The Evolution of Human Behavior: The Darwinian Revolution Continued

The challenge of Darwinism is to find out what our genes have been up to and to make that knowledge widely available as a part of the environment in which each of us develops and lives so that we can decide for ourselves, quite deliberately, to what extent we wish to go along.

-Richard Alexander (1979, pp. 136-137)

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A fast-food restaurant is a little monument to the diet of our ancient ancestors. —Leda Cosmides (quoted in Allman 1994, p. 50)

Oh, yo' daddy's rich, an' yo' ma is good look-in' So hush, little baby, don' yo cry. —"Summertime" (G. Gershwin, D. & D. Heyward, & I. Gershwin 1935)

Hey, Joe. Where you goin' with that gun in your hand? Goin' down to shoot my old lady. You know I caught her messin' around with another man.

-"Hey Joe" (Billy Roberts 1966)

As we saw in the previous chapter, the evolutionary approach pioneered by ethologists provides answers to many ultimate why questions concerning animal behavior. The basic notions of survival and reproductive success, further refined by concepts of kin selection and reciprocal altruism, have time and again provided compelling answers concerning why animals naturally do the things they do and are able to modify their behavior in adaptive, functional ways.

But what about our own species? The Darwinian conclusion that human beings are also a product of biological evolution is scientifically inescapable, meaning that our behavior must also be compatible with and explainable by natural selection. But we humans are undisputably different from all other known organisms in the remarkable flexibility and variability of our behavior and the planning, consciousness, emotions, awareness, and moral sense that often accompany what we do.

In this chapter we will consider both the successes and problems of attempts to use natural selection to understand human behavior since the time of Darwin.

Darwin and His Critics on Animate Behavior

Although Darwin was the first scientist to consider in print the implications of natural selection for human behavior, he took a rather long time to do so. In *The Origin of Species* (published in 1859), in which he introduced the theory of natural selection, he made no explicit mention of human evolution or behavior. It was, however, quite clear from the central argument of this revolutionary book that he believed humans, like all other living organisms, gradually evolved to their present form from nonhuman ancestors. It was this unwritten but clear implication of his work that raised the most criticism and debate. As the wife of the Bishop of Worcester is reported to have worried, "Descended from monkeys? Let us hope that it is not true. But if it is true, let us hope that it does not become widely known" (quoted in Giddens 1991, chapter 2).

Unfortunately for the good bishop's wife, the theory of natural selection turned out to be both true and widely known. But it wasn't until over a decade later (after first publishing two revisions of the *Origin* followed by a book on orchids and another on domesticated animals) that Darwin tackled the emotionally charged and highly controversial issue of human evolution in *The Descent of Man and Selection in Relation to Sex*, first published in 1871 (see Darwin 1874, 1952). Here he maintained that human behavior was in some respects like that of other animals, while in other respects it was unique. He attempted to explain both the similarities and differences as arising naturally from the evolutionary process.

Like all other sexually reproducing animals, humans are (as were our nonhuman ancestors) subject to sexual selection of males by females and of females by males. Darwin saw in human sexual selection an explanation for human racial differences. Since he saw no obvious survival advantages for racial differences in physical attributes such as stature, hair, skin color, and body shape,¹ he reasoned that these variations were the results of differences in perceived sexual attractiveness among different races and the resulting selection of mates.

But more interesting from a behavioral perspective are his conclusions concerning the evolutionary basis for differences in behavioral and mental dispositions of men and women. Here he forged a bold link between humans and the sexual differences found in other animals (1874, pp. 583–584):

No one disputes that the bull differs in disposition from the cow, the wild-boar from the sow, the stallion from the mare, and, as is well known to the keepers of menageries, the males of the larger apes from the females. Woman seems to differ from man in mental disposition, chiefly in her greater tenderness and less selfishness.... Woman, owing to her maternal instincts, displays these qualities towards her infants in an eminent degree; therefore it is likely that she would often extend them towards her fellow-creatures. Man is the rival of other men; he delights in competition, and this leads to ambition which passes too easily into selfishness. These latter qualities seem to be his natural and unfortunate birthright.

He also used sexual selection to explain what he saw as the more violent, aggressive nature of the male sex (1874, p. 583):

There can be little doubt that the greater size and strength of man, in comparison with woman, together with his broader shoulders, more developed muscles, rugged outline of body, his greater courage and pugnacity, are all due in chief part to inheritance from his half-human male ancestors. These characters would, however, have been preserved or even augmented during the long ages of man's savagery, by the success of the strongest and boldest men, both in the general struggle for life and in their contest for wives; a success which would have ensured their leaving a more numerous progeny than their less favored brethren.

It was rather straightforward to provide evolutionary accounts of the human male's more aggressive characteristics. In contrast, understanding the evolutionary origins of the ethical, moral, and religious aspects of human nature was not so easy. Even Darwin's friends and supporters of his theory of evolution (including geologist Charles Lyell, cousin and gentleman scientist Sir Francis Galton, and fellow discoverer of natural selection Alfred Russel Wallace) could not imagine how survival and reproductive success could be at the origin of the kinder and gentler characteristics that often distinguish humans from other animals. According to Richards (1987, p. 206),

Lyell could not conceive that man's intellect and moral sensibility naturally grew by slow degrees from animal stock. Galton and Greg isolated another crucial problem for the Darwinian approach to man: as soon as protomen formed social bonds and through sympathy became solicitous for their mutual welfare, natural selection ought to be disengaged; for sympathy would prevent the salutary elimination of mentally and morally inferior individuals. Wallace . . . pressed these difficulties home. He urged that man's great intellect and refined moral sense far exceeded what was required for mere survival in the wild; hence, natural selection could not have produced them.

Darwin's three responses to these challenges are remarkable for their keen insight and anticipation of theories that became widely appreciated and accepted only much later the next century. First, he imagined that as their reasoning powers increased, our early ancestors would have realized that aiding another individual would increase their chances of being helped later by that individual in return. We saw this idea in the previous chapter, now referred to as reciprocal altruism.

