Climate, Culture, and the Evolution of Cognition

Peter J. Richerson

Department of Environmental Science and Policy

University of California, Davis, California 95616

pjricherson@ucdavis.edu

Robert Boyd

Department of Anthropology

University of California, Los Angeles, California 90024

rboyd@anthro.ucla.edu

Version 2.1. May 6, 1999. Appeared in Evolution of Cognition, Cecelia Heyes and Ludwig Huber (Eds.) MIT Press, 2000, pp. 329-346.

Introduction

What are the causes of the evolution of complex cognition? Discussions of the evolution of cognition sometimes seem to assume that more complex cognition is a fundamental advance over less complex cognition, as evidenced by a broad trend toward larger brains in evolutionary history. Evolutionary biologists are suspicious of such explanations since they picture natural selection as a process leading to adaptation to local environments, not to progressive trends. Cognitive adaptations will have costs, and more complex cognition will evolve only when its local utility outweighs them.

In this chapter, we argue that Cenozoic trends in cognitive complexity represent adaptations to an increasingly variable environment. The main support for this hypothesis is a correlation between environmental deterioration and brain size increase in many mammalian lineages.

We would also like to understand the sorts of cognitive mechanisms that were favored in building more complex cognitions. The problem is difficult because little data exists on the adaptive tradeoffs and synergies between different cognitive strategies for adapting to variable environments. Animals might use information rich, innate decision-making abilities, individual learning, social learning, and, at least in humans, complex culture, alone or in various combinations, to create sophisticated cognitive systems.

We begin with a discussion of the correlated trends in environmental deterioration and brain size evolution and then turn to the problem of what sorts of cognitive strategies might have served as the impetus for brain enlargement.

Plio-Pleistocene Climate Deterioration

The deterioration of climates during the last few million years should have dramatically increased selection for traits increasing animals' abilities to cope with more variable environments. These traits include more complex cognition. Using a variety of indirect measures of past temperature, rainfall, ice volume, and the like, mostly from cores of ocean sediments, lake sediments, and ice caps, paleoclimatologists have constructed a stunning picture of climate deterioration over the last 14 million years (Lamb, 1977; Schneider and Londer, 1984; and Dawson, 1992; Partridge, et al., 1995). The Earth's mean temperature has dropped several degrees and the amplitudes of fluctuations in rainfall and temperature have increased. For reasons that are as yet ill understood, glaciers wax and wane in concert with changes in ocean circulation, carbon dioxide, methane and dust content of the atmosphere, and changes in

average precipitation and the distribution of precipitation. The resulting pattern of fluctuation in climate is very complex. As the deterioration has proceeded, different cyclical patterns of glacial advance and retreat involving all these variables have dominated the pattern. A 21,700 year cycle dominated the early part of the period, a 41,000 year cycle between about 3 and 1 million years ago, and a 95,800 year cycle the last million years.

This cyclic variation is very slow with respect to the generation time of animals, and is not likely to have directly driven the evolution of adaptations for phenotypic flexibility. However, the increased variance on time scales of the major glacial advances and retreats also seems to be correlated with greatly variance at much shorter time scales. For the last 120,000 years, quite high-resolution data is available from ice cores taken from the deep ice sheets of Greenland and Antarctica. Resolution of events lasting only a little more than a decade is possible in ice 90,000 years old, improving to monthly after 3,000 years ago. During the last glacial, ice core data shows that the climate was highly variable on time scales of centuries to millennia (GRIP, 1993; Lehman, 1993; Ditlevsen, et al., 1996). Even when the climate was in the grip of the ice, there were brief spike-like ameliorations of about a thousand years' duration in which the climate temporarily reached near interglacial warmth. The intense variability of the last glacial carries right down to the limits of the nearly 10 year resolution of the ice core data. Sharp excursions lasting a century or less occur in estimated temperatures, atmospheric dust, and greenhouse gases. Comparison of the rapid variation during this period with older climates is not yet possible. However, an internal comparison is possible. The Holocene (the last relatively warm, ice free 10,000 years) has been a period of very stable climate, at least by the standards of the last glacial. At the decadal scale, last glacial climates were much more variable than in the Holocene. Holocene weather extremes have quite significant effects on organisms (Lamb, 1977). It is hard to imagine the impact of the much greater variation that was probably characteristic of most if not all of the Pleistocene. Floods, droughts, windstorms, and the like, which we experience once a century might have occurred once a decade. Tropical organisms did not escape the impact of climate variation; temperature and especially rainfall were highly variable at low latitudes (Broecker, 1996). During most periods in the Pleistocene, plants and animals must generally have lived under conditions of rapid, chaotic, and ongoing reorganizations of ecological communities as species' ranges adjusted to the noisy variation in climate. Thus, since the late Miocene organisms have had to cope with increasing variability in many environmental parameters at time scales on which strategies for phenotypic flexibility would be highly adaptive.

