

Chapter 3

The Evolution of Cognition: Questions We Will Never Answer

Richard C. Lewontin

Editors' Introduction

The idea that many traits of human nature are strongly dependent on inherited characteristics has enjoyed varying degrees of popularity among psychologists and others since the publication of Darwin's *The Origin of Species*. Now, with the amazing advances in our understanding of genetic mechanisms, there has been a resurgence of interest in the influence of inherited characteristics on cognitive and behavioral traits. More and more introductory texts discuss the issue of how genetic mechanisms are expressed in human thought and behavior. But in almost all cases the path from genetic mechanisms to cognition is very long indeed. Genes provide merely blueprints for the synthesis of proteins, and the link between proteins and cognition is remote.

Instead of analyzing the biochemistry of genetic mechanisms, another approach is to try to understand how human cognition might have evolved through the mechanism of natural selection. Here, too, increasing numbers of texts discuss how traits such as emotional expression and language might have evolved. A primary focus in many such discussions is the search for similar (more precisely, homologous) characteristics among species close to us in terms of evolution, such as chimpanzees.

Despite the appeal of explaining human cognition as the result of evolution through natural selection, Richard Lewontin, an expert in genetics and evolution, has strong words of warning. In this elegant chapter outlining the characteristics of evolutionary explanation, he makes a clear and powerful case for why such explanations of human cognition can only be regarded as storytelling. It is hard to accept that we will never come to understand how human nature evolved, but we think this chapter will convince you, as it did us. (Indeed, you might find it amusing to know that Lewontin chided us, the editors, for our initial optimism. You will find some of his remarks to us at the end of the chapter.)

Chapter Contents

- 3.1 An Outline of the Argument 109
 - 3.1.1 An Example from Biology 110
 - 3.1.2 The Application to Human Cognition 110
- 3.2 Traits in Evolution 113
- 3.3 History, Form, and Function 113
 - 3.3.1 Evolutionary Description 114
 - 3.3.2 Functional Changes 115
 - 3.3.3 Evolutionary Constraints 117
- 3.4 Problems of Reconstruction 118
 - 3.4.1 Reconstruction of Relationships 118
 - 3.4.2 Reconstruction of Function and Changes 119

3.5 Specific Problems in the Evolution of Human Cognition	121
3.5.1 Human Relations and Ancestors	121
3.5.2 Ancestors	122
3.5.3 Homology and Analogy	124
3.5.3.1 Linguistic Ability	126
3.6 Function and Selection	128
3.7 A Final Note to the Reader	129
Suggestions for Further Reading	130
Questions for Further Thought	131
References	131
About the Author	131

It is trivially true that human cognition has evolved. The human species has evolved from nonhuman ancestors and, if we go back in time far enough, from one-celled organisms swimming in water. Those one-celled organisms certainly did not have human cognition, if they had cognition at all. They did not have a language, they did not decide to create a government; they did not engage in religious worship. Thus it must be that human cognition, like every other characteristic of the human species, has arisen during the continuous course of human evolution. If, however, it were our purpose in this chapter to say what is actually known about the evolution of human cognition, we could stop at the end of this sentence. This is not to say that a great deal has not been written on the subject. Articles in scientific journals and whole books have been written making claims about the actual course of human cognitive evolution. For example, C. J. Lumsden and E. O. Wilson in their book *Genes, Mind, and Culture* (1981) have built an elaborate theory of the evolution of cognitive functions in which they include, among other manifestations of cognition, "odor and taste discrimination, number ability, word fluency, spatial ability, memory, timing of language acquisition, spelling, sentence construction, perceptual skill" (p. 16). While Lumsden and Wilson offer their theory only as a plausible reconstruction of the evolution of cognition, a much stronger claim about cognitive evolution, specifically the evolution of language, is made by the linguists Steven Pinker and Paul Bloom in a widely discussed article, "Natural Language and Natural Selection" (1990). Rather than offering merely a plausible story, Pinker and Bloom claim that language ability is (1) complex and (2) adaptive, and that "the only way to explain the origin of such abilities is through the theory of natural selection" (p. 708; emphasis added).

Some of these speculations might be true, but we do not know, nor is it clear, as we shall discuss in this chapter, how we would go about finding out. Despite the existence of a vast and highly developed mathematical theory of evolutionary processes in general, despite the abundance of

knowledge about living and fossil primates, despite the intimate knowledge we have of our own species' physiology, morphology, psychology, and social organization, we know essentially nothing about the evolution of our cognitive capabilities, and there is a strong possibility that we will never know much about it. It is the purpose of this chapter to explain why we are in such a position of ignorance. We need to understand how we go about investigating the evolution of a trait or a complex of traits, and how we try to explain the presence or absence of some trait in a particular species. With that understanding, we will see why human cognition is such a difficult case.

3.1 An Outline of the Argument

Claims about the evolution of cognition are built on the outline of the standard theory of evolution by natural selection that we associate with Darwin. That theory stands on three principles.

1. *The principle of variation.* There is variation of physiology, anatomy, and behavior among individual members of a species.
2. *The principle of heredity.* Offspring resemble their parents in these traits more than they resemble unrelated individuals. This similarity is usually a consequence of biological inheritance of genes, but it need not be. Mechanisms of cultural inheritance that cause persistent correlation between parents and offspring over successive generations would also provide the needed heredity for the evolutionary process. The evolutionary consequences of cultural mechanisms of inheritance have been explored by, for example, Luca Cavalli-Sforza and Marcus Feldman in their book *Cultural Transmission and Evolution* (1981).
3. *The principle of natural selection.* Individuals with some traits leave more offspring than others, because the possession of those traits makes them more able to acquire the necessities of life in the struggle for existence and reproduction.

All three of these principles are central to the claim that traits evolve by natural selection. If there were no variation among individuals, there would be nothing to select. If that variation were not heritable, then even if some individuals left more offspring than others, this would have no effect on the composition of the species in the next generation. Even though the strong might leave more offspring than the weak, if the offspring of the stronger are no stronger than the average, then differential reproduction has accomplished nothing. And finally, if there were no differential reproduction and survival, there would be no change in the composition of the population.

3.1.1 An Example from Biology

To see how these principles are, in fact, used by biologists to explain an evolutionary change, let us consider the favorite example of textbooks of evolution, the acquisition of dark coloring (melanism) in the moth *Biston betularia* in England and the European continent. The moth has both a dark- and light-colored form. From extensive museum collections dating to the beginning of the nineteenth century, it can be seen that the dark form has increased from being a rare variant to the most common type in some areas. For example, around Manchester, the dark form was very rare in 1848, but by 1895 represented 98 percent of the population. From experimental breeding of dark and light forms, it has been determined that there is a single gene differentiating the light from the dark forms, and in addition a number of modifying genes that have intensified the dark color. It has been demonstrated in nature that dark- and light-colored forms, when resting on tree trunks, are differentially visible to predatory birds, depending on the color of the trunk. On trees with light gray-green lichen growing on them, the light-colored moths are inconspicuous, while the dark-colored moths stand out. The reverse is true on tree trunks without lichens. The lichen, in turn, is very sensitive to industrial pollutants; as the industrialization of the English Midlands took place during the latter half of the nineteenth century, lichen became rare on tree trunks. As a result, light-colored moths became conspicuous to potential predators, but the dark-colored melanic forms became inconspicuous and thus increased in frequency. This story is not entirely without problems because, for one thing, it is not clear how important bird predation really is in determining the probability of survival of moths, and for another, caterpillars of the genetically dark form appear to have a higher survival rate even though pigment has not yet developed in them. Nevertheless, differential survival does appear to be an important element in this evolutionary event.

