Pleistocene variability selection with Potts' hypothesized increased behavioral flexibility. Harry Jerison's (1973) classic treatment of the evolution of brain size (relative to body size) documented a major trend towards increasing brain size in many mammalian lineages that persists right up to the present. Figure 6 summarizes his data. The data are presented in the form of cumulative frequency distributions of encephalization quotients of carnivores and ungulates over the whole Cenozoic Era. The sample includes:

- (1) archaic creodont carnivores (an extinct order),
- (2) archaic ungulates and carnivores from the extinct orders Condylartha and Amblypoda from the Paleogene (65-22.5 million yrs before present),
- (3) members of the still extant ungulate and carnivore orders from the Neogene (22.5-2.5 million years before present), and
- (4) a selection of living species of ungulates and carnivores.

The time trends illustrated by the figure are complex. There is a progressive increase in average encephalization throughout the Cenozoic. However, there is an interesting tipping of the cumulative curves to the northeast through time as well. Many relatively small-brained mammals persist to the present even in orders where some species have gotten rather large brains. The *diversity* of brain size increases toward the present. Why might variability selection have resulted in this pattern rather than an increase in brain size in all mammalian lineages?

There is good reason to expect that, all-else-equal, selection favors as small a brain as possible. Sophisticated learning systems require larger sensory and nervous systems than simpler ones. The incremental energetic costs of maintaining this extra nervous tissue are quite large (Eisenberg, 1981: 235-6). Mammalian brains vary over about a 25-fold range, controlling for body size (Martin, 1981). Human brains are about 5 times as large as the brains of average mammals of our body weight. Living ungulates and carnivores have average brains. Average living mammals in turn have brains about 5 times as large as those of the smallest brained mammals, such as insectivores and many marsupials. Human brains account for 16% of our basal metabolism (Aiello and Wheeler, 1995). Thus average mammals will have to allocate only about 3% of basal metabolism to their brains, and some get by with less than 1%. Total metabolism runs about 1.8 times that of resting metabolism, mostly because of the mobilization

of large masses of otherwise low-metabolic-rate skeletal muscle during exercise. How nervous system metabolic rate varies with “exercise” is poorly understood. Even disregarding mental exercise, humans must expend something like 9% of their total metabolism on their brain versus a little more than 1% for average animals and well under one for the least brainy mammals. Other costs of big brains, such as increased difficulty at birth and greater vulnerability to head trauma, are no doubt appreciable as well.

Since the fitness costs of large brains are significant, mammals continue to be under strong selection pressure to minimize brain size, and those that find an effective way to cope with climatic deterioration by non-cognitive means will do so. For example, many creatures like opossums cope with high mortality when times are bad by producing large numbers of small-brained offspring when times are good. It is thus not surprising that many mammalian lineages have undergone minimal encephalization despite a great increase in environmental variability. Other lineages evolve larger brains that allow them to exploit the temporal and spatial variability of the environment by using behavioral flexibility instead. Big-brained lineages pay for the cost of encephalization by exploiting the ephemeral niches that species with other responses to variability selection leave under-exploited.

Humans merely anchor the tail of the recently much-stretched distribution of brain sizes in mammals. We are the largest brained member of one of the largest brained mammalian orders (Marino, 1996). The continuum of brain sizes is comforting to a Darwinian hypothesis. Large gaps between species are hard to account for by the processes of organic evolution. That we are part of a larger trend suggests that a large scale, general selective process such variability selection is really operating.

Note that biggest shift per unit time by far is the shift from Neogene to the present. In the 2.5 million years from the late Pliocene to the end of the Pleistocene, encephalization increases were somewhat larger than the steps from Archaic to Paleogene and Paleogene to Neogene, each of which represent tens of millions of years of evolution. Thus, the increase of brain size did closely shadow the Pleistocene climate deterioration, although the precision of the correlation is limited by the low resolution of the brain size data.

Nevertheless, the Pleistocene leap in brain size is part of a trend that reaches back before the beginning of the Cenozoic. Since reasonably detailed records of climatic variability are so far only published for the last 6-7 million years (Figure 4), we cannot say whether a record of climate deterioration, especially high frequency variation, accompanies the earlier increases in encephalization. If Pleistocene increases in variability drove encephalization during the recent past, then the modest increases in encephalization in the early and middle Cenozoic were likely the product of earlier modest climate deterioration. To test this sub-hypothesis we need data on climate fluctuations on fairly short time scales. The analysis of fossilized lake sediments with distinct annual deposition layers might put this part of the hypothesis to the test.

Large Brains for What?

Increases in brain size could signal adaptation to variable environments via enhanced individual learning, for example through the addition of more innate information about the environment, or the addition of the psychological mechanisms that allow social learning. The mathematical models suggest that the individual and social learning work together. Innate rules are necessary to make adaptive decisions in the processes of individual learning and biased transmission. There should be an optimal balance dictated by the spatio-temporal structure of the variability selection imposed upon a species, taking into account how the species niche “filters” raw environmental variation. Given the tight constraints imposed on brains, we would expect to find a tradeoff between social and individual learning abilities. Those species that exploit the most variable niches should emphasize individual learning while those that live in more highly autocorrelated environments should devote more of their nervous systems to social learning. The degree to which innate rules should tightly constrain and bias individual and social learning versus evolving more open, riskier, learning heuristics depends upon the degree to which selection can “detect” predictable patterns of variation in the environment versus the quality of heuristics available for responding appropriately to less predictable variation.

The relationship between individual and social learning has been studied most extensively in birds. Lefebvre (in press) reviews the experimental evidence from a variety of species and reports on a study of feeding innovation rates as observed by field ornithologists. For the most part, the patterns found do not support the hypothesis that individual and social learning are alternative specializations. Both forms of learning tend to be correlated with low neophobia (a low latency to feed on new foods or in a new apparatus), large forebrain size, and opportunistic invasion of new habitats, such as cities. Lefebvre interprets the data to support the hypothesis that large brains in birds usually signal a general-purpose opportunistic resource acquisition strategy using more individual *and* more social learning than the more specialized strategies of smaller brained birds. The former are often social, flocking birds, and the latter are generally territorial and less social. Interestingly, exceptions to the generalization exist. Caching species in the corvids and parids have extraordinary spatial learning abilities associated with enlargements of the hippocampus. However, these abilities are not reflected in improved social learning. Birds include species, such as parrots, with extraordinary imitative abilities (Moore, 1996). Comparative work with birds promises to be one of the most interesting fields for testing general hypotheses about learning and social learning, and their relationship to the innate cognitive structures.

Why might individual learning and social learning be positively rather than negatively correlated? Individual and social learning may not be strongly competing processes and might even be synergistic. Jerison (1973) argued that the expansion of the neocortex, which accounts for most of the tissue involved in encephalization trends, is devoted to “maps” of the environment. Animals with more detailed maps need to acquire the information to fill them out. Both social and individual learning will help do so. Perhaps the information-evaluating neural circuits used in social and individual learning are also substantially shared. Once animals become social, the

potential for social learning arises. If the two systems share the overhead of maintaining the memory storage system and much of the machinery for evaluating the results of experience, the benefits in quality or rate of information gain may be increased by the opportunity for social learning, leading social learners to become better individual learners. If members of the social group tend to be kin, investments in individual learning may also be favored because sharing the results by social learning will increase inclusive fitness.

The hypothesis that the tradeoff between social and individual learning may be modest except at the margin resonates with the mechanisms of social learning found in best-studied cases of social learning. The most common forms of social learning result from very simple mechanisms that piggyback on individual learning (Galef, 1988, 1996; Laland et al. 1993; Heyes and Dawson, 1990). In social species, naïve animals follow more experienced parents, nestmates, or flock members as they traverse the environment. The experienced animals select highly non-random paths through the environment. They thus expose naïve individuals to a highly selected set of stimuli that form the basis for acquisition of behaviors by ordinary mechanisms of reinforcement. Social experiences act to speed up and make less random the individual learning process, perhaps requiring little additional, specialized, mental capacity. Social learning, by making individual learning more accurate without requiring much new neural machinery, tips the selective balance between the high cost of brain tissue and advantages of flexibility in favor of more flexibility. As the quality of information stored on a map increases, selection will favor larger scale maps to take advantage of that fact. Eventually, diminishing returns to map accuracy will limit brain size. At that point only, marginal tradeoffs between individual and social learning may begin to select for cognitive structures specialized for one versus the other.

Data on the encephalization of living mammals suggests that high encephalization is associated with longer times of association with parents, late sexual maturity, extreme iteroparity, and long potential life span (Eisenberg 1981: Ch 23). These life cycle attributes all make social learning easier and hence more likely. Perhaps the opportunity to learn socially from parents allows investments in larger brains necessary for social learning to be amortized over a long life. Even marginally social species may come under selection for behaviors that enhance social learning, as in the well known case of mother housecats to bring partially disabled prey to their kittens for practice of killing behavior (Caro and Hauser, 1992).