Brain Size Evolution in the Neogene

Mammals show clear signs of responding to climate deterioration by developing more complex cognition. Jerison's (1973) classic study of the evolution of brain size documents major

trends towards increasing brain size in many mammalian lineages that persist up through the Pleistocene. The time trends are complex. There is a progressive increase in average encephalization (brain size relative to body size) throughout the Cenozoic. However, many relatively small-brained mammals persist to the present even in orders where some species have evolved large brains. The *diversity* of brain size increases toward the present. Mammals continue to evolve under strong selective pressure to minimize brain size (see section on cognitive economics below), and those that effectively cope with climatic deterioration by range changes or non-cognitive adaptations do so. Other lineages evolved the means to exploit the temporal and spatial variability of the environment by using behavioral flexibility. The latter, we suppose, pay for the cost of encephalization by exploiting the ephemeral niches that less flexible, smaller brained species leave under-exploited.

Humans anchor the tail of the distribution of brain sizes in mammals; we are the largest brained member of the largest brained mammalian order. This fact supports 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 general selective process such as we propose is really operating. Nevertheless, there is some evidence that human culture is more than just a more sophisticated form of typical animal cognitive strategies. More on this vexing issue below.

The largest increases in encephalization per unit time by far is the shift from Miocene and Pliocene species to modern ones, coinciding with the Pleistocene climate deterioration. In the last 2.5 million years 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.

General Purpose Versus Special Purpose Mechanisms

To understand how evolution might have shaped cognitive adaptations to variable environments we need to know something about the elementary properties of mental machinery. Psychologists interested in the evolution of cognition have generated two classes of hypotheses about the nature of minds. A long-standing idea is that cognitively sophisticated mammals and birds have evolved powerful and relatively general purpose mental strategies that culminate in human intelligence and culture. These flexible general purpose strategies replace more rigidly innate ones as cognitive sophistication increases. For example, Donald Campbell (1965, 1975) emphasized the general similarities of all knowledge acquiring processes ranging from organic evolution to modern science. He argued that even a quite fallible cognitive apparatus could nevertheless obtain workable mental representations of a complex variable environment by trial and error methods, much as natural selection shapes random mutations into organic adaptations. Bitterman's (this volume) empirical argument that simple and complex cognitions use rather similar learning strategies is a kindred proposal. Jerison (1973) argued that the main region of enlargement of bird and mammal brains in the Cenozoic has been the forebrain, whose structures serve rather general coordinating functions. He believes that it is possible to speak of intelligence abstracted from the particular cognition of each species, which he characterizes as the ability to construct perceptual maps of the world and use them to guide behavior adaptively. Edelman's (1987) theory of neuronal group selection is based on the argument that developmental processes cannot specify the fine details of the development of complex brains and hence that much environmental feedback is necessary just to form the basic categories that complex cognition needs to work. This argument is consistent with the observation that animals with more complex cognition require longer juvenile periods with lots of "play" to provide the somatic selection of the fine details of synaptic structure. On Edelman's argument, a large measure of phenotypic flexibility comes as a result of the developmental constraints on the organization of complex brains by innate programming. If cognition is to be complex, it must be built using structures that are underdetermined at birth.

Against general-purpose hypotheses, there has long been the suspicion that animal intelligence can only be understood in relationship to the habitat that the species lives in (Hinde, 1970: 659-663). Natural selection is a mechanism for adapting the individuals of a species to particular environmental challenges. It will favor brains and behaviors specialized for the niche of the species. There is no reason to think that it will favor some general capacity that we can operationalize as intelligence across species. A recent school of evolutionary psychologists has applied this logic to the human case (Barkow, Cosmides, and Tooby, 1992; Pinker, 1997; Shettleworth, this volume). The brain, they argue, even the human brain, is not a general problem solving device, but a collection of modules directed at solving the particular challenges posed by the environments in which the human species evolved. General problem solving devices are hopelessly clumsy. To work at all, a mental problem-solving device must make a number of assumptions about the structure of its world, assumptions that are likely to hold only locally. Jack of all trades, master of none. Human brains, for example, are adapted to life in small-scale hunting and gathering societies of the Pleistocene. They will guide behavior within such societies with considerable precision but behave unpredictably in other situations. These authors are quite suspicious of the idea that culture alone forms the basis for human behavioral flexibility. As Tooby and Cosmides (1992) put it, what some take to be cultural traditions transmitted to relatively passive imitators in each new generation could actually be partly, or even mainly, "evoked culture," innate information that leads to similar behavior in parents and offspring simply because they live in similar environments. On this model, human cognition is complex because we have many content rich, special purpose innate algorithms, however much we also depend upon transmitted culture.

This debate should not be trivialized by erecting straw protagonists. On the one hand, it is not sensible for defenders of cognitive generalism to ignore that the brain is a complex organ with many specialized parts, without which no mental computations would be possible. No doubt, much of any animal's mental apparatus is keyed to solve niche specific problems, as is abundantly clear from brain comparative anatomy (Krubitzer, 1995) and from performance on learning tasks (Garcia and Koelling, 1966, Poli, 1986). Learning devices can be only *relatively* general; all of them must depend upon an array of innate processing devices to interpret raw sense data and evaluate whether it should be treated as significant (an actual or potential reinforcer). The more general a learning rule is, the weaker it is liable to be.

On the other hand, one function of all brains is to deal with the unforeseeable. The dimensionality of the environment is very large even for narrow specialists, and even larger for weedy, succeeds-everywhere species like humans. Being pre-programmed to respond adaptively to a large variety of environmental contingencies may be costly or impossible. If efficient learning heuristics exist that obviate the need for large amounts of innate information, they will be favored by selection.