Second, Darwin proposed that natural selection occurring at the level of the *group* could result in the evolution of behavioral traits that, although possibly of no use or even detrimental to the survival and reproductive success of the individual possessing them, would confer a selective advantage to the individual's community. As he reasoned (1874, p. 137):

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.

Finally, he recognized the powerful influence that social praise and blame had on the behavior of individuals (1874, p. 136), an influence that would have been obvious to anyone living in Victorian England. Otherwise, individuals who refused to act for the good of the group (for example, by refusing to fight in the group's wars or not sharing food or other valuable resources) and instead acted only for their own and their family's interest would have greater survival and reproductive success than those who acted for the good of the larger social group. This would prevent the natural selection of altruistic behavior.

All this is not to imply that Darwin's views on the evolutionary origins of human behavior were unproblematic. For one thing, he did not seem to recognize the important role that the environment could play through social and cultural factors in influencing human behavior. This is evident in one of his descriptions of differences between men and women. He noted that "if two lists were made of the most eminent men and women in poetry, painting, sculpture, music (inclusive both of composition and performance), history, science, and philosophy, with a half-adozen names under each subject, the two lists would not bear comparison" and therefore "the average of mental power in man must be above that of woman" (1874, p. 504). It seems inexcusable to us today that he ignored the limited educational and employment opportunities afforded to women in his day and their impact on their lives and career options.

Also evident from this conclusion concerning male-female differences was Darwin's reliance on anecdotal observations of human behavior. This approach may have served him well in his research and conclusions on animal behavior, but animal behavior has much less variation than human behavior. The fact that a male peacock spreads and shakes his tail before a peahen to encourage her to mate is in itself suggestive that other peacocks act similarly. Observing that a panda bear eats bamboo leaves provides a good clue concerning the dining habits of all pandas. But seeing a single instance of human behavior tells us very little indeed about the behavior of humans in general, since humans have so many distinct ways to feed themselves (from hunting and gathering to writing computer programs), dress themselves, shelter themselves, and procure mates. (We will take a look at the large apparent variation in human behavior from another perspective later in this chapter.)

Darwin was also completely unaware of the genetic basis of heredity and so could not understand how traits were passed down from one generation to another, even though Mendel's ground-breaking work on genetics (based on the 30,000 pea plants he had grown) was published in 1865. Without this knowledge, Darwin could not understand how kin selection could be such a powerful force in the evolution of altruistic and cooperative behavior among humans.

Finally, he never abandoned the Lamarckian notion of the inheritance of acquired characteristics in his belief that habits learned during an individual's lifetime could show up as unlearned instincts in one's descendants. He made extensive use of this notion in his book *The Expression of the Emotions in Man and Animals* (1872/1955).

In spite of these limitations, Darwin must be credited for insisting on and providing thoroughly naturalistic explanations for the evolution of human behavior that did not require the divine intervention insisted on by both his harshest critics and some of his closest friends and supporters, such as Lyell, Wallace, and American botanist Asa Gray.

The Post-Darwinian Gap

Because Darwin's theory of evolution had such a great and immediate impact on the scientific world (the entire first edition of the *Origin* was sold out the first day it was put on sale), one might well expect that it would have had a great impact on those social and behavioral scientists interested in accounting for human behavior. But that impact was delayed for quite some time.

One reason for this lack of immediate effect on human psychology was that in spite of Darwin's arguments as summarized above, many simply could not see how evolution by natural selection could account for the emergence of the human mind. Among those who, like Darwin, sought thoroughly naturalistic explanations for the origin of the human species, many remained unconvinced of the theory, preferring instead Lamarck's notion of the inheritance of acquired characteristics. Why was natural selection rejected as the motor of evolution? There were at least three reasons.

First, since natural selection requires gradual accumulation of small variations appearing in each generation, it would take a very long time before an organism as complex as a giraffe or human could evolve from the simplest one-celled organisms. But the best estimates of the age of the earth available in the nineteenth century (provided by Lord Kelvin) were between 10 and 15 million years, far too young even by Darwin's reckoning to have allowed enough time for the evolution of all known extinct and extant species. Lord Kelvin's estimates were based on the temperature of the interior of the earth and rate of decrease of the sun's energy output. However, both radioactivity (which plays a major role in maintaining the earth's high interior temperatures) and nuclear fusion (which is the source of the sun's energy) were unknown phenomena in the nineteenth century. So although the earth is now considered to be about 4.5 billion years old,

providing ample time for evolution to do its stuff, the best estimates during Darwin's time were considered incompatible with his theory of natural selection.

Another reason to doubt the effects of natural selection was the problem of inheritance. Darwin and other naturalists and biologists of his day (except Mendel) believed that inheritance in sexual species involved *blending* characteristics of male and female parents. Reasoning from this assumption, Scottish engineer Fleeming Jenkin pointed out that any new favorable variation would be diluted as the organism possessing it bred with other organisms. Over time, this repeated dilution of new traits meant that little or none of the originally advantageous variation would be retained by succeeding generations, making the emergence of new species impossible.

As noted, Darwin was unaware of Mendel's pioneering experiments in genetics that showed that inheritance did not involve a blending of male and female characteristics but rather was *particulate*; the fact that the offspring of a male-female couple is either male or female and not a blend of the two sexes is just one obvious example of the particulate nature of inheritance. Indeed, the basic notion of the gene that Mendel developed is that of an indivisible unit of biological inheritance that does not blend or dilute itself in the process of reproduction. The modern particulate theory of genetics is therefore thoroughly compatible with Darwin's theory of evolutionary change arising through natural selection of spontaneous variations produced by genetic mutation and sexual recombination of genes. Unfortunately, commonly held but erroneous ideas about inheritance in Darwin's own time were not entirely compatible with the concept of natural selection as the motor behind the evolution of species and emergence of new ones.

The third widely respected argument had to do with how the initial stages of a complex adaptation could become established. It was maintained by one of Darwin's harshest foes (the converted, and later excommunicated, Catholic zoologist St. George Mivart) that a complex adaptation such as a bird's wing was of no use to the animal that possessed it as a tool of flight unless it was fully formed and functional. From this line of reasoning it would seem that if natural selection were a gradual process involving accumulation of very small changes from one generation to the next, there would be no way that such a complex adaptation could ever begin to evolve.