If the relationship between social and individual learning is as tight as this evidence suggests, then we can expect to find social learning in many if not most social species, given that individual learning is so common. Indeed, the food choice system of Norway rats is the best studied example of non-human social learning (Galef, 1996). This species, with an encephalization quotient (brain size relative to body size) of about 0.4, is among those that have participated only modestly in the Cenozoic encephalization trend (Jerison, 1973: 212, 218). Average living mammals have a quotient of 1, whereas humans reach about 7.5. Social learning has been more or less convincingly demonstrated in a long list of animal species (Lefebvre and Palameta, 1988), including recently in guppies (Dugatkin 1996; Laland and Williams, 1998). Social learning need not automatically favor large brains; in species where the costs of large brains are

high relative to the benefits of more accurate maps, brains will remain small even if some social learning occurs.

Aspects of the social learning system in animals do show signs of adaptive specialization. For example, laboratory studies of black rats show that the main mode of social learning is from mother to pups (Terkel, 1996, Chou, 1989, personal communication). Norway rats' social learning is quite different (Galef 1988, 1996). Mothers have no special influence on pups in this species. In the black rat, socially learned behaviors seem to be fixed after a juvenile learning period, whereas Norway rats continually update their diet preferences (the best-studied trait) based upon individually acquired and social cues. Black rats seem to be adapted to more slowly changing and Norway rats more rapidly changing environments. Terkel studied a rat population that has adapted an exotic pine plantation in Israel by the social transmission of the trick to efficiently extract seeds from the tough pinecones, a novel and short-lived niche by most standards, but one that will persist for many rat generations. Norway rats are the classic rats of garbage dumps, where the sorts of foods available change on a weekly basis. Interestingly, in recent decades, Norway rats have been expanding at the expense of black rats (Bentley, 1964). It seems possible that modern garbage dumps present a much more varied resource for rats than traditional ones, and that the spread of Norway rats reflects their better adaptation to human modernity. The theory described here suggests that selection on social learners should tune the social learning system to match the statistical properties of the environmental variation in the specific niche the animal occupies. This very thin bit of data suggests that the hypothesis is worth pursuing.

In the human case, we have at least one highly specialized social learning system, language. On the other hand, we readily learn to make a living using a spectacular array of techniques. As the famous language learnability argument of Chomsky showed, a completely general learning machine cannot work (Pinker, 1994: Ch 9). A finite learner must have a nervous system that in effect makes many “assumptions” about the environment in order even make the most basic map of its environment. For example, primates have a visual system imposes order on nerve impulses coming from the rods and cones to produce a fairly veridical image of objects in the world (Spelke, 1990). The flood of impulses arriving from a large array of sensory cells would overwhelm the capacity of a very general learning mechanism. A functional learning device requires built in expectations about what sorts of objects are out there to sense. For example, the visual system assumes that a set of spatially contiguous points in the visual field that have a similar color, a defined border, and coherent movement is a solid object. This innate physics correctly recognizes a rolling ball as a solid object, though it misidentifies clouds as such. On the other hand, the adaptive reason to have learning and social learning is the flexibility to adapt to unforeseen contingencies. Experience teaches us that the solidity of clouds is an illusion.

The idea that brain size, social learning and individual learning are an adaptive package serving as a rather generalized environment mapping system seems contrary to the attractive, widely held, idea that minds are collections of highly specialized, innate modules (Fodor, 1983). Innatist evolutionary psychologists argue that modular specialization of cognition is to be expected on

general theoretical grounds (Tooby and Cosmides, 1989), and that the nature of the modules can be deduced from the nature of the adaptations they support. The positive correlation between capacities for individual and social learning in birds is perhaps more congenial to the connectionist hypothesis. Connectionists hold that much brain tissue functions as a rather generalized pattern recognition device. A major complexity arises in this debate because, as Fodor insists, different levels of organization have to be kept straight. The structure of the mind may not mimic the structure of its neural machinery. The same is likely to be true of adaptations compared to cognitive structures. Typical adaptations (e.g. ability to capture a certain class of prey) at the phenotypic level integrate many elements of anatomy and physiology. Many of the elements subserving one adaptation also subserve others (e.g. fighting abilities used in dominance struggles and to subdue prey). The same is likely to be true of cognitive structures relative to behavioral adaptations. Relatively general purpose learning and social learning systems could well be based on the operation of a number of rather specialized modules at the cognitive level which in turn are built upon the rather general properties of neural nets at the brain tissue level.

Progress on these questions is limited because we know very little about the adaptive tradeoffs in brain and mind design (Richerson and Boyd, in press; for an introduction to what we do know see Allman, 1999: Chap.7). We would like to build models in which the individual level synergies and tradeoffs between various forms of individual learning and social learning are included alongside the population level tradeoffs heretofore incorporated into them. How much brain space and energy do the various modes of adaptation to variable environments take? It is not yet possible to answer such questions. Neurophysiologists, cognitive scientists, and behavioral ecologists each have something to contribute to the puzzle of how some species can support large brains. Much will depend upon rather general considerations of neurophysiological, cognitive, and adaptive constraints and tradeoffs. Much is also likely to depend upon the details how mammalian brains, if not primate or hominid brains, are constrained by their evolutionary history. However, collaborations between these disciplines to tackle this question have been lacking. Until these tradeoffs are better understood, the support for the social learning hypothesis afforded by the correlation of brain size increase with climatic deterioration is suggestive but certainly not conclusive. The behavioral evidence does suggest that increased social learning was at least one component of the response to Pleistocene variability selection and one component of the cognitive adaptations supporting larger brains.

Perhaps the neocortex of the brain is an adaptation like the beak of birds. The basic beak is nothing more than a moderately complex, functionally integrated, general-purpose forceps-like device. It is usually a food acquisition, handling, and processing organ, fighting weapon, nest building implement, environment probe, and grooming tool, all in one. Nevertheless, despite great commonality of form and function, bird beaks are endlessly stretched, bent, thickened, widened, deepened, and sharpened by selection to support the diverse niches birds occupy. Only occasionally are entirely new parts, like the pouch of pelicans, added to create a new adaptation. The modularity-connectionist debate does not exhaust the possible models for the relationship between form and function in brains (Krubitzer, 1995).

Human Culture Is Derived

The human species position at the tail of the distribution of late Cenozoic encephalization admits of the hypothesis that our system of social learning is merely a hypertrophied version of a common animal system. However, the evidence suggests that human culture is qualitatively different from most, if not all, animal social learning systems.

Human culture differs from that of other species because it involves the assembly of very complex traditions over extended periods of time. Subsistence systems, artistic productions, ideologies, and the like are so multi-parted and intricately integrated that no one individual ever could or did invent them. Nor, merely given the pieces and motivation to produce a complex artifact, would stimulus enhancement provide sufficient clues for a simple social learner to produce a workable version. Think of some relatively simple item like a hunting spear. The maker has to know how to make the stone tools to prepare the shaft, how to knap fine-grained stone to make a good point, how to prepare stout adhesives and fiber to mount the point, what wood makes a spear of the right strength and weight to be useful, how long and stout to make the shaft for the intended purpose (throwing, stabbing, atlatl dart, multipurpose), and so forth. Few of us could make more than a crude approximation of a Stone Age spear, though we could easily learn by being taught, or even just by observing an expert spear-maker. The knowledge of how to make such complex artifacts is built up over many generations by the incremental, marginal modifications of many innovators (e.g. Basalla, 1988). We are utterly dependent on learning such complex traditions to function normally. By contrast, most animal proto-culture involves simple behaviors that individuals can and do learn on their own. The study of the manner in which roof rats open pine cones showed that individuals cannot normally learn to open a pine cone in a way that leads to a net energy gain (Terkel, 1996). However, rats need to learn only one trick to acquire the successful technique. A single individual presumably innovated the trait in the beginning.