When the situation is sufficiently novel, like most of the situations that rats and pigeons face in a Skinner Boxes, every species is forced to rely upon what is, in effect, a very general learning capability. An extreme version of the special purpose modules hypothesis would predict that animals should behave completely randomly in environments as novel as they usually face in the laboratory. The fact that adaptive behavior emerges at all in such circumstances is a clear disproof of such an extreme position. Likewise, humans cannot be too tightly specialized for living in small hunting and gathering societies under Pleistocene conditions. We are highly successful in the Holocene using far different social and subsistence systems.

A Role For Social Learning In Variable Environments

Our own hypothesis is that culture plays a large role in the evolution of human cognitive complexity. The case for a role for social learning in other animals is weaker and more controversial, but well worth entertaining. Social learning and culture furnish a menu of heuristics for adapting to temporally and spatially variable environments. Learning devices will only be favored when environments are variable in time or space in difficult-to-predict ways. Social learning is a device for multiplying the power of individual learning. Systems of phenotypic adaptation have costs. In the case of learning, an individual will have to expend time and energy in learning, incur some risks in trials that may be associated with costly errors, and support the neurological machinery necessary to learn. Social learning can economize on the trial and error part of learning. If kids learn from Mom, they can avoid repeating her mistakes. "Copy Mom" is a simple heuristic that may save one a lot of effort and be almost as effective as learning for

oneself, provided the environment in one's generation is pretty much like Mom's. Suppose the ability to somehow copy Mom is combined with a simple check of the current environment that warns one if the environment has changed significantly. If it has, one learns for oneself. This strategy allows social learners to frequently avoid learning costs but rely on learning when necessary.

We have constructed a series of mathematical models designed to test the cogency these ideas (Boyd and Richerson, 1985; 1989, 1995, 1996; see also Pulliam and Dunford, 1980, Cavalli-Sforza and Feldman, 1973). The formal theory supports the story. When information is costly to obtain and when there is some statistical resemblance between models' and learners' environments, social learning is potentially adaptive. Selection will favor individual learners who add social learning to their repertoire so long as copying is fairly accurate and the extra overhead cost of the capacity to copy is not too high. In some circumstances, the models suggest that social learning will be quite important relative to individual learning. It can be a great advantage relative to a system that relies on genes only to transmit information and individual learning in adaptive directions. When the behavior of models is variable, individuals that try to choose the best model by using simple heuristics like "copy dominants" or "go with the majority," or by using complex cognitive analyses, are more likely to do well than those who blindly copy. Contrariwise, if it easy for individuals to learn the right thing to do by themselves, or if environments vary little, then social learning is of no utility.

A basic advantage common to many of the model systems that we have studied is that a system linking an ability to make adaptive decisions to an ability to copy speeds up the evolutionary process. Both natural selection and the biasing decisions that individuals make act on socially learned variation. The faster rate of evolution tracks a variable environment more faithfully, providing a fitness return to social learning.

Our models of cultural evolution are much like the learning model Bitterman describes in this volume. In fact, one of our most basic models adds social learning to a model of individual learning virtually identical to his in order to investigate the inheritance-of-acquired-variation feature of social learning. Such models are quite simple and meant to be quite general. We expect that they will apply, at least approximately, to most examples of social learning likely to be found in nature.

Social learning strategies could represent a component of general purpose learning system. Social learning is potentially an adaptive supplement to a weak, relatively general purpose learning rule. (We accept the argument that the more general a learning rule is the weaker it has to be.) However, we have modeled several different kinds of rules for social learning. These would qualify as different modules in Shettleworth's terms (this volume). The same rule, with different inputs and different parameter settings, can be implemented as a component of many narrowly specialized modules. Psychological evidence suggests that human culture involves numerous subsystems and variants that use a variety of patterns of transmission and a variety of biasing heuristics (Boyd and Richerson, 1985). Although all non-human social learning systems are, as far as we know, much simpler than human culture, they probably obey a similar evolutionary logic and vary adaptively from species to species (Laland et al., 1996; Chou and Richerson, 1992).

In no system of social learning have fitness effects yet been estimated; the adaptivness of simple social learning warrants skepticism. Rogers (1989, see also Boyd and Richerson, 1995) constructed a plausible model in which two genotypes were possible, individual learners and social learners. In his model, the social learning genotype can invade because social learners save on the cost of learning for themselves. However, at the equilibrium frequency of social learners, the fitness of the two types is equal. Social learners are parasites on the learning efforts of individual learners. Social learning only raises the average fitness of individuals if individual learners also benefit from social learning. The well-studied system of social learning of food preference in rats is plausibly an example of adaptive social learning (Galef, 1996), but the parasitic hypothesis is yet not ruled out. Lefebvre's (this volume) data indicating a positive correlation of individual and social learning suggests an adaptive combination of individual and social learning, although his data on scrounging in aviaries shows that pigeons are perfectly willing to parasitize the efforts of others. We will be surprised if no cases of social learning corresponding to Rogers' model ever turn up.