The reason that the case of *Biston betularia* is so widely used in textbooks is that there is clear factual evidence for all the elements of the evolutionary story. The ancestral population is known with certainty from the museum records, the genes influencing the trait differences have been found using the progeny of experimental cross-breeding, and differential survivorship of adults and caterpillars has been experimentally demonstrated in nature.

3.1.2 The Application to Human Cognition

To follow the same outline of evolution by natural selection, it is incumbent on theorists of cognitive evolution by natural selection to provide evidence that there is heritable variation in cognitive capacities among individuals, and that those with greater capacities leave more offspring.

But, we must remember, this outline is a theory of evolution, a theory of how the present state of the human species came into existence from a different previous state of its ancestors. Thus the evolutionary theorist must convince us that there was heritable variation for, say, linguistic ability, in our remote ancestors when the human species was still evolving into its present form and that those who possessed this ability, in the remote past, left more offspring by virtue of that ability. Notice, that we do not require that linguistic ability, per se, was of reproductive advantage. There might have been some quite different trait that was varying and under natural selection, but whose secondary effect was to produce linguistic competence. Then selection for the first trait would result in selection of linguistic competence. That is, traits may be established by the action of natural selection even when those traits themselves are not of selective advantage. Linguistic competence might be a by-product of having a very large brain, and the human brain may have increased in size for quite other reasons than linguistic ability, or even cognitive ability in general. Aristotle said that the function of the brain is to cool the blood. Indeed, the brain has a very large blood supply and a great deal of our body heat is radiated through the top of our heads. Thus at least in principle, we need some other reasons for rejecting Aristotle's view and claiming that the brain was specifically evolved to provide a greater cognitive function.

Evidence on the evolution of linguistic ability is not easy to come by. Our remote ancestors are not preserved in museum collections, we do not know what kind of heritable variation existed in the past or exists today for the ability to make recursive sentences such as "John thinks that Mary doesn't believe him," and we cannot measure the survival advantage, if any, in our remote ancestors of the ability to do arithmetic. Reconstructions of the evolutionary history and the causal mechanisms of the acquisition of linguistic competence or numerical ability are nothing more than a mixture of pure speculation and inventive stories.

Lumsden and Wilson, in *Genes, Mind, and Culture* (1981), attempt to deal with the problem of heritable variation in number ability or word fluency by referring to pedigree (family tree) studies and comparisons of fraternal and identical twins that are said to "have yielded evidence" of heritable variation in these human cognitive functions. Unfortunately, neither pedigree studies nor the comparisons of identical and fraternal twins are capable of discriminating between similarities of relatives that arise from genetic similarities and similarities of relatives that arise from similar developmental environments. People who are more closely related biologically have, in general, more similar environments because of the family structure of human societies. Even fraternal and identical twins are treated differently. Fraternal twins, who do not resemble each other

physically more than any other pair of brothers or of sisters, are treated by their relatives and friends like any other pair of sibs. But identical twins, who resemble each other physically to a very close degree, are treated in special ways. They are dressed alike, often given very similar names, and in every way the similarity is reinforced in their upbringing. There are even "twin conventions" in which prizes are offered for the most similar twins. On the issue of differential survival and reproduction of cognitive variants, Lumsden and Wilson can offer no evidence at all, because none exists (see section 3.4.2).

The problem of factual evidence is finessed by Pinker and Bloom in "Natural Language and Natural Selection" (1990); they assert that nothing other than natural selection can possibly explain the origin of a "complex adaptive" trait like linguistic ability. Rather than trying to give any direct evidence for a higher survival or reproductive rate of individuals with linguistic ability, they fall back on an old, pre-Darwinian, form of argument called "the argument from design." Before the widespread acceptance of evolutionary theory, one of the chief arguments for special creation and for the existence of a Divine Creator was the complexity of traits that seemed perfectly suited to perform some function. How could extremely complex features that performed complex tasks possibly have come into existence unless they were specially designed by an intelligent engineer? Darwin devoted a considerable effort in *The Origin of Species* to showing that natural selection was a mechanistic explanation of the origin of complex traits. Unfortunately, we are not told by Pinker and Bloom (or Darwin, for that matter) how to measure the complexity of linguistic ability as compared with, say, the shape of our faces nor what (unmeasured) degree of complexity is required for natural selection to be the only explanation. In biology, the notion of complexity, while often appealed to, has been completely without theoretical or empirical force. We still await a definition of complexity that will distinguish between people and frogs and that can be employed in a rigorous theoretical scheme.

Again, while it is an appealing idea that linguistic competence might be adaptive in the Darwinian sense of causing a higher reproductive rate for its possessors, such intuitive appeal is not to be confused with rigorous demonstration. Part of the confusion lies in the failure to distinguish between reproductive advantage to the individual and reproductive advantage to the species as a whole if all individuals possess a particular trait. Evolution by natural selection occurs when individuals within a species possess a trait that give them a reproductive or survival advantage over others within the species that lack the trait. It is an explanation of how a new trait spreads *within* a species, not how the species may replace other species once the trait has been incorporated. Just because a trait may be of advantage to a species when all of its members possess it, it does

not follow that a single individual who first showed the trait in the species would leave more offspring. Thus a species that possesses linguistic competence may indeed take over the earth as a consequence of the technological and managerial capabilities that are the result of language, but in a species lacking linguistic competence, the rudimentary ability to form linguistic elements by a few individuals may be taken as a sign of difference that causes them to be expelled or even killed.

3.2 Traits in Evolution

It is important to understand at the outset that it is not traits but organisms that evolve. There are then two related issues about traits in evolution: How have particular traits come into existence and changed during the evolution of some group of organisms? And how has the trait influenced the organism in its total evolution? That is, particular traits must be understood both as the objects and subjects of the evolutionary process, as both the consequence of a process of historical organic change, and as a cause of change. Thus, for human height, we way well want to know why height became differentiated among different human populations, say, Pygmies and Watutsi. But equally, we need to understand how being the size we are, rather than, say, the size of a Capuchin monkey, has influenced our evolution. One thing is sure: were we only monkey-sized, you would not now be reading this book, because the development of human technological culture required that we be able to break rocks, to mine, to maintain and control fires, activities that elementary physical principles tell us are possible only to creatures large enough to develop considerable kinetic energy with tools. Moreover, the speed of combustion of fuel depends on the ratio of surface area to volume, so that fires cannot be maintained if they are only fed with small twigs. Eighteen-inch monkeys may remind us of humans and seem clever when we watch them in the zoo, but they are too short and too weak to raise a weight high enough and bring it down with enough force to break rocks, or to gather and process the large chunks of fuel wood needed to maintain and control fire, and so they could never mine ore and smelt iron. In like manner, the evolutionary questions about cognition are questions both of the evolution of cognition and the effects of cognition on evolution.