The cumulative complexity of human culture appears to be based on an ability to acquire novel behaviors by observation, “true imitation” in the lexicon of comparative psychologists. As we saw above, much social learning seems to be dependent mostly on the same cognitive strategies used in individual learning. Experimental psychologists have devoted much effort to trying to settle the question of whether non-human animals can learn by true imitation or not (Galef, 1988). True imitation is learning a behavior by seeing it done. True imitation is presumably more complex cognitively than merely using conspecifics’ behavior as a source of cues to stimuli that it might be interesting to experience. Some good experiments indicate a modest capacity for true imitation in many socially learning species (Heyes and Dawson, 1990; Zentall, 1996; Moore, 1996), but it seems to play a modest role in most cases of non-human social learning. Even our closest relatives show quite modest abilities to imitate. Head-to-head comparisons of children’s and chimpanzee’s abilities to imitate show that children begin to exceed adult chimpanzees’ capabilities at about 3 years of age (Whiten and Custance, 1996; Tomasello, 1996; Tomasello and Call, 1997: Chap. 9). Whether or not wild chimpanzees make much use of imitation is unclear. Tomasello is inclined to think that even in this species, there is remarkably little

indication that apes can ape, although *human reared* chimpanzees do show considerable imitation or quasi-imitative “emulation.” Whiten and Custance, on the other hand, argue that the marginal abilities observed under impoverished captive conditions are likely to underestimate abilities in the wild. Arguably, chimpanzee tools are as complex as the simplest known toolkits of humans, those of the Tasmanian Islanders (McGrew, 1992). Chimpanzees exhibit a few tens of traits that are plausibly cultural (Whiten, et al., 1999). Perhaps some chimpanzee tools, especially the hammer-and-anvil nut cracking system found in some West African populations, is a cumulative tradition that is made up of at least two independent inventions, the hammer and then the anvil. Rehabilitated pet orangutans exhibit impressive, though still imperfect, imitations of complex human behavioral routines, such as kindling a fire. Orangutans are not known to have any sign of imitatively acquired behaviors in the wild (Russon and Galdikas, 1993). Parrots seem to have a quite respectable but little understood capacity for imitation (Moore, 1996). On the other hand, monkeys show scant signs of abilities to imitate. Even Capuchin monkeys, who have a higher encephalization quotient than even the great apes, fail imitation tasks (Fragaszy and Visalberghi, 1996; Eisenberg, 1981, 499). Thus, the lesson to date from comparative studies of social learning suggests that very simple mechanisms of social enhancement of cues are much more common than imitation, even in our close relatives and other highly encephalized species. Humans seem to be unique at least in the ease and wide range of behaviors with we can imitate, and in the scale and importance of our complex traditions.

The evidence that imitation is a major cognitive ability distinguishing us from other encephalized mammals, together with the evidence that we use imitation to support complex traditions, suggest that transmitted culture is a central, if not *the* central, problem for *human* evolutionary psychology. We are perhaps the only species that is sufficiently imitative to create complex traditions in the wild, but we do create them with abandon. Anthropologists have long argued on good grounds that complex, transmitted cultural traditions are central to the adaptations of hunter-gathers (e.g. Steward, 1955). How else are we to account for the dramatic variability in technology and social organization among hunter-gatherers or the dramatic historical changes in human behavior under the quiet environmental regime since the end of the Pleistocene? The innate “evoked culture” of Thornhill, Tooby and Cosmides (1997) would equilibrate human behavior to changed circumstances in one generation, whereas cultural traditions exhibit descent with modification over many generations. The conventional social sciences are no doubt guilty of neglecting innate attributes of human minds (Bateson, 1987), but neglecting complex cultural traditions is not progress.

Why Is Cumulative Cultural Evolution Rare?

The hypertrophy of imitation and culture in humans generates the problem of a “great gap” in accounting for human minds by a Darwinian explanation. Humans have apparently penetrated a “cultural niche” that made us a rather successful species under Pleistocene conditions. The gradual cultural assembly of complex traditions allowed humans to occupy environments from the tropics to the glaciers, penetrating to all but the harshest environments. In the Holocene, the development of food plant production has made us the Earth’s dominant organism. If human

traditional culture is a successful adaptation for us, why haven't other species evolved similar capacities?

Perhaps the simplest answer is that we have simply won an evolutionary footrace to be the first animal to occupy the cultural niche. There may be only one cultural niche because the first animal to occupy it excludes all competitors by occupying so many niches using so many different traditional modes of subsistence. Perhaps any one of a number of highly encephalized primate, elephant, or porpoise lineages might have evolved complex culture if hominids had not gotten there first. Some key initial condition may have given our lineage the head start necessary to beat out all competitors. The classic explanation is that upright posture, freeing the hands to make and carry artifacts, was a preadaptation that made complex traditions especially useful (Tobias, 1981). If human evolution was the product of a single breakthrough, we might expect a smooth, rapid entry in the cultural niche and then a stabilization of the imitative adaptation while cultures varied dramatically in response to climatic variability.

The actual paleoanthropological record tells a very different story. The human lineage seems to have been on a progressive, but very complex, trajectory toward a heavy dependence on cumulative cultural including at least four major sequential improvements, the first manufacture of stone tools, presumably by *Homo habilis*, around 2.5 million years ago, the expansion of *Homo erectus/ergaster* out of Africa about 1 million years ago, the evolution of archaic but large brained populations by about 200,000 years ago, and the expansion of anatomically modern *H. sapiens* out of Africa around 50,000-60,000 years ago (Klein, 1999: Chap. 5 & 6). The manufacture of stone tools seems to represent a substantial increase in social learning ability, probably including a significant increment in ability to imitate, over that demonstrated in other living apes. The *erectus* expansion carried hominids to the temperate latitudes of Eurasia. Cultural traditions are a means of adapting to spatially as well as temporally variable environments. The *erectus* expansion gave humans a geographical range that is unusually large for any vertebrate and probably signals the acquisition of a considerable capacity for imitation. *Erectus* and succeeding populations used more sophisticated stone tools than *habilis* and used them to make rather sophisticated tools of wood and probably hide. Wooden throwing spears, weighted for accurate flight like modern javelins, have been recovered from an anaerobic deposit in Germany (Thieme, 1997). However, the rate of evolution of Lower Paleolithic artifacts and their degree of geographical differentiation were restricted compared to modern populations. Between the two invasions from Africa, considerable increases in brain size and artifact sophistication occurred, but cultural evolution was still rather slow and low in regional diversification. Anatomically Modern people made the same Middle Stone Age and Mousterian tool kits as anatomically archaic people for some tens of thousands of years. To judge from the durable artifacts even large-brained Moderns and Neanderthals were not taking full advantage of culture to exploit temporally ephemeral and spatially variable environments. Mitochondrial DNA evidence suggests that Neanderthals and moderns had about 400,000 years of independent evolutionary history (Krings, et al., 1997). For a long time the two species apparently coexisted in Western Asia, physically quite different but culturally quite similar.

This coexistence ended when a cultural revolution, marked by the advent of more complex Late Paleolithic artifacts, apparently gave Moderns a decisive advantage. Nevertheless, Neanderthals in Europe are associated with the modern-appearing Châtelperronian industry, suggesting an ability to make more sophisticated artifacts, perhaps stimulated by contact with Late Paleolithic Moderns. The Anatomical Moderns that invaded Eurasia 50-60,000 years ago generated the Upper Paleolithic Transition in Europe, settled Australia for the first time (requiring tolerably sophisticated boats), and expanded their range into colder and more continental environments than Archaic humans could occupy. The number of artifact types recovered from the sites occupied by invading Moderns, the degree of formalization of types, and the degree of spatial and temporal differentiation of cultural traditions all increase dramatically. On the utilitarian side, Late Paleolithic Moderns were the first humans to make tools of bone, including needles, fish hooks, and spear throwers. They also made the first unequivocal art. They completely replaced relatively small brained late *erectus* populations in East Eurasia but also large brained forms such as Neanderthals in Western Eurasia. Data from the West indicates that invading populations maintained higher population densities, and higher density probably explains the rapid replacement of archaic populations, such as the Neanderthals. These rather dramatic changes in culture suggest some final modernization of human cognition within the last 100,000 thousand years (Stringer and Gamble, 1993; Klein, 1999: 511-572).

On the other hand, the apparent ability of Neanderthals to make Châtelperronian artifacts means that we cannot rule out the hypothesis that the advantages of the Late Paleolithic invaders was mainly cultural, not cognitive. In either case, the existence of seemingly punctuational events separated by periods of slower modernization suggests either the penetration of the complex culture niche is inherently slow or rare concatenations of events are required to penetrate it or both. Conceivably, cultural innovations, such as more effective teaching techniques, might have been as important as genetic changes leading to a capacity to maintain complex traditions, either alone or as part of a coevolutionary sequence. For example, perhaps the invention of the spear-thrower led to the modernization of human physiques in Africa and to higher population densities that in turn could support conspicuously more complex cultures, all without any significant cognitive changes. Perhaps because the very robust Archaic populations were anatomically less suited than gracile Moderns to using spear throwers, they failed to compete successfully with the Modern invasion.