Darwin had a good rebuttal to this objection, and one that is still considered valid today. He recognized that a complex adaptation may have had its beginning in a form that served a quite different function than its current one. For example, it is now believed that wings did not originally emerge as organs of flight but rather as protuberances allowing insects and birds to regulate their body heat. Nonetheless, this was seen by many as another valid argument against natural selection and is still used today by creationists and other opponents of evolution.²

But if Darwin was not swayed by Mivart's argument, he was troubled by those of Kelvin and Jenkin. So much so that by the sixth and final edition of *Origin* he considerably softened his position on natural selection, putting more emphasis on the role of the Lamarckian inheritance of acquired characteristics that he incorporated into his ill-fated theory of *pangenesis*.

His concessions to the antiselectionists did nothing to help his theory gain acceptance. The result was that, beginning in the years shortly before his death in 1882 until well into the twentieth century, biological evolution involving descent with modification was widely accepted among scientists but natural selection was not. Instead, the inheritance of acquired characteristics was seen as the primary motor of evolution, in spite of now obvious fatal flaws of Lamarckian theory.

But whereas the theory of natural selection was rejected by biologists and zoologists, it was embraced by many prominent philosophers and psychologists in Europe and America who saw in the process of variation and selection a mechanism to elucidate the functioning of the human mind. This application of Darwinian theory to the mental realm is part of what I call the "second Darwinian revolution" that is discussed in the next chapter.

Sociobiology's Search for Ultimate Causes

We saw in chapter 7 how biologists such J. B. S. Haldane, William Hamilton, George Williams, and Robert Trivers applied Darwinian concepts in the 1950s through 1970s to find answers to many perplexing

ultimate why questions about animal behavior—including instances of cooperative social behavior—using theories of kin selection and reciprocal altruism. They also applied evolutionary reasoning to human behavior, but since their work was often couched in the complex mathematics of population genetics and directed to other evolutionary biologists, it had little impact at the time on behavioral science. This changed dramatically with the appearance of a book in 1975 that brought a broad Darwinian perspective to the behavior of a remarkable variety of organisms, from microorganisms and slime molds to gorillas and human beings.

The book was *Sociobiology: The New Synthesis* written by Edward O. Wilson, a Harvard entomologist recognized as one of the world's leading experts on ants and other social insects. Defining sociobiology as "the systematic study of the biological basis of all social behavior" (1975, p. 4), Wilson provided many fascinating examples from the world of insects and other animals of the types of behaviors and evolutionary reasoning described and formulated by Hamilton, Williams, and Trivers. Due to the accessibility of his writing and attractive illustrations, *Sociobiology* quickly attracted widespread attention. Although only the last of the twenty-seven chapters dealt with human behavior, it made it clear that Wilson's evolutionary, genetic, and essentially selfish account of the origins of social behavior was fully intended to be applicable to our species as well.

Wilson's book earned him both popularity and notoriety. Many biological and behavioral scientists appreciated the grand scale and synthesis of his work, but others (including some of his Harvard colleagues) accused him of being a racist, sexist, imperialist, right-winger, and genetic determinist. His public appearances were boycotted and disrupted, and he was even doused with a pitcher of ice water at one of his lectures.

But this negative reaction did not stop additional applications of Darwinian theory to human behavior. One year after the publication of Wilson's book, Oxford zoologist Richard Dawkins published *The Selfish Gene*, the first in what was to become a series of popular and influential books on evolution. Dawkins also explored the evolutionary and genetic bases for behavior, including the apparently altruistic behavior of humans toward their fellows. Like Wilson and the new generation of behavioral Darwinians, he emphasized the inherently selfish genetic nature of what may appear to be the kind, altruistic behavior of both animals and humans.

Why did this new application of a Darwinian perspective to human behavior meet with such resistance from so many behavioral scientists and indifference from others? To understand this reaction, we must take a closer look at some of the assumptions, reasoning, and conclusions of Wilson and his sociobiologist colleagues.

The first assumption is that the human species, like all other species of living organisms, evolved from simpler forms of life by natural selection. The second assumption is that since the evolution of a species is directed by the survival and reproductive success of individual organisms (including the survival and reproductive success of new generations), and that this success is influenced by an organism's behavioral characteristics, various human behaviors can be understood as adaptations that promote (or at least promoted in the past) survival and reproductive success. The third assumption is that there is a genetic basis for human behavior in the same way that there is an inherited, genetic basis for the behavior of other animals and for the physical structure of both.

All three of these assumptions are quite in keeping with modern biological theory and clearly consistent with what was learned from studies of animal behavior as discussed in chapter 7. So why all the fuss about applying them in an attempt to discover ultimate explanations for human behavior?

At least part of the resistance was (and is) due to misinterpretation of certain aspects of sociobiological theory. Perhaps the most common charge is that of *genetic determinism*, the idea that humans inherit genes that in effect force them to behave one way or another. It is true that Wilson and other sociobiologists discussed the possibility of human genes underlying such human behavioral characteristics as homosexuality and social conformity (for example, see Wilson 1975, pp. 555, 562). But it is also clear that these scientists were aware that genes must interact with environmental factors for them to have any effect on the structure or behavior of an organism, human or otherwise. As Wilson explained (1975, p. 26):

Blue eye color in human beings can be proved to be genetically different from brown eye color. But it is meaningless to ask whether blue eye color alone is determined by heredity or environment. Obviously, both the genes for blue eye color and the environment contributed to the final product. The only useful question . . . is whether human beings that develop blue eye color instead of brown eye color do so at least in part because they have genes different from those that control brown eye color. The same reasoning can be extended without change to different patterns of social behavior.

Wilson also included a section in the last (human) chapter of *Sociobiology*, entitled "Plasticity of social organization," in which he presented the hypothesis "that genes promoting *flexibility* in social behavior are strongly selected at the individual level" (1975, p. 548; emphasis added).