3.3 History, Form, and Function

The theory of evolution is meant to explain the pattern of similarities and differences among organisms. Why do people look more like monkeys than like elephants, say, and why have there never been any animals that

look like the Hindu god Ganesha, with the body of a man and the head of an elephant? Evolutionary biology since Darwin, and even before, has consisted of three partly contradictory strains of explanation of these patterns.

One strain (section 3.3.1) is descriptive and explains the patterns by closeness of historical relationship. If we and monkeys have a more recent common ancestor than we have with elephants, then fewer changes have occurred in the evolutionary divergence between us and monkeys. After all, we look more like our cousins than like totally unrelated humans. A second strain (section 3.3.2) explores functional changes by appealing to adaptive events and natural selection. We and monkeys both are omnivores that need to capture their prey by being nimble, agile, and sharp-sighted, while elephants browse on leaves at the top of trees in open plains and so are selected to move over flat areas and reach high in trees to get their food. The third strain (section 3.3.3) emphasizes constraints on evolution by focusing on developmental and physiological constraints on the building and functioning of organisms. Putting an elephant's head on a human body would, in this view, simply not work physiologically, nutritionally, and behaviorally. Indeed, some constraints are yet more basic. There are no animals with wheels presumably because there is no way to make an appendage that rotates on an axle and still can be supplied with blood and nerves.

3.3.1 Evolutionary Description

If, as now seems certain, all complex organisms form a single tree stemming from a single ancestral line in the remote past, then all organisms of which we have a record are related to each other, and we can trace a path from one branch to another through their most recent common ancestors. But by the very nature of genetic inheritance, we expect related organisms to carry similar genes, derived from their common ancestors. The more distant in time those common ancestors were, the more likely that mutations in the genes will have occurred, so that distant relatives are less likely to have identical genes than close relatives. In general, then, for purely historical reasons we expect the degree of genetic similarity of two organisms to reflect their ancestral relationships, which is itself simply an expression of how long ago the organisms shared a common ancestor. But the observable traits of organisms, their forms, and their functions are a consequence of the genes they carry; thus we expect, in general, that more genetically similar organisms will also be more similar in morphology, physiology, and behavior.

This approach of evolutionary reconstruction emphasizes the historical process of random mutational divergence from a common form as the essential feature of evolution. The question is, who is related to whom,

and how closely? And the answer is provided by similarity of form and function, which is supposed to reveal an underlying genetic similarity. In this view, evolution is a descriptive science, and its rhetoric is in the form of chronicles, like the "begats" of the Book of Genesis. Just as "Mahalal lived sixty and five years and begat Jared and Nahalel lived after Jared eight hundred and thirty years and begat sons and daughters," so a human paleontologist might say that *Australopithecus africanus* lived between 2 and 3 million years ago, had a cranial capacity of 450 cc, and was an ancestor of *Homo habilis*, a form that lived between 1.5 and 2 million years ago, with a cranial capacity of about 750 cc, and that was an ancestor of modern *Homo sapiens*. Unfortunately, as we shall see, it is far from clear that *Australopithecus africanus* really "begat" *Homo habilis*. This chronicle is only one of many that can be unfolded from the fossil record. Indeed, *Australopithecus africanus* may have begotten many "sons and daughters," any or none of whom may have been our ancestor.

The descriptive task for cognitive traits includes not only the drawing of patterns of relationships and the history of changes in observed characteristics of living and ancestral forms but inferences about unobservable characteristics of ancestors. It is not sufficient for the purposes of reconstructing the cognitive evolution of human beings to describe changes in cranial capacity, the length and pattern of other bones, and the fossil material found in association with the fossil remains of prehumans. If we are concerned with the evolution of cognition in particular, we need to reconstruct from those materials the likely patterns of locomotion, of manual dexterity, of food gathering, of communal activities, of all those actions that we associate with and are prerequisite to various kinds of cognitive functions. Can we infer erect posture and bipedal locomotion from the skeleton? If so, were the hands used to carry and manipulate objects, freeing the mouth for better things? Was the cranial capacity large enough, and were the frontal and temporal lobes of the brain sufficiently developed that we may suppose a linguistic capability? Are there the broken bones of prey, are there tools, art, fire? These are all part of the evidence about supposed cognitive functions of our ancestors and relatives, some bits more compelling than others, but all related only inferentially to cognition. Any notion of what we mean by human cognition must regard the drawings of bison on the walls of the Lascaux caves in southwest France by our Upper Paleolithic ancestors 14,000 years ago as cognitive activity of a very advanced nature, but it is much more problematic to infer cognitive activity of earlier forms from, say, their brain size.

3.3.2 Functional Changes

The second strain of evolutionary explanation focusses on functional changes. In contrast to the purely historical relations between organisms

arising from random mutational divergence from common forms, there are similarities and differences that arise for functional reasons. The theory of evolution by natural selection is the theory that the shapes and activities of organisms are a consequence of the differential survival and reproduction of organisms of different types. Thus organisms that are not closely related may come to resemble each other beginning with more divergent ancestors because natural selection has driven them to similar morphologies and functions. Conversely, beginning with very similar ancestors, evolved forms may diverge very dramatically because of natural selection. Such convergence and divergence from natural selection can be manifest even at the level of genetic similarity. The function of an enzyme molecule, for example, depends on its three-dimensional structure and amino acid composition. But the amino acid composition is determined by the genetic code. If selection drives two unrelated forms to be more similar or two unrelated forms to be quite different at the level of the enzyme structure, these changes will also be manifest at the level of the genetic code. To the extent that some changes in organisms are reproduced while others are rejected by natural selection, the similarity between closely related species may be diminished and fail to reveal ancestral relations, and distantly related organisms, beginning with very different materials, may come to resemble each other because natural selection has favored similar morphologies and physiologies. Evolutionary convergence is particularly striking in the marsupial mammals of Australia when they are compared with the placental mammals of the rest of the world. The lines leading to the marsupials and placentals have been separated since the very origin of mammals over 100 million years ago (some believe they even descend from two different reptilian ancestors). Yet each group, independently, has developed some remarkably similar forms. There are marsupial "wolves," marsupial insectivores, marsupial "bears," marsupial "mice," "rats," and "moles." On the other hand, selection can result in extreme dissimilarity of closely related forms. Virtually all the differences between cows, goats, and deer have arisen in the last 10 million years—only about 10 percent of the total time since the origin of the mammals. It is this possibility of very rapid divergence of closely related forms that makes the evolution of cognition such a difficult problem. Our nearest nonhuman relatives are the chimpanzee and the gorilla, with which we had a common ancestor around 10 million years ago. Our proteins are about 98 percent identical with those of chimpanzees and gorillas, about the same as two species of mice; on this basis, we might consider those primates as our close relatives. Yet a major difference in the consequences of cognitive power has taken place during human evolution that makes the cognitive difference between gorillas and chimpanzees trivial as compared to our cognitive distance from them. Moreover,

what evidence we have from paleontology and archaeology, from cranial capacity and tool making, shows that most of the difference has evolved in less than 200,000 years.