Theoretical models suggest the evolution of a capacity for complex cumulative traditions faces a bootstrap problem—a capacity for complex cumulative culture cannot increase when rare even if it would be quite adaptive once it became common (Boyd and Richerson, 1996). The mathematical result is quite intuitive. Suppose that to acquire a complex tradition, learners need efficient imitation skills. Suppose that efficient imitation requires considerable costly, or complex, cognitive machinery to support an imitation capacity. If so, there will be a coevolutionary failure of capacity for complex traditions to evolve. The capacity is a great fitness advantage, but only if there are cultural traditions to take advantage of. But, obviously, there cannot be complex traditions without the cognitive machinery necessary to support them. A rare individual with a mutation coding for an enlarged capacity to imitate will find no complex traditions to learn, and

will be handicapped by an investment in nervous tissue that cannot function. If it takes a number of generations for a complex tradition to evolve, the offspring of the initial mutant individual will be almost as handicapped as their parent. Worse, a quite large population of sophisticated imitators might still take a considerable length of time to evolve enough useful traditions to make the imitative capacity pay for itself. The hypothesis depends upon there being a certain lumpiness in the evolution of the mind. If even a small amount of imitation requires an expensive or complex bit of mental machinery, or if the initial step in the evolution of complex traditions does not result in particularly useful ones, then there will be no smooth evolutionary path from simple social learning to complex culture.

The failure of a capacity for complex cumulative culture to evolve when rare is an example of the sort of process that gives evolution its commonly contingent, historical character (Boyd and Richerson, 1992). Natural selection is often portrayed as causing populations to climb fitness peaks. There are numerous processes that cause fitness topographies to be rugged, like real mountain ranges. Because it maximizes only locally, natural selection will tend to get stuck on local peaks. Selection is like a blind mountain climber; it cannot “see” distant higher fitness peaks across valleys and instead just goes up the current hill. If a relatively abrupt environmental change occurs, the initial adaptations will tend to be globally sub-optimal, represented by the tops fitness knolls near the initial phenotypes of adapting populations, far from the more nearly globally optimal high peaks. The problem is well understood in the context of the engineering of complex systems (Kirkpatrick, et al., 1983). Complex design problems typically have an extremely large number of possible designs, including a huge number of locally optimal designs (“best” in the sense that all small modifications of the design are worse). There are also typically quite a few nearly equivalent globally “best” solutions that are qualitatively different from each other. In the longer run, various kinds of historical happenstance cause populations to escape local optima and climb higher on the topography. The notion of preadaptation captures the idea that traits evolved for one function sometimes put populations at the foot of a slope leading to a quite different adaptation. Some populations thus find an indirect route, via preadaptations, up a complex topography that has left competitors stuck in the foothills. Other processes, such as genetic drift and the constant small-scale wiggling of the topography due to environmental variability, likewise allow populations to move to higher peaks. Given enough time, some population will reach one of the more or less equivalent near-global optima. If this picture applies to human evolution, we expect to find that the perfection of our rather novel cognitive adaptation to Pleistocene environments is slow, roundabout, and punctuated by rushes from lower local optima to higher ones.

Some evidence supports the hypothesis that the utility of having a capacity for learning complex traditions is constrained by the number of others who have the capacity. Among modern humans, the maintenance of complex traditions is not unproblematic. The Tasmanians’ originally normally complex toolkit shrank in size and sophistication after their isolation from Australia by the Holocene rise in sea level. The loss probably resulted from a sort of cultural drift (Diamond, 1978). In a small population, complex skills will occasionally be lost by accident. With few people to invent and reinvent, and no possibility of reacquiring complex traditions by diffusion,

the Tasmanians were helpless to prevent a gradual erosion of their more complex cultural traditions. Even given a capacity for complex traditions, the number of participants in a cultural system may be critical to the complexity that can be maintained. A few rare, unsophisticated imitators could not possibly have maintained even marginally complex traditions if fully modern humans have trouble maintaining them if regional populations are too small. On a grander scale, cultural evolution in Eurasia has proceeded along the trajectory toward politically and technically more sophisticated societies faster than in Africa and the New World. The likely reasons are two (Diamond, 1997). First, Eurasia is the largest continent, thus encompassing more cultural evolutionary experiments than Africa and the New World. Second, it is extended in the east-west rather than north-south direction, connecting ecologically similar regions of the continent and facilitating the rapid diffusion of relevant innovations, including the re-diffusion of any that are lost in a given population. Thus, some direct evidence supports the hypothesis that cultural traditions of the complexity created by the last major modernization of the culture capacity could not have increased when rare. Plausibly, the earlier increases in the sophistication of culture were slowed by similar bootstrap problems. For example, perhaps imitation and complex traditions were first restricted to a narrow domain, say food acquisition. Each extension to a new domain, say to social organization, may have faced a similar problem of not being favored when rare.

The paleoanthropological record strongly is consistent with the idea that the evolution of human cognition and culture occurred on a complex fitness topography. The two invasions from Africa seem to mark two major increases in the sophistication of the cultural adaptation. The first is poorly dated, but could have been an evolutionary response to the beginning of the dominance of the 95,800 year Milankovich cycle in the climate record. The second is not associated with any known change in the pattern of climate change. The evolution of the rather diverse populations of archaic but increasingly large brained hominids between the first and second invasions occurs without any conspicuous change in the pattern of climate variation. A million or so years seems to have been spent slowly enlarging brains and increasing the sophistication of artifacts, leading to a rather sudden and late emergence of modern culture. Most likely, evolving human populations encountered a number of local optima and adaptive valleys of the useless-when-rare sort over the 2.5 million years after the first signs of minimal imitative capacities appeared in the archaeological record.

If multiple major impediments to the evolution of complex traditions existed, evolution must have traveled a round-about path to achieve get the frequency of the capacity high enough to begin to bring it under positive selection for its tradition-supporting function. The exact path that evolution took to reach modern culture capacities is probably vain to seek; disciplined speculation is often the best that evolutionary science has to offer. What sort of evolutionary situation might finesse the problem of imitation not being adaptive when rare? The best-developed suggestion along these lines is that primate intelligence generally was originally an adaptation to manage a complex social life (Humphrey, 1976; Whiten and Byrne, 1988, Kummer et al., 1997). In primates generally there is a correlation between group size and the size of the neocortex relative to the rest of the brain (Dunbar, 1991). Perhaps in our lineage the

complexities of managing the sexual division of labor or some similar social problem favored the evolution of abilities to understand the intentions of others, the rudiments of a generative language, or some similar preadaptation. Such a capacity might then incidentally make efficient imitation possible, launching the evolution of complex traditions that could drive the evolution of still more sophisticated imitation. This hypothesis might apply to the original stone tool revolution or to the later modernizations leading up to the range extensions out of Africa. Perhaps it underpins all three in one way or another.

The second invasion out of Africa is plausibly associated with the evolution of language. Language is an extraordinarily powerful device for encoding and transmitting cultural traditions. The productivity of language allows humans to express a huge number of ideas and link them in patterned arrays. According to one well-known hypothesis, modern skull anatomy is required to make room for a vocal apparatus capable of making the modern range of vowel sounds (Lieberman, 1984). Even otherwise advanced hominids like the Neanderthals may have had only limited speech. Highly specialized neurological structures are required to code and decode speech at the rates we normally converse (Friederici, 1996). Language is potentially an example of the failure of a capacity for imitation to evolve when rare. If a complex capacity to learn grammar, form words, and decode words is required for speech to be a significant improvement to silent mimicry in acquiring cultural traditions, then it also cannot increase when rare. With no language to learn, there is no advantage to a capacity to learn one.

Language is much used for social purposes (Dunbar, et al., 1995; Thompson, 1995) and this use could be the key link in the origin of the capacity for complex traditions. Plausibly, small steps in the increase of communication complexity allowed the coevolution of a language capacity and a cultural linguistic system. Communication about who-did-what-to-whom-when-and-why is the sort of thing that is hard to communicate accurately without grammatical structure. Social actors often want to communicate information about social events that occur out of the presence of their hearer. Even a talented mime has trouble conveying such information. Even a marginal increase in competence may allow one to convey a bit more information about a social relationship. Finally, a fully generative language arose, with the capacity to encode an unlimited number of messages. Even if the original function of language was gossip about social relations, it is a ready vehicle for transmitting complex traditions, starting with the language itself.