The complex cognition of humans is one of the great scientific puzzles. Our conquest of *the* ultimate cognitive niche seems to explain our extraordinary success as a species (Tooby and Devore, 1987). Why then has the human cognitive niche remained empty for all but a tiny slice of the history of life on earth, finally to be filled by a single lineage? Human culture, but not the social learning of most other animals, involves the use of imitation, teaching and language to transmit complex adaptations subject to progressive improvement. In the human system, socially learned constructs can be far more sophisticated than even the most inspired individual could possibly hope to invent. Is complex culture the essence of our complex cognition, or merely a subsidiary part?

The Problem of Cognitive Economics

To understand how selection for complex cognition proceeds, we need to know the costs, benefits, tradeoffs, and synergies involved in using elementary cognitive strategies in compound architectures to adapt efficiently to variable environments. In our models we have merely assumed costs, accuracies, and other psychological properties of learning and social learning. We here sketch the kinds of knowledge necessary to incorporate cognitive principles directly into evolutionary models.

Learning and decision-making require larger sensory and nervous systems in proportion to their sophistication, and large nervous systems are costly (Eisenberg, 1981: 235-6). Martin (1981) reports that mammalian brains vary over about a 25-fold range, controlling for body size. Aiello and Wheeler (1995) report that human brains account for 16% of our basal metabolism. Average mammals have to allocate about only 3% of basal metabolism to their brains, and many marsupials get by with less than 1%. These differences are large enough to generate significant evolutionary tradeoffs. In addition to metabolic requirements, there are other significant costs of big brains such as increased difficulty at birth, greater vulnerability to head trauma, increased potential for developmental snafus, and the time and trouble necessary to fill them with usable information. On the cost side, selection will favor as small a nervous system as possible.

If our hypothesis is correct, animals with complex cognition foot the cost of a large brain by adapting more swiftly and accurately to variable environments. Exactly how do they do it? Given just three generic forms of adaptation to variable environments-innate information, individual learning, and social learning-and two kinds of mental devices-more general and less general purpose—the possible architectures for minds are quite numerous. What sorts of tradeoffs will govern the nature of structures that selection might favor? What is the overhead cost of having a large repertoire of innate special purpose rules? Innate rules will consume genes and brain tissue with algorithms that may be rarely called upon. The gene-to-mind translation during development may be difficult for complex innate rules. If so, acquiring information from the environment using learning or social learning may be favored. Are there situations where a (relative) jack-of-all-trades learning rule can out-compete a bevy of specialized rules? What is the penalty paid in efficiency for a measure of generality in learning? Are there efficient heuristics that minds can use to gain a measure of generality without paying the full cost of general purpose learning device? Relatively general purpose heuristics might work well enough over a wide enough range of environmental variation to be almost as good as several sophisticated special purpose algorithms, each costing as much brain tissue as the general heuristic (See Gigerenzer and Goldstein, 1996, on simple but powerful heuristics).

Hypothesis building here is complicated because we cannot assume that individual learning, social learning, and innate knowledge are simply competing processes. For example, more powerful or more general learning algorithms may generally require more innate information (Tooby and Cosmides, 1992). More sophisticated associative learning will typically require more sense data to make finer discriminations of stimuli. Sophisticated sense systems depend

upon powerful, specialized innate algorithms to make useful information from a mass of raw data from the sensory transducers (Shettleworth, this volume, Spelke, 1990). Hypothesis building is also complicated because we have no rules describing the efficiency of a compound system of some more and some less specialized modules. For example, a central general-purpose associative learning device might be the most efficient processor for such sophisticated sensory data because redundant implementation of the same learning algorithm in many modules might be costly. Intense modularity in parts of the mind may favor general-purpose, shared, central devices in other parts. Bitterman's (this volume) data are consistent with there being a central associative learning processor that is similar by homology across most of the animal kingdom. However, his data are also consistent with several or many encapsulated special purpose associative learning devices that have converged on a relatively few efficient association algorithms. Shettleworth's (this volume) argument for modularity by analogy with perception has appeal. If the cost of implementing an association algorithm is small relative to the cost of sending sensory data large distances across the brain, selection will favor association algorithms in many modules. However, the modularity of perception is surely driven in part by the fact that the different sense organs must transduce very different physical data. Bitterman's (this volume) data show that, once reduced to a more abstract form, many kinds of sense data can be operated on by the same learning algorithm, which might be implemented centrally or modularly. The same sorts of issues will govern the incorporation of social learning into an evolving cognitive system.

There may be evolutionary complications to consider. For example, seldom used special purpose rules (or the extreme seldom-used ranges of frequently exercised rules) will be subject to very weak selection. More general-purpose structures have the advantage that they will be used frequently and hence be well adapted to the prevailing range of environmental uncertainty. If they work to any approximation outside this range, selection can readily act to improve them. Narrowly special purpose algorithms could have the disadvantage that they can be "caught out" by a sudden environmental change, exhibiting no even marginally useful variation for selection to seize upon, whereas more general-purpose individual and social learning strategies can expose variation to selection in such cases (Laland, et al., 1996). On the other hand, we might imagine that there is a reservoir of variation in outmoded special purpose algorithms, on which selection has lost its purchase, that furnishes the necessary variation in suddenly changed circumstances.