An important consequence of nonrandom, natural selective divergence of species is that similarity of traits in two species may differ widely from trait to trait. To say that we are "closely" or "distantly" related to chimpanzees and gorillas on the basis of our average protein similarity or on the basis of the time since our common ancestor is to give a false impression of a uniformity in divergence that may lead to false inferences. The 20 million years of evolution that separates us from the chimpanzee (we are each 10 million years from our common ancestor) makes us rather distantly related on the timescale, compared to, say, dogs and wolves, which have been separated only by a few thousand years. Humans and chimpanzees are nevertheless very similar in their proteins, on the average, but vastly different in the sizes of their brains and in their ability to write books about each other. Small differences in protein structure can be magnified in the development of an organism into very large differences in shape, size, and function.

3.3.3 Evolutionary Constraints

A third strain in evolutionary reasoning accepts both the historical and functional elements in the determination of similarity but emphasizes a set of general constraints on the possibility of change. For reasons that are not at all clear but must be related to the possible range of mutations that can occur from a given gene, there is tremendous "inertia" of form in evolution. For example, all the vertebrates have only four limbs and none has ever succeeded in adding an extra pair in the billion years of evolution that have gone on since the origin of fish. When birds arose from dinosaurs, they had to sacrifice their front limbs to make wings, as did bats. Yet, of course, animals can be constructed with more than four legs. Insects have six in addition to wings. On the other hand, all insects have six legs and none has ever acquired eight. That is reserved for a completely separate evolutionary line, the spiders and mites. When mammals reentered the sea to become seals and whales, they turned their limbs into flippers and flukes, but maintained the same basic skeletal architecture that characterizes the legs of their terrestrial relatives. There appear, then, to be basic body plans that are maintained through immensely long evolutionary periods despite dramatic changes in the life activity patterns of organisms and the functions of their parts. This means, in turn, that when new functions arise in evolution, they often do so through a process of recruiting previously existing organs or physiological activities.

Thus, while natural selection modifies the similarity between organisms that would appear from purely historical relations, the existence of basic

body plans shows that history constrains the outcome of natural selection. Evolution under natural selection is historically contingent. The available material upon which selection acts is itself one of the determinants of what natural selection can produce. That is, natural selection cannot produce all possible results but is constrained to certain possibilities by the starting material. If the genes of an organism cannot mutate appropriately, it will be impossible to develop another set of appendages, no matter how advantageous that might be if it were possible. That only human beings can write books and make recursive sentences is not a demonstration that selection might not favor similar functions in ants. They just may not have the genes for it. Moreover, the particular morphological changes that have occurred in the human brain that facilitate authorship and speech are built on previously existing structures which served other functions and which were recruited for new purposes (see section 3.5.3.1).

3.4 Problems of Reconstruction

3.4.1 Reconstruction of Relationships

As we see, reconstruction of the evolution of traits involves both historical and ahistorical causal elements. From the historical standpoint, it must be possible to describe the relevant characteristics of an ancestral species and of closely related collateral relatives. But, in turn, such a description requires two kinds of information. First, it must be possible to reconstruct lines of relationship of species in order to know which forms are truly ancestral and which are merely collateral relatives not in a direct ancestral line of living forms. Moreover, it must be possible to make inferences about the degree of genetic relationship of living species to know which are "close" and which are "distant" relatives. Second, for the traits of interest, we require a description of their state in the various living and extinct ancestral and collateral lines. This includes the possibility that the trait simply does not exist in some or all related lines, that it is a novelty, and so has no observable evolutionary history. The temptation is strong to stretch the description of the trait so that at least some rudimentary manifestation can be seen in ancestors. But even when the trait seems obviously present to various degrees in several species, it is by no means certain that we are dealing with the same trait in the genetic, anatomical, and physiological sense. Is vocalization in apes and monkeys a rudimentary form of human speech, connected to speech by an unbroken line of neuroanatomical transformation, or is it merely a superficial analogy with speech?

Unfortunately, the problems of drawing lines of ancestry and of proper description of traits in relatives are not independent. How do we decide

whether two forms are closely or distantly related, except by way of their manifest similarities and differences? If we use brain size and form to infer relationship, we cannot then turn around and use the inferred relationship to make assertions about the evolution of brain size and structure. Thus in the creation of a structure of inferred relationships we must try to find a set of characteristics of organisms that are evolutionarily independent of the traits whose evolution we want to reconstruct. We can use overall similarity in DNA, or an average similarity in randomly chosen proteins to establish lines of relationship. These inferred relationships can then be used to reconstruct brain evolution, on the reasonable grounds that overall DNA and protein similarity averages out particular functional changes and provides an estimate of average genetic similarity among organisms.

3.4.2 Reconstruction of Function and Changes

When we turn from the chronicles of events, the "begats" of evolutionary history, to causal stories involving function and natural selection, quite different problems arise. First, we must distinguish between the forces that influenced the acquisition of traits and the functional forces that operate on them currently. That is, we must not confound past functional forces with current function. For example, no one would deny that an insect's wings are "for flying" in the sense that many insects do indeed depend upon them for flight and that in a normally winged species, an individual with defective wings will not long survive. Yet, because rudimentary wings provide no aerodynamic lift, and because single gene mutations cannot cause a full wing to develop from other structures, wings could not have originated in evolution by natural selection for flight. Recent experiments strongly support the view that wings originated as thermoregulatory devices and only functioned as flying appendages when they reached a critical size. Yet the fact that rudimentary wings can serve as thermoregulatory devices does not exclude other possibilities for their origin. Perhaps they were used as mating signals, or to repel competitors for food, or for any one or combination of other functions that an imaginative mind can invent. The problem of origin is the problem of reconstructing the function of traits in long-extinct forms living in long-extinct environments together with other long-extinct forms. While, on purely mechanical grounds, we may exclude some explanations, we cannot choose among many allowable ones. Did the dinosaur stegosaurus use the large leaflike plates along its back for physical defense, for appearing deceptively large to potential predators, for sexual attraction, for thermoregulation, for all four, for some at one time and others at another, or none of the above? We will never know.

The second problem is to determine the possible selective forces operating even on modern forms accessible to observation and experiment.