Donald's (1991) admirably well specified scenario for the origins of human cultural complexity involves a stage of sophisticated motor mimicry preceding and laying the neurological basis for language. Donald argues that quite complex behavior can be acquired by mimicry in the absence of language. 19th Century accounts of the abilities of deaf-mutes to acquire many sorts of useful economic and social skills without language suggest that they could easily learn to most non-linguistic skills, including most social graces, by observation, without any linguistic aids. Donald argues that *Homo erectus* had evolved the basic memetic capacity, which accords well the pattern of the first invasion of Eurasia by hominids. These populations could probably sustain complex traditions of resource exploitation that allowed them to occupy an unprecedented

diversity of niches. Fine motor skills are neurologically closely related to linguistic skills, suggesting that mimetic capacities were the preadaptation for language. A possible objection to Donald's hypothesis is that it does not explain why utilitarian artifacts made by *erectus* and its immediate successors evolved so slowly and were so similar across wide areas. Modern people who acquire such traits as stone knapping and woodworking substantially by direct imitation imitate fine details of performances but also readily invent new variants, generating rapid evolution. Deaf-mute Moderns would seem to be capable of much more. Young children, whose imitative capacities might be models for *H. erectus*, play inventively and imaginatively with toys. Would not free mimicry lead to something approaching the innovativeness of modern people as regards those functional aspects of tool technology that are easy to mimic? Perhaps innate constraints on learning and social learning were still relatively strong in *erectus* and its immediate descendants. The large-brained archaic toolmakers, such as Neanderthals, made considerably more complex tools than *erectus*. Whether this increase in sophistication was gradual or more discontinuous is hard to say given a sparse and poorly dated record.

The dramatic increases in tool complexity in some parts of the world about 50-60,000 years ago postdate the anatomical modernization of skeletons by perhaps another 50,000 years. If we suppose that anatomical modernization reflects something like the modern ability to speak language, then what took the further 50,000 years before moderns were able to make the more sophisticated tools that supported the second invasion from Africa? If moderns 100,000 years ago had relatively modern language, the imitative sophistication in the linguistic mode did not yet spill visibly into artifact production. Perhaps learning to make archaic tools required a relatively primitive imitative capacity. Perhaps the manufacture of artifacts of the complexity made by large-brained archaics was still innately constrained in ways that the imitation of moderns is not. The relative crudity and uniformity archaic tools, even the Mousterian and Middle Stone Age tools made for tens of thousands of years by anatomical moderns, suggest that a relatively small number techniques were inherited and that controlled innovation that might lead to cumulative complexity is rare or at least rarely imitated. The stereotypy of archaic tool traditions in time and space suggests a very conservative form of transmission, with strong innate elements or tightly controlled teaching by parents. Or perhaps, only the basic steps of toolmaking could be imitated, and much refinement of technique by individual learning was still necessary. In this way, function and raw material properties might have dictated final form to a much greater extent than was the case for Late Paleolithic artisans who could easily copy minute nuances, whether stylistic or functional, of each others' artifacts. The penultimate hominid population preceding fully modern humans might have been linguistically advanced but still retarded in their abilities to imitate in other domains.

The linguistic system, even if first modernized for social communication not cultural transmission, could have made more complex cultural traditions possible by making it easy to express, memorize, and teach cultural principles verbally. Once language became fully productive, talk would occasionally turn from band politics and sex to technology. In this way, elements of material culture that were initially complex in the oral mode of transmission may then have selected for more facile mimetic capabilities for those common learning tasks where a picture is

worth a thousand words. Once complex non-linguistic cultural traditions began to be built by linguistic means, selection might favor devoting costly brain tissue to learning them more efficiently by imitation. Donald's (1991) evidence for a close neurological relationship between language and mimicry is silent as to which came first. Perhaps a back-and-forth coevolution between mimicry and language was involved. We are used to thinking that language is the ultimate human cultural achievement. The evidence that much of the complexity of language is innate (Pinker, 1994) suggests that this system is actually more primitive than other cultural systems that appear to have a much smaller innate component, such as late Pleistocene and Holocene technology. If children have enough innate information to create a new language in one generation (Bickerton, 1984), this system may not really depend upon the existence of complex traditions, although it produces them as a byproduct. Perhaps modern motor mimicry abilities postdate the evolution of modern linguistic skills.

Of course, these scenarios, like any number of others that imaginative scholars can produce, is exceedingly difficult to test given the quality of the archaeological record. We can recover relatively little information about past behavior and past environments from the paleoanthropological record. If the notion that the evolution of our capacity for cumulative culture was a complex design problem is correct, *Homo* might have taken any of a number of paths through the complex topography to reach the present state of human culture capacities. If the possible pathways are many and the historical data sparse, we will never be able to rule out a considerable number of alternative evolutionary trajectory our species might have taken. Likewise, predicting the details of modern cognitive capabilities by considering the adaptive function of cognition in the Pleistocene will be difficult. The more complex the fitness topography, the more unpredictable evolution becomes. We know from the commonness of analogous adaptations (the wings of birds, bats, insects, and airplanes) that many different structures may serve the same adaptive function. Selection puts constraints on the evolution of adaptations, but when there are many alternative evolutionary outcomes, these constraints are often not sufficient to predict the details of how the machinery will be organized. At the level of cognitive details, there are probably many more or less equivalent ways to make a mind capable of complex culture and the other things modern humans do. Even at the gross functional level the evolution of *Homo* is very puzzling. Archaic populations lacked something that prevented rapid innovations to adapt to local environmental circumstances. On the other hand, the artifacts that they did make are often quite impressive, especially compared to what other apes produce. Moderns would certainly well exercise their good imitation skills to learn how to make them, but would have a hard time not using these same skills to launch a trajectory leading quite shortly to much fancier things. Late archaics had brains as large as ours, but apparently used them quite differently. How differently is highly uncertain. If this complexity tells us anything it tells us that past hominids are not just simpler versions of ourselves. They seem to have had quite different mixtures of capabilities and constraints than moderns do.

Evidence from human paleodemography suggests that some sort of rare evolutionary accident led to the final modernization of human culture capacities, as dated by appearance of modern artifacts during the last glacial. Human mitochondrial DNA records evidence of a human

population explosion of the modern human lineage between 33,000 and 150,000 years ago (Rogers and Harpending, 1992). In small populations, genetic drift limits the diversity of mitochondrial genomes in the population. The age of diversification of mitochondrial DNA lineages can be estimated from the number of mismatches separating different lineages. If a small population rapidly expands, a large number of new mitochondrial lineages will arise more or simultaneously and will be preserved against loss by drift. As these lineages accumulate more mismatches over time they generate a clock that allows us to estimate the time of the original population explosion. Although confidence intervals are wide, the data suggest that the population ancestral to all modern humans was quite small around 60,000 years ago, when began to expand rapidly. The pre-expansion population was between 1,000 and 7,000 breeding females for an extended period, although exactly how long is unclear. At the time of the final modernization of the human mind, we were most likely a rare and, given the nature of the Pleistocene, endangered species. Our numbers were probably much smaller than those of the archaic populations that we replaced after the explosion. The date of the explosion is consistent with the dates of the appearance of more sophisticated tools in Europe. Similar considerations apply to other genetic elements (Harpending, et al., 1998). If critical events happened in a small population traversing a rugged fitness topography, recovering evidence about the exact evolutionary process led to our final modernization is likely to prove most difficult. If our lineage had gone extinct, who knows how many more glacial cycles would have passed with big-brained hominids poised on the threshold of the complex culture adaptation without crossing it?

The contribution of psychology to the study of human evolution is likely to prove to be at least as great as the contribution of evolutionary studies to psychology. The social psychology of living humans is available for study, while the behavior of our long dead ancestors is heavily veiled. The ability of clever experimentalists to dissect the function of organisms with only a little help from evolutionary theory is well illustrated by physiology, cell biology, and molecular biology. Evolutionary biologists have turned all of these sciences to good account, while the reverse is less frequent. Inferences about what selection pressures must have shaped the social life of our ancestors derived from the social psychology of living humans are generally going to be more secure than inferences about living behavior from an inevitably poorly understood past. The details of how cognition is organized may bear some stamp of its complex historical trajectory. Reductionist psychology gives us the means to reverse engineer a complex design by tearing it to pieces to see how it works. The intricacies of a particular complex design are apparent in such exercises. We certainly should not discount roles for evolutionary theory or for paleoanthropology in understanding human behavior. They have essential tools, so long as these tools' limitations as well as their strengths are understood. Guessing from basic evolved functions about how an organism will fulfill these functions is forward engineering. If the design problem is complex, even great guesses will almost certainly only lead to organisms that might have been. Like economics and meteorology, evolutionary science is only weakly predictive. Nevertheless we take full advantage these sciences' weak predictions because in important domains they are the best we can do. Still, a good understanding of living human minds, a reasonably paleoanthropological record, and a body of well-verified theory may altogether be

insufficient to trace the *details* of the trajectory a complex adaptation took through a rugged fitness topography.