However, he and other sociobiologists were on occasion less careful in describing the role of genes in human behavior. For example, Wilson asserted in his Pulitzer prize-winning book *On Human Nature* that "the question of interest is no longer whether human social behavior is genetically determined; it is to what extent" (1978, p. 19). The use of the word "influenced" (which implicitly recognizes the effect of other factors) instead of "determined" (which can be easily taken to mean that genes are the *only* cause of human behavior) would have given his opponents less cause for criticism.

Another charge is that sociobiologists often infer a specific genetic basis for apparently universal human behaviors without considering how such behaviors could have arisen from more general aspects of the form and abilities of the human organism interacting with the environment. For example, Wilson stated that "in hunter-gatherer societies men hunt and women stay at home. This strong bias presents in most agricultural and industrial societies and, on that ground alone, appears to have a genetic origin" (1975; quoted in Lewontin, Rose, & Kamin 1984, p. 255). But it is quite easy to imagine how this division of labor could be the indirect effect of physical differences between men and women such as men's greater size, strength, running speed, and throwing ability, which are characteristics best suited to hunting, and women's ability to bear and nurse babies, which is better suited to staying at or near one's home and taking care of children. As three of sociobiology's harshest critics remarked, Wilson's "argument confuses the observation noted, with the explanation. If its circularity is not evidence, one might consider the claim that, since 99 percent of Finns are Lutheran, they must have a gene for it" (Lewontin, Rose, & Kamin 1985, p. 255).

Another example is that all normal able-bodied humans use their hands to eat. This could therefore be considered a universal, species-specific aspect of human behavior (and a social behavior insofar as it is done with other humans). But does this then indicate that a specific human gene or group of genes causes us to use our hands to eat, which if changed would result in a human who did not use his or her hands to eat? This appears unlikely, as it is obvious that a hungry human who has learned to use his or her hands for manipulating objects would also use them to place food in his or her mouth. Of course, there is a genetic basis for the human behavior of eating with one's hands, since without human genes a human would not have hands to begin with, or the neurological system to achieve fine motor control of its fingers. But it is simply unconvincing to argue that a specific gene or set of genes must exist for a particular behavior simply because all (or nearly all) humans do it. Philosopher Daniel Dennett has made this same point using yet another example (1995, p. 486):

Showing that a particular type of human behavior is ubiquitous or nearly ubiquitous in widely separated human cultures goes *no way at all* towards showing that there is a genetic predisposition for that particular behavior. So far as I know, in every culture known to anthropologists, the hunters throw their spears pointy-endfirst, but this obviously doesn't establish that there is a pointy-end-first gene that approaches fixation in our species.

None of this is to deny that using one's hands to eat, dividing labor between the sexes, and throwing spears pointy-end-first may well be adaptive behaviors that facilitated the survival and reproduction of individuals who practiced them. But given the structure and abilities of human brains and bodies together with the environments in which they live, it seems implausible that any such universal human behaviors have a *specific* determining genetic basis. Instead, it is more likely that such behaviors are the outcome of the more general problem-solving abilities our species possesses that are themselves products of the interaction of our genetic endowment with our environment. As will be proposed later in this chapter, the entire enterprise of attempting to separate genetic from environmental (or social) causes of behavior is itself an indication of confusion.

These criticisms and problems notwithstanding, the evolutionary approach taken by sociobiologists has been of considerable value in addressing certain ultimate why questions about human behavior. The major contribution to our understanding is the realization that human behavior, like the behavior of all organisms, was shaped over evolutionary time as a function of its survival and reproductive consequences. As for any other species, a human behavior having an inherited basis that increases an individual's survival and reproduction, or the survival and reproduction of closely related individuals, will over time spread through the population. In contrast, heritable behaviors with less positive effects will over time be eliminated.

The Darwinian approach taken by sociobiologists to study human behavior yielded interesting hypotheses, predictions, and answers. We will now consider some of these as they relate to male-female differences and parental care of children.

Men and women differ in many obvious ways, but an important one that is not immediately apparent is their capacity for reproduction. With each ejaculation a man can provide up to 100 million sperm that are then quickly replaced. In contrast, a woman produces only about 400 eggs during her entire lifetime. In addition, a woman must make a very large investment in producing and rearing a child. The fetus develops in her body from which it draws its nourishment, the woman gives birth to the child at considerable risk to her own health, and the child must be nursed and cared for a considerable length of time. In contrast, a man needs do nothing more than copulate to produce a child, although, of course, many men (but certainly not all) also make substantial investments in their children. Thus a man's potential reproductive capacity is much greater than a woman's.

As in other animals, these striking differences in reproductive functions and capacities should, from an evolutionary perspective, lead to similarly striking differences in certain behaviors. Since the limiting factor for male reproductive success is the availability of fertile women, we should expect to find keen competition among males for fertile female mates, and evidence shows that such competition exists in all human societies. In fact, many cases of homicide are related to men competing for women (Daly & Wilson 1988).

Also, since each copulation by a man with a fertile woman has the potential of producing one or more children carrying half of the man's genes even with no further involvement by him, we would expect men to be more easily sexually aroused and more interested in mating with many different women. Because women have much less to gain from multiple partners (only one man at a time can father a child), they should be less easily sexually aroused and less interested in having several sex partners. The facts that married men are much more likely to engage in sex outside of marriage than their wives (Symons 1979), that many men pay women for sex but women do this much more rarely, and that a huge worldwide pornographic industry is supported by men who are willing to pay to just look at images of young scantily clad and nude women, are all consistent with evolution-based predictions by sociobiologists concerning male-female differences in sexual behavior. These findings are also consistent with male-female differences in animal behavior as discussed in chapter 7.

Men and women also differ in mate choices. A man may maximize his reproductive potential by establishing a relationship with a younger woman with many reproductive years ahead of her. So we should expect men to prefer younger mates, especially as they grow older. In contrast, a woman may maximize her reproductive success by finding a man with sufficient material resources to provide for her and her children, and such a man is likely to be older than she. As expected, men's preference for younger women and women's preference for older men were found in at least thirty-seven countries (Buss 1989; Kenrick & Keefe 1992). A rather blunt way to summarize these findings is to note that men tend to see women as sex objects (preferring mates and wives who are young and physically attractive), and women tend to see men as resource objects (preferring older and wealthier men with less concern for physical attractiveness).