The ascertainment of function is not the same as the determination of natural selection. Selection occurs if there is difference in the probability of survival and reproduction of different forms. But it is not always obvious that the presence or absence of some function will have a significant influence on reproductive rates. The ability to create well-formed sentences is a characteristic of normal human cognition, whose social and individual functions seem manifold and obvious. Yet no one has ever measured the reduction, if any, of survivorship and reproductive rate consequent on the lack of this ability. Plausible stories about what might be the reproductive consequences of aphasia are not sufficient. The issue, after all, is not whether linguistic ability might have been favored by natural selection (obviously it might have been), but whether, in fact, it was.

There are three requirements for a demonstration of the operation of natural selection. First, it must be possible to find contrasting groups, those possessing the trait and those without it, or those possessing the trait to different degrees, in order to measure the reproductive effect of variation in the trait. One reason we cannot measure natural selection for linguistic ability is that there are too few aphasics, and anyway, they have suffered traumas that interfere, in themselves, with survivorship and reproduction. Second, even when there are contrasting groups as part of the natural variation of the species, the differences in reproductive rate must be large enough to measure. A one percent difference in reproductive rate between types represents an enormous evolutionary force that would result in quite rapid changes in the prevalence of a trait in a species. Yet to measure a one percent difference in reproductive rate in a species like *Homo sapiens* that spreads its reproduction over many ages requires immense numbers of observations. In human beings, it would require the complete survivorship and reproductive histories, from birth, of an impractically large number of individuals in the contrasting groups (of the order of 100,000), an enormously costly enterprise that has never been carried out for any human trait. Third, it must be possible to demonstrate that genetic differences underlie the different forms of the trait. Even if there are differences in reproductive rates of different groups, those differences cannot be the cause of evolution unless the groups differ genetically. If the differences in morphology, physiology, and behavior are not passed from parent to offspring, then differential reproduction cannot change the distribution of a trait in the population. Unfortunately, it is extremely difficult to obtain evidence of the biological heritability of traits, especially behavioral traits, and most especially in humans. Evidence about inheritance comes from the similarity of biological relatives. But because many animals, certainly all mammals, have a family structure, offspring will resemble their parents both because of biological inheritance and because of environmental similarity. For behavioral traits, there

is the added complication of learned behavior. The problem is to distinguish between genetic similarity and similarity from environment and learning. This is impossible unless offspring can be raised apart from their parents in randomized environments. While this is possible for a few domesticated or laboratory species, it cannot be done, for example, in humans (see section 3.1.2 above for the discussion of twin studies). Thus we simply do not know how genes are implicated in most trait differences. There are a few "natural experiments" that make some inferences possible. For example, it is clear that differences in phonemic structure between say, Slavic, Germanic, and Romance languages are not genetic because the offspring of Polish, German, and Italian speakers in North America can all speak unaccented American English. On the other hand, human stature has both genetic and environmental causation of group differences. The offspring of Japanese immigrants to North America are taller than their parents, but shorter, on the average, than the North American mean. Curiously, the stature has increased again in the second generation, thus there may be a multigenerational cultural effect.

Finally, we need to note a contradiction between the claim that a trait has been established by natural selection and the attempt to measure the actual force of that selection. When traits have been established by the force of selection, we do not expect to find much variation for the trait because selection will have eliminated the variant types. Yet the possibility of measuring the force of natural selection depends precisely on the availability of contrasting types whose reproductive rates are to be measured! Only rarely can we catch natural selection in flagrante delicto in the process of causing the replacement of one form by another or changing the average value of a trait in a species. More often, the deed has already been done, leaving no trace of its action behind.

3.5 Specific Problems in the Evolution of Human Cognition

3.5.1 Human Relations and Ancestors

The first serious problem in the reconstruction of human cognitive evolution is that we do not have any close relatives, nor do we know who our ancestors were. Relationships among living forms can be judged on the basis of overall similarity in DNA sequences. It is possible to make use of DNA similarity because of a remarkably constant rate of divergence of DNA per unit of evolutionary time. In part, this rate constancy arises because not all changes in DNA are reflected in changes in proteins. Both within genes and in the spaces between genes on the chromosome there is DNA whose changes are functionally "silent." For such DNA, the divergence between species is simply the clocklike accumulation of

mutations of no functional significance. But even for DNA changes that do matter to the anatomy and physiology of the organism, because some genes evolve slowly and others rapidly, the average overall difference is roughly independent of individual selection events.

Using DNA similarity, it now seems clear that the two closest relatives of *Homo sapiens* are the chimpanzee (*Pan troglodytes*) and the gorilla (*Gorilla gorilla*). Using the average rate of DNA divergence for a broad range of organisms, it is estimated that there was a common ancestral form of human, chimpanzee, and gorilla about 7–10 million years ago, so that 14–20 million years of evolution separate us from either the gorilla or the chimpanzee. (The less convincing paleontological evidence suggests a much older separation.) For comparison, this is roughly the evolutionary time separating giraffes and deer, while deer and moose are separated by less than a million years. The value of close living relatives in evolutionary reconstruction is that the close relatives will share characteristics or have close similarity, in contrast to the differences that separate the relatives, as a group, from more distantly related forms. But a great deal of evolutionary time separates us from the chimpanzee and the gorilla; thus, a priori, we cannot expect that we will share many characteristics with them that differentiate us and them, as a group, from other primates. Indeed, the standard classification of the primates based on morphology places the chimpanzee and gorilla in the same family, Pongidae, as the orangutan; and some classifications put the Pongidae together with the gibbon in a single family.

A further difficulty about the relatives of *Homo sapiens* is that they are so few. Only two species form the group of our "close" relatives, and only three others, the orangutan, gibbon, and siamang are included in our superfamily, the Hominoidea. All other primates (monkeys, lemurs, etc.) are very far from us indeed. When there are so few forms that are even moderately related, it becomes very difficult to trace the successive changes of a trait. The evolutionary space is too sparsely populated to be able to connect the points sensibly.

3.5.2 Ancestors

In contrast to the paucity of living related species, there is a relative richness of fossil forms that seem to be relevant to human evolution. The oldest of these is about 4 million years old. Considerable intellectual blood has been spilt over the interpretation of the diverse collection of fossil remains. The discoverer of each claims it as a definitive human ancestor, while revisionist critics continue to reorganize the relationships of the remains. There is no consensus, but a very conservative view is that the hominoid fossils belong to only two genera, separated from each

other on the basis of characteristics of the skull and limbs. The older genus, *Australopithecus*, runs from about 4 million to 1.2 million years ago, while the younger one, *Homo* (including us) begins about 2 million years ago and runs to the present. What is not clear, however, is whether any of these fossil forms is, in fact, a direct human ancestor.