Conclusion

Humans are a difficult species. The Darwinian project is committed to bringing us into the same basic explanatory framework as all other organisms. In his M notebook on August 16 1838, while he was in full cry in pursuit of his first formulation of natural selection, Darwin wrote “Origin of man now proved.—Metaphysics must flourish.—He who understand baboon would do more toward metaphysics than Locke” (Barrett, 1974: 281). Darwin realized that failing to account for human behavior left a dangerous gap in his theory through which opponents could and did try to attack his whole theory. When, in the *Descent of Man*, Darwin reluctantly undertook to explain our species, a hostile commentator in the *Quarterly Review*, whom Darwin believed to be his persistent critic St. George Mivart, took advantage of perceived problems in the human story to attack the whole edifice. The reviewer gloated, it “offers a good opportunity for reviewing his whole position” (and rejecting it, Anonymous, 1971). If the gap between humans and our animal ancestors is too large, it is difficult to explain how ordinary evolutionary processes could explain our origins. If one species escapes the net of evolution by natural selection, the whole of so comprehensive a theory is brought into question. On the other hand, a considerable gap between our ape ancestors and ourselves exists and must be explained, if only to account for our ecological success. Our nearest living ancestors are forest dwelling creatures with modest ranges and abundances. Our more immediate fossil ancestors began to extend their ranges beyond Africa a million or so years ago. Even then, the range of *Homo erectus* and related hominids was not strikingly greater than that of some large carnivores like lions and pumas. However, by latest Pleistocene times, *Homo sapiens sapiens*, using toolkits of great sophistication, penetrated to the furthermost reaches of the Old World. With the waning of the ice at the end of the Pleistocene we exploded into the New World. In the Holocene, human societies have rapidly become very complex, rivaling in this regard the eusocial insects. In the industrial era, we are coming to have climatic impacts that rival the drivers of the Pleistocene.

Only in the late 20th Century did evolutionary biologists become markedly more sophisticated than Darwin about the evolution of behavior. W.D. Hamilton’s (1964) famous papers on inclusive fitness launched the theoretical study of social evolution, and a growing corps of empirical ethologists began conducting theoretically relevant investigations. Richard Alexander’s (1974) review paper and Edward Wilson’s (1975) treatise *Sociobiology* left no doubt that evolutionary biologists were going to apply this theory to humans with little or no respect for claims of disciplinary autonomy based on superorganic claims for cultural processes. At the same time, the population geneticists Lucca Cavalli-Sforza and Marcus Feldman (1973) initiated the study of cultural evolution using a style of mathematical modeling borrowed from population genetics. Other threads important to the problem of understanding humans in a comparative framework were picked up in that period. For example, Bennett Galef (1977) began his important work on social learning in Norway rats, and the first deep-ocean cores

began to reveal the true dimensions of Pleistocene climates. Advances in paleoanthropology in recent years have likewise been spectacular.

25 years of relatively intensive work have many important questions outstanding. This essay is an attempt to link the results from theoretical modeling the evolutionary properties of culture with some relevant sets of empirical work to produce a synthetic hypothesis to explain the origin of human culture. We make no strong claims for its particular postulates. Our frequent repetition of the word “perhaps” and its relatives emphasizes our belief that many important questions remain to be answered. We believe much more strongly that the main hypothesis here has the right general ingredients to be a successful explanation. It takes a stab at addressing the adaptive economics of large brains and connecting these considerations to the environmental changes that must have driven the encephalization trends of the Cenozoic. It takes a stab at explaining how humans, so lately derived from ancestors with relatively modest systems of social learning, could at once be spectacularly successful using culture but yet not have a crowd of competitors for the cultural niche.

The hypothesis makes predictions that are testable. If it is true, the pattern of climatic deterioration of the Cenozoic should predict the pattern of mammalian encephalization. The correlation is good back 6 million years, and it appears that the step-wise climate deterioration is mirrored in events in hominid evolution (deMenocal and Bloemendal, 1995). It should also hold for the more modest mammalian brain size increases of the middle and early Cenozoic. If selection cannot favor a capacity for complex culture when it is rare, we should expect that apes will show *preadaptations* for culture. That is, they should have cognitive capacities that are homologous to those that we use to support complex, cumulative culture, but that are subsidized, if not entirely supported by, other functions. Chimps and orangutans have some capacity for imitation that is apparently little if at all used in the wild. What function does it serve? Similarly, if parrots and other animals do prove to have capacities for imitation that might support complex cultural traditions, they should serve other functions. Do humans adaptively vary in their relative reliance on cultural tradition versus individual learning as the theoretical models suggest that they should? Do the simple systems of social learning that are probably common in social animals serve the function of adaptation to autocorrelated variable environments? The empirical support for the climate deterioration hypothesis comes from climate proxy data that are mostly very far from measuring variations relevant to the fitness of particular organisms. Only the beautifully detailed ice core data permits us to look at variation on the generational time scale. Beyond about 420,000 years ago, the ice core record disappears and we have only the coarser scale of deep-sea cores. Much more will be revealed in the future, for example from cores from deep, old lakes like Lake Tanganyika.

The hypothesis that social learning is a common adaptation to variable environments could be refined if the proximal features of cognition were better understood. The cognitive economy of brains is, despite much recent attention to other aspects of cognition, poorly understood. Is the incremental cost of improving simple social learning at a given level of individual learning really small? Is it true that even relatively rudimentary imitation requires costly cognitive machinery,

making it impossible for selection to favor true imitation incrementally, beginning with rather simple traditions and working smoothly towards complexity on the human scale? What are the advantages and disadvantages of coding adaptations to variable environments as innate rules versus using more general rules supplemented by learning or social learning? How do individual learning, and social learning interact to support complex cognitive abilities? The rudimentary considerations introduced here suggest that something much more complex than a simple tradeoff between them.

The simple models about the evolutionary significance of culture, upon which the climate driven hypothesis is based, make only very general predictions about how organisms will respond to a variable environment, but they hold out the hope of robust results. Improving upon such predictions is difficult. This does not mean that we need to despair about ever understanding the origins of the human mind. Success in reconstructing the evolution of human minds will come from triangulating on our mysterious past from many different perspectives. No one technique such as strategic modeling by itself will advance understanding more than marginally. In this chapter, we have tried to show how testing the models' predictions against the large scale patterns of mammalian brain enlargement, and of the environmental changes that presumably drove encephalization, sheds some light on the issue. These data constrain the universe of plausible hypotheses, and will exert tighter constraints as they get better. Other kinds of data constrain them still further.

We must take care not to ask science to solve the insoluble. Meteorologists have had to get comfortable with the idea that chaotic dynamics put fundamental limits on weather prediction. Brandon (1990) observes that evolutionary accounts are generally "how possibly" rather than "how actually" explanations because of practical if not fundamental limits on what we know and can hope to know about evolutionary trajectories. How possibly explanations do give us real insights into evolutionary processes even if we cannot hope to nail a particular explanation. We can at least aspire to better understand whether or not the evolution of human cognition was a complex design process or not. If so, we should get comfortable with the idea that the multi-optimality of complex design problems, combined with the paucity of data about the past, put fundamental limits on our ability to understand how we came to be what we are. Not to mention what we might become. Some research programs—we have singled out innatist evolutionary psychology—defy what seem to us to be fundamental limits on the level of detail that strategic modeling can hope to produce.

Thus, the challenge of the origin of the human mind is much the same as it was in Darwin's day. Humans must have evolved by the same basic processes as other organisms yet we are highly unusual in our mode of adaptation by cultural traditions and in our ecological success. Quite likely, the climatic deterioration of the late Cenozoic, especially of the Pleistocene, played a key role in the evolution of culture. Capacities for social learning expanded as a means of adapting to the highly variable environment of the ice age, probably in many mammalian lineages. However, only our species went on to evolve the capacity to acquire complex cultural traditions by imitative social learning. The events leading up to the late Paleolithic expansion in cultural

complexity remain obscure, but some form of preadaptive breakthrough hypothesis is supported by the current evidence.