The high dimensionality of the variation of Pleistocene environments puts a sharp point on the innate information versus learning/social learning modes of phenotypic flexibility. Mightn't the need for enough information to cope with such complex change by largely innate means exhaust the capacity of the genome to store and express it? Recall Edelman's (1987) neuronal group selection hypothesis in this context. Immelman (1975) suggested that animals use imprinting to

identify their parents and acquire a concept of their species because it is not feasible to store a picture of the species in the genes or to move the information from genes to the brain during development. It may be more economical to use the visual system to acquire the picture after birth or hatching by using the simple heuristic that the first living thing one sees is Mom and a member of one's own species. In a highly uncertain world wouldn't selection favor a repertoire of heuristics designed to learn as rapidly and efficiently as possible?

As far as we understand, psychologists are not yet in a position to give us the engineering principles of brain design the way that students of biological mechanics now can for muscle and bone. If these principles turn out to favor complex, mixed designs with synergistic, non-linear relationships between parts, the mind design problem will be quite formidable. We want to avoid asking silly questions analogous to "which is more important to the function of a modern PC, the hardware or the software?" However, in our present state of ignorance, we do run the risk of asking just such questions!

With due care, perhaps we can make a little progress. In this chapter, we use a method frequently use by evolutionary biologists, dubbed "strategic modeling" by Tooby and Devore (1987). In strategic modeling, we begin with the tasks that the environment sets for an organism and attempt to deduce how natural selection should have shaped the species' adaptation to its niche. Often, evolutionary biologists frame hypotheses in terms of mathematical models of alternative adaptations which predict, for instance, what foraging or mate choice strategy organisms with a given general biology should pursue in a particular environment. This is just the sort of modeling we have undertaken in our studies of social learning and culture. We ask: how should organisms cope with different kinds of spatially and temporally variable environments?

Social Learning Versus Individual Learning Versus Innate Programming?

Increases in brain size could signal adaptation to variable environments via individual learning, social learning, or more sophisticated innate programming. Our mathematical models suggest that the three systems work together. Most likely increases in brain size to support more sophisticated learning or social learning will also require at least some more innate programming. There is likely an optimal balance of innate and acquired information dictated by the structure of environmental variability. Given the tight cost/benefit constraints imposed on brains, at the margin we would expect to find a tradeoff between social learning, individual learning, and innate programming. For example, 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.

Lefebvre (this volume) reviews studies designed to test the hypothesis that social and opportunistic species should be able to learn socially more easily than the more conservative species, and the conservative species should be better individual learners. Surprisingly, the prediction fails. Species that are good social learners are also good individual learners. One explanation for these results is that the synergy between these systems is strong. Perhaps the information-evaluating neural circuits used in social and individual learning are partly or largely shared. Once animals become social, the potential for social learning arises. The two learning systems may share the overhead of maintaining the memory storage system and much of the machinery for evaluating the results of experience. If so, the benefits in quality or rate of information gained may be large relative to the cost of small bits of specialized nervous tissue devoted separately to each capacity. 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. On the other hand, Lefebvre notes that not all learning abilities are positively correlated. Further, the correlation may be due to some quite simple factor, such as low neophobia, not a more cognitively sophisticated adaptation.

The hypothesis that the brain tissue tradeoff between social and individual learning is small resonates with what we know of the mechanisms of social learning in most species. Galef (1988, 1996), Laland et al. (1996), and Heyes and Dawson (1990) argue that the most common forms of social learning result from very simple mechanisms that piggyback on individual learning. 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 then lead to acquisition of behaviors by ordinary mechanisms of reinforcement. Social experience acts, essentially, to speed up and make less random the individual learning process, 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 mental map increases, it makes sense to enlarge the scale of maps to take advantage of that fact. Eventually, diminishing returns to map accuracy will limit brain size.

Once again, we must take a skeptical view of this adaptive hypothesis until experimental and field investigations produce better data on the adaptive consequences of social learning. Aside from Roger's parasitic scenario, the simplicity of social learning in most species and its close relationship to individual learning invites the hypothesis that most social learning is a byproduct of individual learning that is not sufficiently important to be shaped by natural selection. Human imitation, by contrast, is so complex as to suggest that it must have arisen under the influence of selection.

Eisenberg's (1981: Ch 23) review of a large set of data on the encephalization of living mammals suggests that high encephalization is associated with extended association with parents, late sexual maturity, extreme iteroparity, and long potential life-span. These life cycle attributes all seem to favor social learning (but also any other form of time-consuming skill acquisition). We would not expect this trend if individual and social learning were a small component of encephalization relative to innate, information rich modules. On the latter hypothesis, animals with a minimal opportunity to take advantage of parental experience and parental protection while learning for themselves ought to be able to adapt to variable environments with a rich repertoire of innate algorithms. Eisenberg's data suggest that large brains are not normally favored in the absence of social learning and/or social facilitation of individual learning. The study of any species that run counter to Eisenberg's correlation might prove very rewarding. Large brained species with a small period of juvenile dependence should have a complex cognition built disproportionately of innate information. Similarly, small-brained social species with prolonged juvenile dependence or other social contact may depend relatively heavily on simple learning and socially learning strategies. Lefebvre and Palameta (1988) provide a long list of animals in which social learning has been more or less convincingly documented. Recently, Dugatkin (1996) and Laland and Williams (1997) have demonstrated social learning in guppies. Even marginally social species may come under selection for behaviors that enhance social learning, as in the well known case of mother housecats who bring partially disabled prey to their kittens for practice of killing behavior (Caro and Hauser, 1992).