It is important to understand that the appropriate metaphor for the evolution and diversification of a group of species is not a "tree," but rather a "bush." Beginning with a remote ancestor, a very large number of parallel lines and sublines evolve so that at any moment in time there may exist many species that are cousins and second cousins. Some of these family lines die out, while others give rise to yet further groups of cousins. If we then pass back along this bushlike array of collateral relatives, finding a form here and there as fossils, we cannot know how two forms are related. Most important, if one form follows another in time, we cannot tell whether the older form is a direct parent or only an uncle or a cousin of a previous generation (a cousin once removed). Thus, of all the human fossils, we do not know which, if any, was a direct ancestor. Even other species that are classified into the genus *Homo* may be only collateral and not direct lineal ancestors. Indeed, we are not even sure that Neanderthal man, classified together with us in the species *Homo sapiens*, is a direct ancestor rather than a parallel line that died out without issue. The only form we are sure of is one that is already indubitably human, like the Cro-Magnon forms of the Upper Paleolithic. But Cro-Magnon man is already us and so throws no light at all on our ancestors.

The genus *Homo* consists essentially of three species: *H. habilis*, running from roughly 2 million to 1.5 million years ago, with a cranial capacity of 750 cc; *H. erectus*, running from 1.8 million to 300,000 years ago, with a cranial capacity of about 1,000 cc; and *H. sapiens*, (including the extinct Neanderthal man), starting around 400,000 years ago, with a cranial capacity of about 1,300 cc. All of these species have been placed in the genus *Homo* on the basis of purely morphological evidence, but quite independently all have been found in association with shaped stone tools. Such tools have not been found in association with any earlier fossils. Thus the cognitive ability needed to manufacture tools appears suddenly about 2 million years ago as a novelty. It is true that a refinement of these tools is seen in later deposits. The earliest objects from Olduvai in Tanzania, Africa (near the Serengeti Park about 100 kilometers southeast of Lake Victoria) are stone cores that have been partly shaped by chipping off pieces to sharpen them. Then, at about 1.5 million years ago, there appear at the same site tools made from large stone flakes that had been chipped off larger stones. The flakes are worked on both surfaces and carefully chipped around the edges to make a variety of scrapers and cutters. These sophisticated flake tools coexisted with older cave tools for

half a million years, before the earlier types disappear from the record. Whether this long coexistence is evidence of different isolated human groups or simply the maintenance of an older, still adequate technology is a matter for pure speculation. The refinement of tools does not, of course, demonstrate biological evolution of their makers. The Arabic numerals represent a vast technological advantage over the Roman numerals and even the refined and sophisticated classical Chinese culture lacked a convenient method of multiplication and division. Yet we do not suppose that the technical progress in calculation is evidence of the biological evolution of cognitive ability.

When we consider other evidence of high cognitive function—language, planning, political organization, technology beyond stone tools—we have absolutely no evidence. Even fire does not seem to have been domesticated before 100,000 years ago, when our ancestors were already indistinguishable from us morphologically and presumably had begun to feel the chill of advancing glaciers.

3.5.3 Homology and Analogy

To make any use at all of information from different species, we must be able to distinguish between characteristics that are only similar in function and form between species, *analogous* traits, and those connected with each other by an unbroken line of inheritance in evolution, *homologous* traits. The rear flipper of a seal and the tail fluke of a whale serve similar functions in swimming and are in the same terminal position in both animals, but the seal's rear flippers are modified hind legs, while the whale's flukes are appendages attached to the tail vertebrae. They are then only analogous to each other. We cannot reconstruct the evolution of a seal's flippers from anatomical knowledge of whale flukes, but a great deal is to be learned about evolutionary origins from comparing them with dogs' legs, because both the seal's flippers and the dog's rear leg are derived from the same appendage in their common carnivore ancestor.

The problem of analogy versus homology is particularly serious for cognition. What are we to take as the comparable characteristics in different species? What, indeed, is the mark of cognition, and how are we to tell homology from analogy? On the one hand, if we are extremely loose in our definition of cognition, too many utterly unrelated organisms will appear to possess the trait. Recognition, for example, is not informative because all living organisms have some form of recognition system that distinguishes one species from another, one family from another, one individual from another. There is a chemical recognition of mating types (sexes) in molds; female insects recognize males of their own species; mice recognize their own newborns by odor; and dogs know their masters by

sight, smell, and sound. What about communication then? But all sorts of animals communicate information about themselves and the outer world to other individuals. Bees, by the movements of their bodies and wings, communicate the direction, distance, and amount of food sources to other bees in the hive (see Gallistel, chap. 1, this volume). Birds give alarm calls at the approach of a predator. Other birds signal their feeding territories by song. Even problem solving is much too general a character to provide evolutionary hints, if by problem solving we mean the flexible construction of sequences of action in response to various situations, leading to an adaptive end. Squirrels are remarkable at finding their way along complex pathways and over obstacles to gather food, as anyone who has ever tried to keep a squirrel away from a birdfeeder knows. Behavioral experiments have shown these small-brained rodents to be considerably better at solving the particular problem of finding their way around barriers to food than are large dogs. Even plants solve problems. Tropical vines, when they germinate from seed, find their way to tree trunks by being positively geotropic (hugging the ground) and negatively phototropic (heading toward dark objects as they grow). On reaching the tree trunk, they become negatively geotropic and positively phototropic and thus climb the tree into the light. Particular organisms are good at solving particular problems, the problems that have been set by how they make a living. "Problem-solving ability" is too general a category to make homologous comparisons, and specific problem-solving abilities are too much contingent on the particularities of an organism's life history.

In contrast, we might define cognition in an extremely restrictive way, as the ability to communicate the difference between past and future, say, or as the ability to make tools. These, however, are so human-centered that, in fact, no other species possesses them in even a rudimentary form, so that no evolutionary inferences are possible. In the case of tools, it is important to distinguish tool making from tool use. Other animals use tools. A finch in the Galapagos digs insects out of holes with a twig held in its beak, and thrushes break snails against stone "anvils." Thus the fact that chimpanzees use sticks to dig cannot be taken as showing homology, although their peeling of twig tools with their teeth and hands does represent deliberate fashioning. On the other hand, only the genus *Homo* has ever used one tool to shape another into a form particularly suited to some function. Only *Homo* has manufactured the means of production; other animals use whatever they find.

Finally, we must avoid the process of ad hoc adjustment of our definition of cognition so as to include just *Homo* and a few related genera, for then, by definition, we will invent a characteristic whose evolution is already predetermined by its definition. We must decide to begin by delimiting that "cognitive ability" whose evolution we want to study, and

then accept the possibility that it is a *de novo* state with no homologues in other known organisms.

3.5.3.1 Linguistic Ability

A paradigm of the problem of homology and analogy in cognition is the question of the evolution of linguistic competence. Chimpanzees and gorillas vocalize, grunt, screech, hoot, and make a variety of lip, tongue, and mouth gestures that signal pleasure, anger, threat, and other internal states. Are these the rudimentary forms of speech? Are the grunts of a chimpanzee the primitive homologues of Hamlet's soliloquy?