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of mutation. Guided variation's behavior to track more closely than can genes that follow strict rules, or mixed innate variation for other behaviors during the evolution of a social species.

models we have used to describe. Readers who already know some of models tedious may never, however, that theorists have problems in systems of (Boyd & Richerson, 1996). As in evolution and gene-culture coevolving, motivating the use of

social learning are adaptations to basic models of the individual. Lines: Suppose that the virtually all animals show animals like birds and they have the opportunity to learn. Animals have two sources of information: experience of individuals and two different kinds of social learning (Boyd & Richerson, 1985; Ch. 11 & Richerson, 1989), we have little dependence on the

organisms live in one of two environments. In each one of two behaviors can benefit for behaving alone (or forage alone if wet). Individuals can also opt to imitate social versus individual learning threshold, d , to determine. While growing up, individuals can depend on their parents. Because of the noisy environment, the limitations of individuals' knowledge about whether the environment is dry or wet can be correct. Even if the

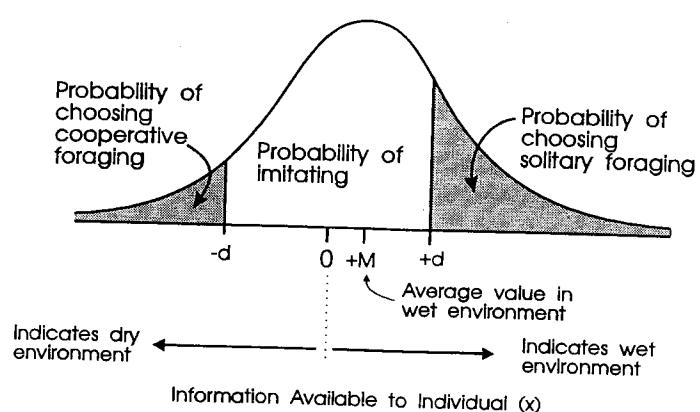


Figure 1. The effect of the learning threshold (d) on the probability of acquiring the best behavior by individual learning or tradition. The curve shows the probability of obtaining a given estimate, x , of the average difference in yield between two environments from a small sample of years of experience of a young forager, assuming that the environment really is in a certain state, wet in this case. The task of the young forager is to decide what to do. If experience seems to show that the environment is indeed rather wet ($x > d$) the forager opts to forage alone. If experience seems to indicate that the environment is dry ($x < -d$), our forager, incorrectly in this case, opts to forage cooperatively. If experience is ambiguous ($-d < x < d$), the young forager follows tradition (adopts parent's behavior). The width of the curve is a measure of the quality of information available from individual learning. In the curve illustrated, individual learning is fairly error prone, and selection is likely to favor setting wide values of d so as to avoid the chance of making an error based on noisy personal experience. However, if the environment is changing rapidly enough, it may be better for young foragers to depend on their own experience in spite of the risks because the risk that their parents are out of touch is also great (from Boyd & Richerson, 1989). First published in Lectures on Mathematics in the Life Sciences, published by the American Mathematical Society.

environment is dry on average, some individuals will experience an unusual run of rainy years. These individuals are vulnerable to mistakenly deciding that the state of the environment is wet when it is really dry. The confidence parameter d tells us how heavily individuals weigh their noisy samples. If d is large, individuals look for quite definitive evidence that the environment really is in the wet or dry state, say entirely quite wet or quite dry during their formative years. If they do not see such evidence, and most will not if the evidence available to individuals comes from an environment with noisy variation, they imitate an experienced individual of the parental generation, such as their mother. If d is small, information from personal experience is virtually always deemed definitive, and learners depend almost entirely on their personal experience.

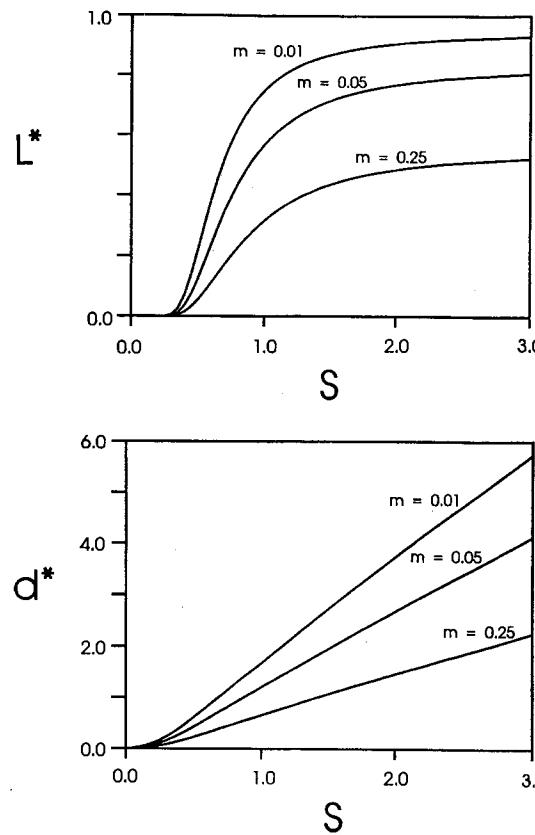


Figure 2. The values of d , the learning threshold and L , the fraction of young foragers acquiring their foraging mode by social learning, as a function of reliability of personal experience (S) and the amount environmental variability from generation to generation (m). The * indicate that these are the evolutionary equilibrium values of L and d , those that maximize fitness. Note that for environments that are harder to figure out (S large), the best thing to do is to rely more on social learning (d^* and L^* increase). Contrariwise, as the real change in the environment increases from generation to generation (m increases), it is best to trust more in own experience even at the risk happening to get the wrong answer by chance. (From Boyd and Richerson, 1989.) First published in Lectures on Mathematics in the Life Sciences, published by the American Mathematical Society.

fitness advantages of a conventional combination of genes and individual with learning a Lamarckian combination of social learning and individual learning. Suppose that there is some cost to being able to learn socially. Under what circumstances might selection favor adding social learning to the standard system where genes represent the wisdom of evolutionary

? The analysis varied the autocorrelation between their potential teachers. If a relationship between experienced individuals of environmental change in the long term, the change

in Figure 3. The social de range of conditions. when the environmental correlation is high, but chosen for illustration at often fairly high, on the a 25% dependence on environments become well, and the advantage ts that social learning species living in variable

rules of social learning random member of the For example, a socially models. If they exhibit two can out and retain the one population are probably exempt on their own. Pla number of plausible initial own experience to choose guided variation process lar evolution that result ion."

tural systems to evolve lations. This subdivision o evolve rapidly. Much shuttling off gene flow the flow of extraneous adaptations can be per son, such groups are spe c roles (Barth, 1969). ge, dress, religious prac w of ideas in spatially

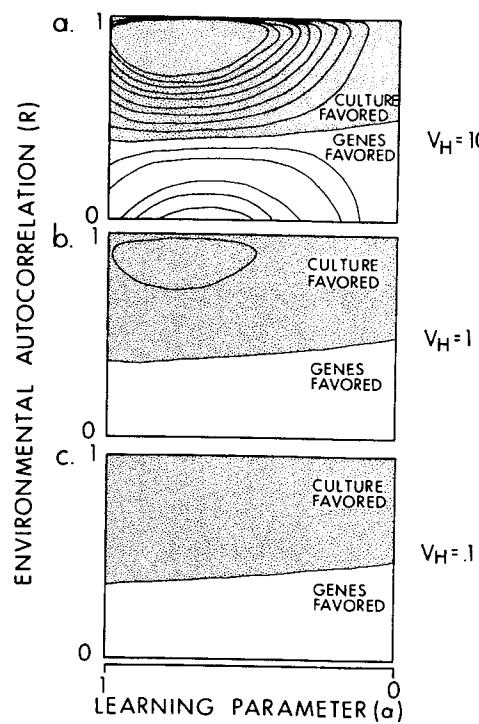


Figure 3. Contour plot of the differences in the fitness of populations using culture or social learning versus genetic transmission to convey information from the older to the younger generation. Both populations use the same individual learning rule, the only difference is that the cultural population has the inheritance of acquired variation so that both learning and natural selection drive behavior in an adaptive direction. The cultural system is assumed also to have a higher random error rate. Here (a) measures the amount of social learning, R the environmental autocorrelation (the degree to which offspring's environments resemble those of their parents), and V_H the amplitude of the environmental variation. The exact shape of the topography depends upon variables not pictured here, but the qualitative results hold for a wide range of those parameters. Cultural transmission is favored whenever the resemblance of parental to offspring environments is sufficiently high. It is especially favored when the environmental change is quite large but fairly slow on the generational time scale. In the situation where the advantage of the cultural system is maximal, the dependence on social learning is substantial, around $\alpha = 0.75$. Note that if R gets large enough, genes win again because in a stable environment the higher "mutation" rate of social learning favors the more exact system of transmission. (From Boyd and Richerson, 1985: 127.) Copyright © 1985 by the University of Chicago.