Some examples of non-human social learning are clearly specialized, such as bird song imitation, but the question is open for other examples. Aspects of the social learning system in other cases do show signs of adaptive specialization, illustrating the idea that learning and social learning systems are only general purpose *relative* to a completely innate system. For example, Terkel (1996) and Chou (1989, personal communication) obtained evidence from laboratory studies of black rats that the main mode of social learning is from mother to pups. This is quite unlike the situation in the case of norway rats, where Galef (1988, 1996) and coworkers have shown quite conclusively that mothers have no special influence on pups. 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 environment than norway rats. Terkel studied a rat population that has adapted to open pinecones in an exotic pine plantation in Israel, 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.

Human Versus Other Animals' Culture

The human species position at the large-brained tail of the distribution of late Cenozoic encephalization suggests the hypothesis that our system of social learning is merely a hypertrophied version of a common mammalian system based substantially on the synergy between individual learning and simple systems of social learning. However, two lines of evidence suggest that there is more to the story.

First, human cultural traditions are often very complex. Subsistence systems, artistic productions, languages, and the like are so complex that they must be built up over many generations by the incremental, marginal modifications of many innovators (Basalla, 1988). We are utterly dependent on learning such complex traditions to function normally.

Second, this difference between humans and other animals in the complexity of socially learned behaviors is mirrored in a major difference in mode of social learning. As we saw above, the bulk of animal social learning seems to be dependent mostly on the same techniques used in individual learning, supplemented at the margin by a bit of teaching and imitation. 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. Although there are some rather good experiments indicating some capacity for true imitation in several socially learning species (Heyes, 1996; Zentall, 1996; Moore, 1996), headto-head comparisons of children's and chimpanzee's abilities to imitate show that children begin to exceed chimpanzees' capabilities at about 3 years of age (Whiten and Custance, 1996; Tomasello, 1996, this volume). The lesson to date from comparative studies of social learning suggests that simple mechanisms of social learning are much more common and more important than imitation, even in our close relatives and other highly encephalized species.

Why Is Complex Culture Rare?

One hypothesis is that an intrinsic evolutionary impediment exists, hampering the evolution of a capacity for complex traditions. We show elsewhere that, under some sensible cognitiveeconomic assumptions, a capacity for complex cumulative culture cannot be favored by selection when rare (Boyd and Richerson, 1996). The mathematical result is quite intuitive. Suppose that to acquire a complex tradition efficiently, imitation is required. Suppose that efficient imitation requires considerable costly, or complex, cognitive machinery, such as a theory-of-mind/imitation module (Cheney and Seyfarth, 1990: 277-230, Tomasello, this volume). If so, there will be a coevolutionary failure of capacity for complex traditions to evolve. The capacity would be 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 who has 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. 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 traditionary path from simple social learning to complex culture.

If such an impediment to the evolution of complex traditions existed, evolution must have traveled a round-about path get the frequency of the imitation capacity high enough to begin to bring it under positive selection for its tradition-supporting function. Some have suggested that primate intelligence was originally an adaptation to manage a complex social life (Humphrey, 1976; Byrne and Whiten, 1988, Kummer et al., 1997; Dunbar, 1992, this volume). Perhaps in our lineage the complexities of managing the sexual division of labor, or some similar social problem, favored the evolution of a sophisticated theory-of-mind capacity. Such a capacity might incidentally make efficient imitation possible, launching the evolution of elementary complex traditions exist, the threshold is crossed. As the evolving traditions become too complex to imitate easily, they will begin to drive the evolution of still more sophisticated imitation. This sort of stickiness in the evolutionary processes is presumably what gives evolution its commonly contingent, historical character (Boyd and Richerson, 1992).

Conclusion

The evolution of complex cognition is a complex problem. It is not entirely clear what selective regimes favor complex cognition. The geologically recent increase in the encephalization of many mammalian lineages suggests that complex cognition is an adaptation to a common, widespread, complex feature of the environment. The most obvious candidate for this selective factor is the deterioration of the Earth's climate since the late Miocene, culminating in the exceedingly noisy Pleistocene glacial climates.

In principle, complex cognition can accomplish a system of phenotypic flexibility by using information rich innate rules or by using more open individual and social learning. Presumably, the three forms of phenotypic flexibility are partly competing, partly mutually supporting

mechanisms that selection tunes to the patterns of environmental variation in particular species' niches. Because of the cost of brain tissue, the tuning of cognitive capacities will take place in the face of a strong tendency to minimize brain size. However, using strategic modeling to infer the optimal structure for complex cognitive systems from evolutionary first principles is handicapped by the very scanty information on tradeoffs and constraints that govern various sorts of cognitive information processing strategies. For example, we do not understand how expensive it is to encode complex innate information rich computational algorithms relative to coping with variable environments with relatively simple, but still relatively efficient, learning heuristics. Psychologists and neurobiologists might usefully concentrate on such questions.