But youthfulness is just one factor involved in female reproductive capability, with health and fertility being others. One indicator of female health and fertility is the ratio of waist to hip size. Healthy women in their prime childbearing years (early teens to middle age) have waist-to-hip ratios between 0.67 and 0.80, although conditions such as hypertension, diabetes, gallbladder disease, and (obviously) pregnancy tend to increase this ratio. A small waist-to-hip ratio is also indicative of high levels of the female hormone estrogen and therefore of fertility. We should thus expect men to find young women with low waist-hip ratios to be most attractive. This was in fact found in the United States and many other cultures where a ratio of 0.7 is considered most attractive by men (Singh 1993, 1997).

The care that parents invest in raising children has also been a subject of considerable interest among sociobiologists, using as their basic working hypothesis that men should invest less in their mate's child if they know or suspect that the child was fathered by another man. Perhaps one of the most interesting findings concerning parental care of children has to do with the Ifaluk people of the Caroline Islands in the South Pacific. Their society is characterized by a relatively high degree of sexual permissiveness so that a man has little certainty that he is the father of his wife's children. Evolutionary analysis would predict that a man in this situation would withhold at least some parental support from his wife's children. In the case of the Ifaluk, a man provides support not for his wife's offspring but rather for his sister's, to whom he is more likely to be related, by becoming their "uncle-father" (Alexander 1979). In the somewhat less exotic setting of the Canadian city of Hamilton, Ontario, children over the age of four living with a step-parent were forty times more likely to suffer some form of parental abuse than those living in families with both biological parents (Daly & Wilson 1985).

A final example of the value of a sociobiological approach to human behavior deals with two major practices that are used throughout the world to help one's child obtain a desirable spouse. Because a man's reproductive capacity is limited primarily by his access to fertile women, we would expect that a man and his parents would be willing to give up some material resources to obtain a wife, the payment of which to the woman's family is often referred to as a *bride price*. This was the custom among the inhabitants of southern Sudan when I made several visits there in the early 1980s. I found it interesting to compare prices for brides in different localities, with a typical price being in the neighborhood of fifteen goats. But when I explained to my male Sudanese hosts that in other places such as India it is the bride's family that provides money and other goods (that is, a *dowry*) to the groom's family, they were incredulous. Why on earth would a young woman's parents pay an unrelated man's family in addition to giving away the services of their daughter?

At the time I could provide my African friends with no reasonable explanation for the Indian custom of the dowry. Since then I learned that providing a bride price is much more common than paying a dowry throughout the world (Murdock 1967). Paying for a bride is particularly prevalent in societies where men often take more than one wife (polygyny) since this practice increases competition for wives (if some men have more than one wife, other men must have none) and hence their worth to men. In contrast, the woman's family providing a dowry is about fifty times more likely to be found in socially stratified, monogamous societies than in nonstratified, polygynous societies (Gaulin & Boster 1990). In such societies men's wealth and earning potential vary greatly, and because a man's resources cannot be diluted by the acquisition of many wives, it pays for a woman's family to find her a wealthy husband, even if considerable cost is incurred in doing so. So these strikingly different practices of bride price versus dowry can be understood as different ways of achieving the common goal of maximizing reproductive success in two different cultural contexts.

Evolutionary Psychology's Search for Proximate Causes

The work of sociobiologists provides interesting hypotheses and useful explanations for aspects of human behavior by focusing on the survival and reproductive consequences of behaviors in different social contexts. It must be kept in mind, however, that uncovering the ultimate, evolutionary origins of certain preferences and behaviors does not explain proximate here-and-now reasons for a behavior. To use an analogy, studying and understanding the history of the invention and development of the automobile does not provide an explanation for why my car (usually) accelerates when I step on the gas.

This is perhaps made most clear by an example of animal behavior. The European cuckoo is a bird that is referred to as a *brood parasite*, meaning that the female lays each of her eggs in other birds' nests and then abandons them. The cuckoo egg hatches before those of the host bird, and the intruding hatchling proceeds to dump the other eggs out of the nest by balancing each egg on its back between its extended wings while walking backward up the side of the nest.

Coming up with an ultimate, evolutionary explanation for the young cuckoo's egg-dumping behavior is not difficult. By eliminating the eggs of its genetically unrelated hosts, the cuckoo monopolizes the care and food given to it by its duped adoptive parents. Since today's cuckoos descended from cuckoos that practiced egg dumping, they continue the practice. But eliminating its nestmates to have more food for itself is not likely what the cuckoo has in mind when it sends its hosts' eggs tumbling out into the void. Its actual proximate goal is almost certainly something much simpler, such as to remove all objects of a certain size, shape, and color from the nest with no knowledge that achieving this immediate goal will have a longer-term positive effect on its survival and later reproductive success. That this behavior had the effect of increasing the survival and reproduction of cuckoos in the past provides no proximate explanation at all for why the individual cuckoo still does what it does. The latter can be determined only by empirical testing of various hypotheses by introducing objects of varying shapes, colors, and sizes into the cuckoo's adoptive nest and observing its behavior to determine what perceptual variables it is controlling. In this way, the young cuckoo's immediate behavioral goals can be determined, goals that evolution selected because of their ultimate side effects of facilitating survival and reproductive success.

Now let us consider an example of human behavior. It was noted that men throughout the world, particularly older men, prefer women who are considerably younger than themselves. The ultimate, evolutionary explanation for this preference that was offered was that younger women are fertile and have many reproductive years ahead of them. Men who in the past chose younger mates left more descendants than those who chose older, less fertile mates, so this inherited preference for younger women spread throughout the population of human males.