The evidence that we have in this matter comes from the comparative neuroanatomy of related species, the experimental functional anatomy of the brain and, for humans, information about the function of people who have had various parts of their brain injured, destroyed, or isolated in accidents or as a by-product of surgery. In humans there are several areas of the brain involved in speech. In the frontal lobe there is a motor area that is responsible for movements of the face, tongue, and larynx. Just adjacent, in the left hemisphere for most people, is Broca's area, which seems to play a primary role in syntactic function. If Broca's area is damaged, a particular aphasia results, in which speech and comprehension are possible but of an impoverished kind. Broca's aphasics can move their tongues, lips, and mouths on command but cannot respond to sequence commands, such as "Stretch out your tongue, then pout your lips, then open your mouth." They can create and comprehend simple declarative sentences in which object follows subject and in which there are adjectives. But they cannot comprehend passive constructions in which subject and object are in reverse order, nor use connective terms like *by*, *for*, *which*, *or*, and so on. They have the same problems both in written and spoken language.

Behind and to the side of the frontal lobe, in the temporal lobe, is Wernicke's area, which is concerned with auditory inputs. Disturbances in this area interfere with auditory comprehension of speech but not with hearing acuity. Finally, there are larger areas in the parietal and temporal lobes where electrical stimulation results in a variety of speech and comprehension disorders such as misnaming, confused counting, and inability to repeat heard utterances. The major areas are connected to each other, so that the primary motor area is connected to Broca's area, which in turn is connected to Wernicke's area. If this latter connection is broken, there is no loss of comprehension or performance of speech, but there is interference with the ability to repeat a heard utterance.

If we turn to the lower primate brain, where comparative experiments have been performed, there are anatomical homologues to the human language areas and also substantially the same connections between the

different areas. Electrical stimulation studies show important functional similarities and differences, however. In the macaque, vocalization is produced when the primary motor area is stimulated, and when the same area is stimulated in humans, grunts and vocalizations are also produced. When the homologue of Broca's area is stimulated in monkeys, movement of the lips, tongue, and face is produced, but no vocalization. From a study of brain lesions in monkeys, it is known that their anatomical homologue of Wernicke's area mediates the distinction between self-produced and externally produced vocalizations.

It is clear that speech is not simply vocalization writ large. The motor areas for the production of sound and the movement of lips, tongue, and mouth have remained more or less anatomically and functionally conserved, but other areas, while anatomically homologous, have changed functionally. That is, one of the regions of the monkey brain associated with muscles of the lip, tongue, face, and larynx became Broca's area, in which syntactic functions now reside. At the same time, a region of the temporal cortex associated with discriminating self-produced vocalization from sounds made by other individuals, became Wernicke's area, the center for auditory comprehension of phonemic differences and the syntactic structure of heard speech. The nerve tracts connecting these regions have remained present in humans, coordinating heard speech with the organization of what is to be spoken. In sum, areas of the lower primate brain have been recruited from their former functions to serve the novel functions of speech. We know of no areas of the monkey brain that serve a function that might correspond to speech, nor is it clear what other behavior of monkeys beyond vocalization we would regard as homologous to speech.

The phenomenon of recruitment in the origin of new functions is widespread in evolution. Birds and bats recruited bones of the front limbs to make wings. In the bat, the wing is suspended from a long lower arm bone and four extremely long fingers. Birds, in contrast, have a greatly elongated wrist and one digit supporting a wing that is almost all feather. The three bones that form the inner ear of mammals were recruited from the skull and jaw suspension of their reptilian ancestors. The panda's thumb is really a wrist bone recruited for stripping leaves from bamboo. Given the general conservation of body plan that characterizes large groups of species, the recruitment of previously existing morphological features into new function is the only path open to evolution when needs for functional novelties arise. Consequently, there may be no function at all in the ancestral species that is homologous to the function in the descendants, even though they share homologous anatomical features.

The problem of homology is directly relevant to the experiments in training chimpanzees and gorillas to communicate with humans. There

have been repeated claims that chimpanzees and gorillas have been taught to create syntactical structures, using computers to help them say things like "Me pour water." There have been many arguments that call into question the claimed homology with human linguistic function. From an evolutionary standpoint, however, the possibility of teaching a gorilla to produce a sentence is not, in itself, critical evidence for the evolution of human speech. Dolphins have also been taught to distinguish sentences, for example, the difference between "Put the ball in the ring" and "Put the ring on the ball." Yet the Cetacea, the order to which dolphins belong, have been separate from the primates since near the beginning of mammalian divergence, and we are no closer to them evolutionarily than we are to mice. To show a homology between ape and human "language" rather than a mere analogy requires that as much energy and ingenuity be put into attempting to teach linguistic competence to cows, dogs, horses, and mice as has been expended on the chimpanzee and gorilla. Only when a wide range of comparisons over the mammals is available will it be possible to judge the homology of the ape behavior to the human. The choice of our closest hominid relatives for the experiment is simply an anthropocentric bias. Given the neuroanatomical evidence discussed above and the results obtained with dolphins, it is not likely that the computer-aided communication of primatologists with chimpanzees and gorillas involves reciprocal homologous processes between the two species. What the trainers say to the apes is probably only analogous to what the apes "say" to the primatologists.

3.6 Function and Selection

Whenever cognition came from, one would like to make arguments about the forces of natural selection that established it. On the face of it, generalized problem solving and linguistic competence might seem obviously to give a selective advantage to their possessors. But there are several difficulties. First, even if it were true, we have no way of measuring the actual reproductive advantages, and it must be a reproductive advantage that accrued to the early hominids who had rudimentary linguistic competence. Second, any imaginative reconstruction of that advantage must show that individuals or family groups, rather than the species as a whole, had such an advantage. Natural selection operates within populations to increase the frequency of some types and decrease others through differences in reproductive rates of individuals. Unless a more cognitively competent individual or its immediate family leaves more offspring than other families, selection will not increase the frequency of the selected character. Thus stories about how the species as a whole would be benefited by speech are not to the point.

Third, the claim that greater rationality and linguistic ability lead to greater offspring production is largely a modern prejudice, culture- and history-bound. The view of our individualistic, competitive, and entrepreneurial society that the smart and articulate win power may not apply to our primitive ancestors. Instead, our hunting ancestors, living in small bands, may have had a social organization much more akin to the cooperative hunting bands of present-day hunters and gatherers, where bonds of mutual obligation result in widespread sharing of resources. It may have been that more adventurous and inventive Australopithecines actually had a lower probability of survival and reproduction than their stodgier and more risk-averse relatives. We do know, for example, from the work of the anthropologist John Moore (1990), that Cheyenne chiefs or war bands had much shorter life spans and smaller family sizes than chiefs of peace bands. Is that the appropriate comparison? The problem is that we do not know and never will. We should not confuse plausible stories with demonstrated truth. There is no end to plausible storytelling.