Human cognition raises the ante for strategic modeling because of its apparently unique complexity and yet great adaptive utility. We can get modest but real leverage on the problem by investigating other species with cognitive complexity approaching ours, which in addition to great apes may include some other monkeys, some cetaceans, parrots and corvids (Moore, 1996, Heinrich, Clayton, this volume). Our interpretation of the evidence is that human cognition is mainly evolved to acquire and manage cumulative cultural traditions. This capacity probably cannot be favored when rare, even in circumstances where it would be quite successful if it did evolve. Thus, its evolution likely required, as a preadaptation, the advanced cognition achieved by many mammalian lineages in the last few million years. *In addition*, it required an adaptive breakthrough, such as the acquisition of a capacity for imitation as a byproduct of the evolution of a theory-of-mind capacity for social purposes.

Acknowledgements: Thanks to Cecelia Heyes, Ludwig Huber, the Konrad Lorenz Institute staff and other participants for a most interesting conference, to Monique Borgerhoff Mulder's lab group for useful comments, and to Scott Richerson for editorial assistance.

Literature Cited

- Aiello, L.C., and P. Wheeler. 1995. The expensive tissue hypothesis: The brain and the digestive system in human and primate evolution. Current Anthropology 36: 199-221.
- Barkow, J.H., L. Cosmides, and J.Tooby. 1992. The Adapted Mind: Evolutionary Psychology and the Generation of Culture. Oxford: Oxford University Press.

Basalla, G. 1988. The Evolution of Technology. Cambridge: Cambridge University Press.

- Boyd, R. and P.J. Richerson. 1996. Why culture is common, but cultural evolution is rare. Proc. Brit. Acad. 88: 77-93.
- Boyd R. and P.J. Richerson. 1995. Why does culture increase human adaptability? Ethol. Sociobiol. 16: 125-143.
- Boyd, R, and P.J. Richerson. 1992. How microevolutionary processes give rise to history. In: M.H. and D.V. Nitecki, eds., History and Evolution. Albany: The State University of New York Press. Pp. 179-209.
- Boyd, R. and P.J. Richerson. 1989. Social learning as an adaptation. Lectures on Mathematics in the Life Sciences 20: 1-26.
- Boyd, R. and P.J. Richerson. 1985. Culture and the Evolutionary Process. Chicago: Chicago University Press.
- Broecker, W.S. 1996. Glacial climate in the tropics. Science 272: 1902-1903.
- Byrne, R.W. and A. Whiten, eds. 1988. Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. Oxford: Oxford University Press.
- Campbell, D.T. 1975. On the conflicts between biological and social evolution and between psychology and moral tradition. Amer. Psychol. 30: 1103-1126.
- Campbell, D.T. 1965. Variation and selective retention in sociocultural evolution. In H.R. Barringer, G.I. Blanksten, and R.W. Mack, eds., Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory. Cambridge, Mass.: Schenkman. Pp. 19-49.
- Caro, T, and M. Hauser. 1992. Is there teaching in nonhuman animals? Quart. Rev. Biol. 67:151-174.
- Cavalli-Sforza, L.L. and M.W. Feldman. 1973. Models for cultural inheritance. I. Group mean and within group variation. Theoret. Pop. Biol. 4: 42-55.

- Cheney, D.L. and R.M. Seyfarth. 1990. How Monkeys See the World: Inside the Mind of Another Species. Chicago: University of Chicago Press.
- Chou, L., and P.J. Richerson. 1992. Multiple models in social trasmission among Norway rats, *Rattus norvegicus*. Animal Behaviour 44: 337-344.
- Chou, L-S. 1989. Social Transmission of Food Selection by Rats. PhD Dissertation, University of California—Davis.
- Dawson, A.G. 1992. Ice Age Earth: Late Quaternary Geology and Climate. London: Routledge.
- Ditlevsen, P.D., H. Svensmark, and S. Johnsen. 1996. Contrasting atmospheric and climate dynamics of the last-glacial and Holocene periods. Nature 379: 810-812.
- Dugatkin, L.A.1996. Copying and mate choice. In: C.M. Heyes and B.G. Galef, Jr., eds., Social Learning in Animals: The Roots of Culture. San Diego: Academic Press. Pp. 85-105.
- Dunbar, R.I.M. 1992. Neocortex size as a constraint on group size in primates. J. Human Evolution 20: 469-493.
- Edelman, G.M. 1987. Neural Darwinism: The Theory of Neuronal Group Selection. New York: Basic Books.
- Eisenberg, J.F. 1981. The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior. Chicago: University of Chicago Press.
- Galef, Jr., B.G. 1996. Social enhancement of food preferences in norway rats: A brief review. In: C.M. Heyes and B.G. Galef, Jr., eds., Social Learning in Animals: The Roots of Culture. San Diego: Academic Press. Pp. 49-64.
- Galef, Jr., B.G. 1988. Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In: T.R. Zentall and B.G. Galef, Jr., eds., Social Learning: Psychological and Biological Perspectives. Hillsdale, New Jersey: Lawrence Erlbaum. Pp. 3-28.