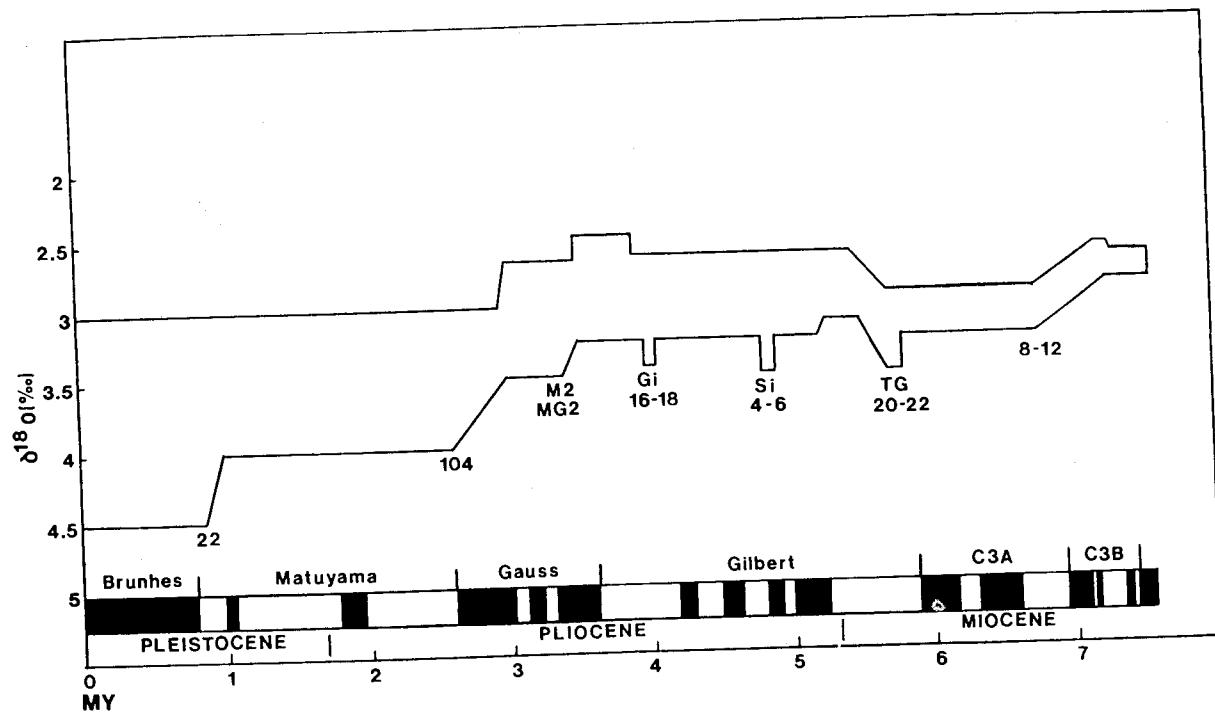


Figure 4. The envelope of variations in the oxygen isotope record for the last 7 million years in marine sediments. The oxygen isotope record, based on samples of foraminiferan shells, is a proxy measure of volume of ice locked up in continental glaciers. Greater concentrations of the heavy ^{18}O isotope indicate cold, high ice conditions. Thus, the climate over the last 7 million years has gotten cooler on average and very much more variable. A significant increase in variability occurred just after 6 million years ago, and again in the middle Pliocene. Another sharp deterioration occurred in the middle Pleistocene. (From Opdyke, 1995.) Copyright © 1995 by Yale University.

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Figure 4. The envelope of variations in the oxygen isotope record for the last 7 million years in marine sediments. The oxygen isotope record, based on samples of foraminiferal shells, is a proxy measure of volume of ice locked up in continental glaciers. Greater concentrations of the heavy ^{18}O isotope indicate cold, high ice conditions. Thus, the climate over the last 7 million years has gotten cooler on average and very much more variable. A significant increase in variability occurred just after 6 million years ago, and again in the middle Pleistocene. (From Opdyke, 1995.) Copyright © 1995 by Yale University.

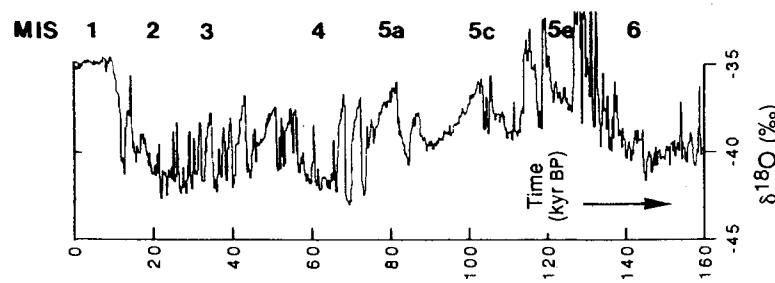


Figure 5. The oxygen isotope paleoclimate proxy from the Greenland Ice Core Project core drilled nearly 3,000 m to bedrock on a nearly stationary part of the Greenland ice cap. Ice depleted in the heavy isotope of oxygen (more negative values) indicates that large volumes of fresh water, depleted in ^{18}O , are stored in the continental glaciers. Note the very sharp peaks and troughs during the last cold period (Marine Isotope Stages 2–4). These are the Dansgaard-Oeschger and Heinrich fluctuations. The replicate GISP2 core agrees remarkably well with the GRIP core back to MIS 5c. The deeper part of the record, MIS 5e and 6, may be disturbed by ice flow (Grootes et al., 1993). Note that the last 10,000 years have been very much less variable than the other parts of the record. Reprinted with permission from Nature, GRIP (1973), copyright © 1993 Macmillan Magazines Limited.

CO_2 content (deMenocal, 1995; Raynaud et al., 1993). Thus, during glacials overall plant productivity was lower, but a higher percentage of plant communities were tundra, shrub desert, and steppe, which favor large herbivores. Ocean currents shifted dramatically (Lehman, 1993). The causes of the Pleistocene climate deterioration are not well understood. They are probably the result of basic geological processes, such as the isolation of the Antarctic continent from warm ocean currents by circum-Antarctic currents flowing through the gap created by continental drift between Antarctica and South America (Partridge et al., 1995).

As time series analysts say, the climate record of the past few million years is highly non-stationary. Not only does the climate vary, but also the statistics that describe the variation—the mean, variance and patterns of autocorrelation—change with time. The amplitude of fluctuations in temperature (and many other climate variables) increased as mean temperature dropped, as Figure 4 shows. The pattern of fluctuation in climate is very complex. Much of the variation seems to arise from an enhanced sensitivity to radiation changes caused by periodic variations in the Earth's orbit and its orientation with respect to the sun. The radiation income in high northern latitudes has a 20% range of variation due to these effects (Milankovitch, 1941; Broecker & Denton, 1990). The eccentricity of the Earth's orbit varies on a 95,800 year time scale, the inclination of its axis with a periodicity of 41,000 years, and the precession of the equinoxes with a periodicity of 21,700 years. As the deterioration has proceeded, different

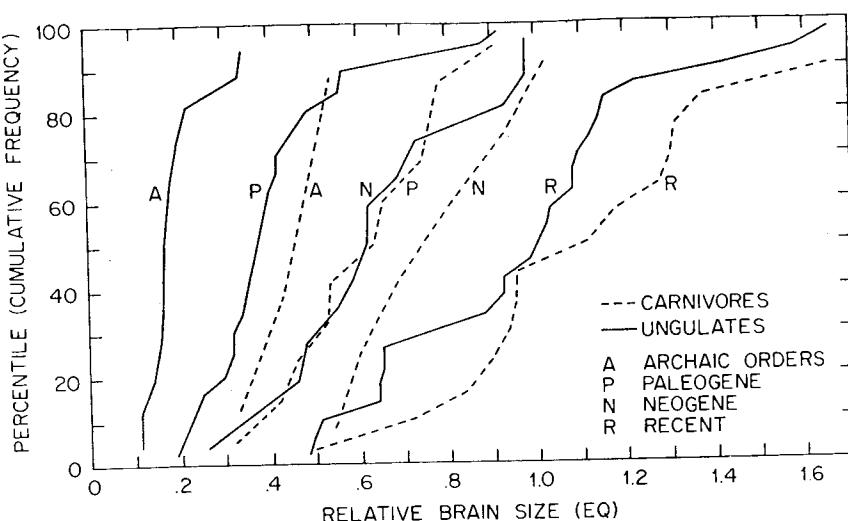


Figure 6. Cumulative frequency distributions of encephalization quotients in fossil and Recent ungulates and carnivores. Encephalization coefficients measure brain size corrected for body weight. (From Jerison 1973: 311.) Copyright © 1973 Academic Press.

However, many relatively small-brained mammals persist to the present even in orders where some species have gotten rather large brains. The diversity of brain size increases toward the present. Why might variability selection have resulted in this pattern rather than an increase in brain size in all mammalian lineages?

There is good reason to expect that, all-else-equal, selection favors as small a brain as possible. Sophisticated learning systems require larger sensory and nervous systems than simpler ones. The incremental energetic costs of maintaining this extra nervous tissue are quite large (Eisenberg, 1981, pp. 235–6). Mammalian brains vary over about a 25-fold range, controlling for body size (Martin, 1981). Human brains are about 5 times as large as the brains of average mammals of our body weight. Living ungulates and carnivores have average brains. Average living mammals in turn have brains about 5 times as large as those of the smallest brained mammals, such as insectivores and many marsupials. Human brains account for 16% of our basal metabolism (Aiello & Wheeler, 1995). Thus average mammals will have to allocate only about 3% of basal metabolism to their brains, and some get by with less than 1%. Total metabolism runs about 1.8 times that of resting metabolism, mostly because of the mobilization of large masses of otherwise low-metabolic-rate skeletal muscle during exercise. How nervous system metabolic rate varies with “exercise” is poorly