But this ultimate, evolutionary explanation does not necessarily provide information concerning the proximate reasons as to why an individual man prefers and pursues younger women. In the case of the cuckoo, the ultimate, evolutionary explanation for any behavior or preference need not correspond to the proximate explanation. But since humans can plan ahead and consider the long-term consequences of behaviors, choices, and preferences, the proximate reason may be that older men prefer younger women because they really do consciously desire to have many children and see a younger woman as a means to this goal. But a more likely explanation is that men have evolved a preference for young women because our male ancestors who had such a preference left more descendants than those who did not, and that preference may have nothing to do with any perceived reproductive advantages. Again, the ultimate, evolutionary explanation for a behavior need not necessarily provide information concerning proximate mechanisms. This is particularly clear for nonhuman organisms that are unable to consider the long-term survival and reproductive consequences of their behavior. But the distinction between ultimate and proximate explanations is valid for humans as well.

Sociobiologists have not always been careful to distinguish between the two types of behavioral explanations, sometimes taking ultimate, evolutionary explanations as proximate ones. As John Tooby commented (quoted in Allman 1994, p. 49):

Many sociobiologists have this view of people as *fitness maximizers*. They assume that since evolutionary biology says "We all evolved to propagate genes," the purpose of humans is to propagate genes. They believe that beneath all of our complicated human behaviors there is an underlying hidden logic of "gene propagation." So when you are being nice to your child, they say, all you are *really* doing is selfishly trying to propagate your own genes. A lot of sociobiological work carries this cynical interpretation of human behavior-a view of the world for which sociobiologists have been rightly criticized. The problem is that sociobiologists confuse the mechanisms of the mind with the process that built the mind, and in fact these are two separate things. Evolutionary biology is not a theory of human nature. Rather, it is a theory for how human nature came to be-and a useful tool for discovering what human nature actually is. A mother really does love her child--it's not that somewhere deep inside her mind there is a selfish motive to spread her genes. In fact, it's really the other way around: Human beings love their children because those ancestors who loved their children had more surviving children, and we're descended from them and not the others who didn't love their kids. So in the "grand evolutionary biological" sense of Why do you love your kids? You love them because it is part of your human nature that evolved as part of our ancestors' brain mechanisms. There is nothing in those brain mechanisms that says That kid has your genes; he's propagating your genes, and so you should love him.

John Tooby and his wife, Leda Cosmides, two founders of the new field of evolutionary psychology, are primarily interested in discovering psychological mechanisms that serve as the proximate causes of human behavior while looking to evolutionary theory for clues to these mechanisms and their ultimate origins. This Darwinian approach is still in its beginning stages, but it has already made two important theoretical contributions. The first, as mentioned, is the distinction between ultimate (evolutionary) and proximate (psychological) causes of human behavior. The second is the realization that almost all human evolution took place while our species lived in small groups of hunter-gatherers, long before the development of agriculture, large urban communities, and modern technology. This means that many behaviors and preferences that were adaptive in their original evolutionary contexts may no longer be adaptive today.

An example is our taste preference for sugar, salt, and fat—which are, coincidentally, the main ingredients of concoctions served in fast-food restaurants that have invaded almost all corners of the world. During the Pleistocene epoch, which ended 10,000 years ago, such nutrients were difficult for our hunter-gatherer forebears to obtain, yet vital for their survival. So individuals who consumed as much sugar, salt, and fat as they could when available would have had survival and reproductive advantages over those who did not. Because there was little danger during this time of consuming too much of these nutrients (being in such scarce supply), humans evolved a strong craving for the taste of foods with these nutrients.

But today millions of people live where they have virtually unlimited access to foods containing all the sugar, salt, and fat they can eat, and the associated health problems of obesity, diabetes, hypertension, and heart disease are all too common in modern industrial societies. So whereas a craving for these nutrients was adaptive in early human environments, recent changes in the environment for many modern humans rendered these dietary preferences less adaptive if not downright maladaptive. This distinction between what evolutionary psychologists call the "environment of evolutionary adaptiveness" (often abbreviated EEA) and our current environment is important in understanding how certain human preferences and behaviors that appear nonadaptive today may nonetheless have an adaptive evolutionary origin.

Changes in survival and reproductive consequences of certain behaviors and preferences in modern environments not anticipated by evolution often give useful clues to the proximate mechanisms of human behavior. For example, behaviors and preferences that in the past typically resulted in many offspring were selected by evolution. But what was actually selected? Is it a basic human desire to have many children? Or is having many children a side effect of achieving other proximate goals?

The finding that over the last century family size declined in Western societies and that today it tends to be smaller for wealthier families

(Vining 1986) suggests the latter. This decline and its negative correlation with wealth is one consequence of the availability of contraceptive methods that permit heterosexual couples to copulate while limiting the number of children they have or avoiding having children altogether. The fact that contraception is widely used, particularly by wealthier couples who in the past would have been expected to produce the most children and grandchildren, is a good indication that having many children is not a universal human goal resulting from natural selection, but is rather a side effect of other inherited preferences, notably the desire for frequent sexual intercourse, particularly with young, attractive females (for men) and wealthy, high-status men (for women).

The picture that emerges is one in which evolution selected organisms who had goals (and the means to achieve them) that resulted in better than average survival and reproductive success. But survival and reproduction are not the goals per se that the organism pursues. Rather, organisms, humans included, evolved preferences (and the means to achieve them) that in past environments led to survival and reproductive success with no guarantee that they will do so today. Overconsumption of sugar, salt, and fat and the practice of birth control are two examples of the lessening fit of evolved preferences and behaviors to survival and reproduction.

But humans do differ from other organisms in the flexibility they show in achieving their goals. A farmer can change the crops he plants depending on weather and economic conditions. In contrast, the leaf-cutting ant, having discovered agriculture millions of years before humans did, is limited to its crop of leaf-based fungus and cannot change its way of feeding if for some reason cultivating fungus is no longer practical or possible. In other words, humans have higher-order goals that are achieved by manipulating lower-order goals as necessary. Other organisms also provide evidence of a hierarchy of goals in their behavior (recall the examples of flexible insect behavior in chapter 7), but their hierarchies are not as extensive as those of humans. Thus certain goals (such as what to eat) cannot be varied to the extent that humans can adaptively modify their goals (which is why you will never find a vegetarian dog or a cat on a self-imposed diet).