3.7 A Final Note to the Reader

After reading an earlier draft of this chapter, the editors of this volume of *An Invitation to Cognitive Science* asked me if I could not add material that would relieve what seemed to them an "unremitting attack" on the study of the evolution of cognition. In addition, they thought it would be useful to readers if there were a general section on how to use evolutionary concepts in studying other behaviors that might be more amenable to such study. My response to them was the following:

I have not added a last section relieving the "unremitting attack" because I cannot. It may be true that we cannot keep people from storytelling, but I cannot see that my response to that should be to tell stories. Indeed, in one place you even invite me to do so using the word "hypothesis" (in reference to the question of why more advanced and less advanced stone tools coexisted for so long in section 3.5.2). But calling a story a "hypothesis" does not make it more scientific. We should reserve the notion of "hypothesis" for assertions that can be tested.

As to writing a last section that might tell people how to use evolutionary concepts and methods for other things beside human cognition, that is quite impossible, except by taking up specific cases in sufficient detail to make them nonobfuscating. So I would need a half chapter to talk about the evolution of, say, birdsong acquisition, about which we know rather more than we do about human

cognition, and in the end it, also, would be an “unremitting attack.” In birds, where we have a lot of information from closely related species and the advantage of being able to do all sorts of dreadful blinding and deafening experiments that would bring down the wrath of decent people if they were done on primates, it is clear that every species has its own path to song acquisition, from nearly totally (I emphasize “nearly”) hard-wired to totally learned.

There are, however, certain common neural regions in the production of sounds that are species-specific in what sound they mediate. In birds, one cannot generalize from one species to another, and it would take me nearly a chapter to explain why, and the result would not be an *evolutionary* story because the species are so different in their acquisition mechanisms. About the evolution of insect navigation (see Gallistel, chap. 1, this volume) I know nothing, but I am damned sure that moths will tell me nothing about flies and cicadas because they are even more distantly related than any two mammals.

Finally, I must say that the best lesson our readers can learn is to give up the childish notion that everything that is interesting about nature can be understood. History, and evolution is a form of history, simply does not leave sufficient traces, especially when it is the forces that are at issue. Form and even behavior may leave fossil remains, but forces like natural selection do not. It might be interesting to know how cognition (whatever that is) arose and spread and changed, but we cannot know. Tough luck.

Suggestions for Further Reading

An overview of what is known about the genetic differences between individual human beings and between geographical populations can be found in Lewontin (1982). This book is at pains to draw the distinction between the observed variation in form, behavior, and culture on the one hand and the genetic differences that can be established.

For a discussion of evolutionary theory that emphasizes the role of natural selection and inclines strongly to the view that it is proper for evolutionists to imagine plausible reconstructions of evolutionary scenarios, the reader should consult Maynard Smith (1966). A paleontologist's view of the grand sweep of animal evolution with specializations on what it all means for human life, is contained in one of the great classics of the field, George Gaylord Simpson's *The Meaning of Evolution* (1967). A lighthearted but scientifically sound exposition of evolutionary biology, using cartoons and text has been created by Miller and Van Loon. Although amateurs, they have got it right where it counts. A collection of articles from *Scientific American* (1978) deals with a range of issues of interest in evolutionary biology written by a variety of specialists.

The controversies about human evolution, our relationships to the great apes and the significance of various fossil finds are treated with great care and discrimination in a book by the paleontologists Eldredge and Tattersall (1982).

Questions for Further Thought

- 3.1 Why is anyone interested in the evolution of human cognition? It is sometimes said that knowing the evolution of cognition will enable us to “better understand” it. Specifically, what does that mean? How will recovering information about cognition in human ancestors, or the evolutionary forces that gave rise to it, help us to “better understand” our current state? Can it help us to predict the future?
- 3.2 What is the value of animal models in understanding cognition? What does it tell us about cognition to study cognitive function in birds? Dogs? Monkeys? Chimpanzees? What problems exist in interpreting animal models? Are these more or less worrisome when we study species closer to us, as opposed to distant species? Are they more or less difficult when we study physiological functions like digestion or the reaction to a drug, as opposed to cognition?
- 3.3 How would one go about determining whether individuals with a particular intellectual or temperamental trait leave more or fewer offspring than others? How important are historical comparisons and comparisons among geographically and culturally different groups for making evolutionary predictions and explanations?
- 3.4 Can you develop a definition of “cognition” that would be useful in studying its evolution? Can you do this without human bias? If not, does it matter? After all, it is human cognition whose evolution we are trying to understand.
- 3.5 Do you think that evolution by natural selection optimizes various features of organisms? What does “optimal” mean for organisms? How would you tell whether a feature is optimal? Is there any difference between a feature that is optimal for a species and a feature that is optimal for individual organisms within the species?
- 3.6 This chapter claims that linguistic function is a novel trait that arose relatively recently in evolution rather than being the homologue of some behavior in our primate ancestors. How would one go about demonstrating that language is indeed novel and that there are no homologous traits in gorillas and chimpanzees?

References

- Cavalli-Sforza, L. L., and Feldman, M. (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton, NJ: Princeton University Press.
- Eldredge, N., and Tattersall, I. (1982). *The myths of human evolution*. New York: Columbia University Press.
- Lewontin, R. C. (1982). *Human diversity*. New York: Freeman.
- Lumsden, C. J., and Wilson, E. O. (1981). *Genes, mind, and culture*. Cambridge, MA: Harvard University Press.
- Maynard Smith, J. (1966). *The theory of evolution*. 2d ed. Baltimore: Penguin.
- Miller, J., and Van Loon, B. (1982). *Darwin for beginners*. New York: Pantheon.
- Moore, J. H. (1990). The reproductive success of Cheyenne war chiefs: a contrary case to Chagnon's Yanomamo. *Current Anthropology*, 31, 322–330.
- Pinker, S., and Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Science*, 13, 707–784.
- Scientific American*. (1978). *Evolution*. New York: Freeman.
- Simpson, G. G. (1967). *The meaning of evolution*. Rev. ed. New Haven: Yale University Press.

About the Author

Richard C. Lewontin is a member of the Department of Organismic and Evolutionary Biology and the Museum of Comparative Zoology at Harvard University. Professor Lewontin is

an evolutionary geneticist working both on the mathematical theory of population genetics and on experimental determination of genetic structure of natural populations. He works particularly at the molecular level and was a pioneer in the study of molecular population genetics about twenty-five years ago. He is also active in the philosophy of science and has written a number of papers with philosophers of science on questions of evolutionary theory. Professor Lewontin spends a good deal of energy on relating genetics and evolution to social issues, and in this connection has written several books including *Not in our genes: biology, ideology, and human nature*, 1984, *Human Diversity*, 1982, and *Education and class: the irrelevance of IQ genetic studies*, 1986. In particular, he has been concerned for a very long time with the questions about the inheritance or noninheritance of human behavioral traits like IQ and temperament. On the nonacademic side, he has been an architectural engineer, designing domes for Buckminster Fuller, and on the political side, he has been active for many years in the radical science movement.