- Garcia, J., and R.A. Koelling. 1966. Relation of cue to consequence in avoidance learning. Psychonomic Science 4: 123-124.
- Gigerenzer, G., and D.G. Goldstein. 1996. Reasoning the fast and frugal way: models of bounded rationality. Psychological Review 103: 650-669.
- GRIP (Greenland Ice-core Project Members). 1993. Climate instability during the last interglacial period recorded in the GRIP ice core. Nature 364: 203-207.
- Heyes, C.M. 1996. Introduction: identifying and defining imitation. In: C.M. Heyes and B.G. Galef (eds.) Social Learning In Animals: The Roots of Culture. San Diego: Academic Press. Pp. 211-220.
- Heyes, C.M., and G.R. Dawson. 1990. A demonstration of observational learning using a bidirectional control. Quart. J. Exper. Psychol. 42B: 59-71.
- Hinde, R.A. 1970. Animal Behaviour: A Synthesis of Ethology and Comparative Psychology. New York: McGraw Hill.
- Humphrey, N.K. 1976. The social function of intellect. In: P.P.G. Bateson and R.A. Hinde, eds., Growing Points in Ethology. Cambridge: Cambridge University Press. Pp. 303-317.
- Immelman, K. 1975. Ecological significance of imprinting and early learning. Ann. Rev. Ecol. and Syst. 6: 15-37.
- Jerison, H.J. 1973. Evolution of the Brain and Intelligence. New York: Academic Press.
- Krubitzer, L. 1995. The organization of the neocortex in mammals: are species differences really so different? Trends in the Neurosciences 18: 408-417.
- Kummer, H., L. Daston, G. Gigerenzer, and J.B. Silk. 1997. The social intelligence hypothesis.In: P. Weingart, S.D. Mitchell, P.J. Richerson, and S. Maasen, eds., Human by Nature: Between Biology and the Social Sciences. Mahwah, New Jersey. Pp. 157-79.

- Laland, K.N., P.J. Richerson, and R. Boyd. 1996. Developing a theory of animal social learning. In: C.M. Heyes and B.G. Galef (eds.) Social Learning In Animals: The Roots of Culture, San Diego: Academic Press. Pp. 129-154.
- Laland, K.N. and K. Williams. 1997. Shoaling generates social learning of foraging information in guppies. Animal Behaviour 53: 1161-1169.
- Lamb, H.H. 1977. Climatic History and the Future. Princeton: Princeton University Press.
- Lefebvre, L. and B. Palameta. 1988. Mechanisms, ecology, and population diffusion of socially learned, food finding behavior in feral pigeons. In: T.R. Zentall and B.G. Galef, Jr., eds., Social Learning: Psychological and Biological Perspectives. Hillsdale, New Jersey: Lawrence Erlbaum. Pp. 141-64.
- Lehman, S. 1993. Climate change: Ice sheets, wayward winds and sea change. Nature 365: 108-9.
- Martin, R.D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293: 57-60.
- Moore, B.R. 1996. The evolution of imitative learning. In: C.M. Heyes and B.G. Galef, Jr., eds., Social Learning in Animals: The Roots of Culture. San Diego: Academic Press. Pp. 245-65
- Partridge, T.C., G.C. Bond, C.J.H. Hartnady, P.B. deMenocal, and W.F. Ruddiman.1995. Climatic effects of late Neogene tectonism and vulcanism. In: E. S. Vrba, G. H. Denton, T. C. Partridge, L. H. Burckle, eds., Paleoclimate and Evolution With Emphasis on Human Origins. New Haven: Yale University Press. Pp. 8-23.
- Pinker, S. 1997. How the Mind Works. New York: Norton.
- Poli, M.D. 1986. Species-specific differences in animal learning. In: H. Jerison and I. Jerison, Intelligence and Evolutionary Biology. Berlin: Springer. Pp277-297.
- Pulliam, H.R. and C. Dunford. 1980. Programmed to Learn: An Essay on the Evolution of Culture. New York: Columbia University Press.

Rogers, A.R. 1989. Does biology constrain culture? American Anthropologist 90: 819-831.

- Schneider, S.H. and R. Londer. 1984. The Coevolution of Climate and Life. San Francisco: Sierra Club Books.
- Spelke, E.S. 1990. Principles of object perception. Cognitive Science 14: 29-56.
- Terkel, J. 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In: C.M. Heyes and B.G. Galef, Jr., eds., Social Learning in Animals: The Roots of Culture. San Diego: Academic Press. Pp. 17-47.
- Tomasello, M., .1996. Do apes ape? In: C.M. Heyes and B.G. Galef, Jr., eds., Social Learning in Animals: The Roots of Culture. San Diego: Academic Press. Pp. 319-46.
- Tooby, J. and L. Cosmides. 1992. Psychological foundations of culture. In: J.H. Barkow, L. Cosmides, and J.Tooby (eds.). The Adapted Mind: Evolutionary Psychology and the Generation of Culture. Oxford: Oxford University Press. Pp. 19-136.
- Tooby, J and I. DeVore. 1987. The reconstruction of hominid behavioral evolution through strategic modeling. In: W.G. Kinzey, ed., The Evolution of Human Behavior: Primate Models. Albany: State University of New York Press. Pp. 183-237.
- Whiten, A., and D. Custance. 1996. Studies of imitation in chimpanzees and children. In: C.M. Heyes and B.G. Galef, Jr., eds., Social Learning in Animals: The Roots of Culture. San Diego: Academic Press. Pp. 291-318.
- Zentall, T. 1996. An anlysis of imitative learning in animals. In: C.M. Heyes and B.G. Galef, Jr., eds., Social Learning in Animals: The Roots of Culture. San Diego: Academic Press. Pp. 221-243.