This emphasis on the flexibility of human behavior is another way in which evolutionary psychology distinguishes itself from sociobiology. In the terminology of Robert Wright whose book *The Moral Animal* (1994) introduced evolutionary psychology to a large audience, we can look at human nature as made up of "knobs and tunings." Knobs are basic preferences selected by human evolution, and tunings are influenced by environmental factors. The preference for a variety of sex partners may be a basic knob that all human males inherit as part of their evolutionary legacy. But the extent to which this preference is realized (tuning) may well depend on the particular experiences of the particular man. Learning that other men who are sexually promiscuous pay no obvious penalty for their adventures and are able to maintain a stable family life and high social status may result in the knob being set on the high end of the scale. In contrast, living in a society where male sexual promiscuity is punished (for example, by exposure as scandalous, leading to loss of social status and esteem) may result in a much lower setting of that specific knob.

Such variation in tunings of basic inherited preferences may well explain much of the cultural diversity that is found among human societies, a diversity that has led many anthropologists and sociologists to reject the notion of universal human behavioral characteristics that were shaped by our evolutionary past. But we have seen that whereas the cultural practices of bride price and dowry are superficially very different, both can be understood as having positive effects on reproductive success in their social contexts. Still, these positive reproductive consequences are likely only a side effect of men competing for wives in polygynous societies and women attempting to secure high-status, resourceful husbands in monogamous, stratified societies.

When one looks under the surface in this way, similarities among diverse human societies are more striking than differences. Donald Brown, in his book *Human Universals* (1991), described characteristics that appear to be universally present in all human cultures. Steven Pinker (1994, pp. 413– 415) outlined some of them, summarized here.

With respect to oral language, all human societies have:

Gossip. Lying. Verbal humor. Humorous insults. Poetic and rhetorical speech forms. Narrative and storytelling. Words for days, months, seasons, years, past, future, body parts, inner states (emotions, sensations, thoughts), behavioral propensities, flora, fauna, weather, tools, space, motion, speed, location, spatial dimensions, physical properties, giving, lending, numbers (at the very least "one," "two," and "more than two"), proper names, possession. Kinship categories, defined in terms of mother, father, son, daughter, and age sequence. Binary distinctions, including male and female, black and white, natural and cultural, good and bad. Measures. Logical relations including "not," "and," "same," "equivalent," "opposite," general versus particular, part versus whole. Conjectural reasoning (inferring the presence of absent and invisible entities from their perceptible traces).

Concerning nonlinguistic vocal communication, all human communities have:

Cries and squeals. Interpretation of intention from behavior. Recognized facial expressions of happiness, sadness, anger, fear, surprise, disgust, and contempt. Use of smiles as a friendly greeting. Crying. Coy flirtation with the eyes. Masking, modifying, and mimicking facial expressions. Displays of affection.

With respect to emotions we find all human communities having:

Sexual attraction. Powerful sexual jealousy. Childhood fears, especially of loud noises, and, at the end of the first year, strangers. Fear of snakes. "Oedipal" feelings (possessiveness of mother, coolness toward her consort).

Concerning activities, humans everywhere have:

Dance. Music. Play, including play fighting.

Aspects of universal human technology include:

Manufacture of, and dependence upon, many kinds of tools, many of them permanent, made according to culturally transmitted motifs, including cutters, pounders, containers, string, levers, spears. Use of fire to cook food and for other purposes. Drugs, both medicinal and recreational. Shelter. Decoration of artifacts.

For social conventions, we find in all human communities:

A standard pattern of time for weaning. Living in groups, which claim a territory and have a sense of being a distinct people. Families built around a mother and children, usually the biological mother, and one or more men. Institutionalized marriage, in the sense of publicly recognized right of sexual access to a woman eligible for childbearing. Socialization of children (including toilet training) by senior kin. Children copying their elders. Distinguishing of close kin from distant kin, and favoring of close kin. Avoidance of incest between mothers and sons. Great interest in the topic of sex. Exchange of labor, goods, and services. Reciprocity including retaliation. Gifts. Social reasoning. Coalitions. Government, in the sense of binding collective decisions about public affairs. Leaders, almost always nondictatorial, perhaps ephemeral. Laws, rights, and obligations, including laws against violence, rape, and murder. Punishment. Conflict, which is deplored. Rape. Seeking of redress for wrongs. Mediation. In-group/out-group conflicts. Property. Inheritance of property. Sense of right and wrong. Envy. Concerning sex and age differences, found universally are:

Division of labor by sex and age. More child care by women. More aggression and violence by men. Acknowledgment of differences between male and female natures. Domination by men in the political sphere.

As discussed, universal human behavioral patterns and preferences cannot in themselves be used as evidence that they have a specific genetic basis. Instead they may be the result of the interaction of more general abilities and desires with physical and social environments that are similar enough in all cultures to produce these behaviors. But this essential interaction of genes and environment does not in any way detract from a Darwinian approach to explaining their origins since any behavior, preference, or trait depends on an interaction of genes and environment, of nature and nurture.

Sociobiologists and evolutionary psychologists respect this essential gene-environment interaction insofar as they usually refrain from stating that any human trait or behavior is either solely genetically or environmentally determined, but they make other errors as a result of not adequately respecting this interaction. For instance, it is not unusual for a Darwinian-inspired behavioral scientist to state that some behavior or trait is more due to genes than environment, or vice versa. E. O. Wilson commented on the extent to which human social behavior is genetically determined. A more blatant and potentially pernicious example of such thinking can be found in Herrnstein and Murray's controversial book The Bell Curve (1994). The authors used a maze of statistical analyses to argue that differences between American blacks and whites in performance on general intelligence tests are almost exclusively due to genetic racial differences and not to striking differences in environments in which individuals of these two races typically grow up and remain. Yet if all behavior and psychological abilities result from an interaction of genes and environment, what can it actually mean to say that either genes or environmental factors are more important for a behavior or trait?

One way of simplifying this issue is to consider the surface area of a rectangle, which is a function of both its length and width. Specifically, its length and width interact in a multiplicative fashion so that its area in square units is its length multiplied by its width. The way in which the length and width interact in determining area means that the effect of length on area depends on width. Similarly, the effect of width on area depends on length. So increasing a rectangle's width from 5 to 6 units will have more of an effect on its area if it is 16 units wide rather than 15 units wide. Increasing width from 16 to 17 units will have more effect on area if it is 6 units rather than 5 units long. Note that this interactive relationship makes it nonsensical to ask whether a rectangle's length or width is more important in determining its area.

Consider the implications of a similar multiplicative gene-environment interaction for human abilities and behaviors, such as those related to a child's success in school. If genes and environmental factors interact in determining school achievement, it makes no sense to consider whether nature or nurture is more important or which contributes more to the observed differences in this regard among a group of children.

Here's another example, a hypothetical case I call "The Case of the Stuttering Triplet," like the surface area example above, inspired by psychologist Donald Hebb's important 1953 paper on the roles of heredity and environment in behavior. Two psychologists, Dr. A and Dr. B, are interested in the causes of stuttering. Dr. A finds a boy named Stu who stutters and learns that Stu has a fraternal (dizygotic) twin living in the same house who does not stutter. Dr. A concludes from these findings that Stu's stuttering is genetically determined, since his brother, who has a different genome but shares the same home environment, does not stutter.

Meanwhile, Dr. B discovers a boy, also named Stu, who stutters. During his investigation Dr. B learns that this Stu has an identical (monozygotic) twin who was separated from Stu at birth, lives with a different family, and does not stutter. Dr. B concludes that Stu's stuttering is due to environmental factors since Stu's identical brother, who has an identical genome but lives in a different environment, does not stutter.

The punch line is that Dr. A and Dr. B have both found and studied the very same stuttering boy but have learned different things about him. Stu is actually one of *triplets*, two of them identical (one of them being Stu) and one fraternal. Dr. A's knowledge of Stu's nonstuttering fraternal twin living in the same home led him to conclude that Stu's stuttering had a genetic cause. In contrast, Dr. B's discovery of Stu's nonstuttering identical twin in a different home led to a very different conclusion, that Stu's stuttering must be due to his environment. What is really going on (obvi-

ous to us since we know of both Stu's identical and fraternal nonstuttering brothers) is that a certain *combination* of environmental and genetic factors led to Stu's stuttering, with neither genes nor environment being more or less important than the other in bringing about this phenomenon.

But there is yet another way in which genes and environment interact to influence behavior that goes beyond the multiplicative model suggested by the rectangle example. Research indicates that certain environmental factors can cause chemical changes in the body that affect certain genes that in turn produce proteins that ultimately influence the brain. Since changes in the brain influence behavior and the resulting environment, we have another circle of causality that defies one-way cause-effect analysis. We will see in the next chapter a particularly striking example of how at least a portion of a person's genes are not fixed at birth but rather continue to evolve throughout life in response to certain environmental conditions. To return briefly to the rectangle, it is as if changing its length also influences its width, which then influences its length, and so on.

What all this means for a Darwinian approach to human behavior is that neither genes nor environment (including culture) can be considered in isolation. Even to ask the question as to whether nature or nurture is more important in determining a human structural or behavioral trait is an indication of confusion. Since so much of humankind's environment is a function of human behavior and preserved for succeeding generations in the form of culture (which includes homes and schools), we must consider coevolution of both to make sense of human behavior. As the noted Ukrainian-born American geneticist Theodosius Dobzhansky remarked (quoted in Wilson 1978, p. 21), ". . . in a sense, human genes have surrendered their primacy in human evolution to an entirely new, nonbiological or superorganic agent, culture. However, it should not be forgotten that this agent is entirely dependent on the human genotype." And, of course, the human genotype has from its very beginning also been dependent on human culture.

This interaction of nature and nurture also blurs the distinction that is still often made between innate and learned behavior. We noted in the preceding chapter how the learning capabilities of animals were shaped by natural selection. That is, the ability to modify behavior in useful ways as a result of experience is inherited. Insofar as such learning abilities have survival and reproductive consequences, they in turn help to shape further evolution of the organism.

Strengths and Dangers of a Darwinian Approach to Human Behavior

The Darwinian approach to human behavior that emerged in the 1990s in the form of evolutionary psychology has begun to offer new insights into the behavior of our species.³ Like its sociobiological forerunner, evolutionary psychology recognizes the importance of Darwinian evolution, including kin selection and reciprocal altruism, to provide ultimate explanations. In addition, it attempts to discover proximate psychological mechanisms underlying various human actions, recognizing that certain evolved behaviors and preferences may no longer be adaptive in a world so very different from the physical and social world in which we evolved.

But this approach has potential dangers that must be guarded against. One is the tendency to analyze human behavior by attempting to separate genetic from environmental factors, when these factors interact so that any such separation is meaningless at best and seriously misleading at worst.

Another potential danger is application of basic human universals or observed group differences (such as those based on sex or race) to individuals. By way of illustration, let us consider a proposed human universal from the preceding list where it was noted that all human societies make use of music and dance for various social functions. But finding music and dance in all human societies does not mean that all individual humans engage in musical behavior. Rather, since evolution depends on variation in traits and abilities, we should expect to find individual variation in participation in and abilities for such activities. Similarly, not all mature humans engage in sexual activities (while others do so frequently) and not all individuals participate in gift giving (while the great majority of us do). It is therefore important to keep in mind that human universals suggested by an evolutionary perspective are universal only in the sense that they are found in all human cultures and societies, and not in the sense that they apply to every human being on earth.

We must also guard against applying observed group differences to individuals. For example, consideration of human spatial abilities from an evolutionary perspective led to the hypothesis that since our male ancestors were primarily hunters of mobile, far-ranging game while our female forebears were mostly foragers of immobile, nearby vegetable foods, there should be sex differences in those abilities that are most important for hunting (where men should show an advantage) and foraging (where women should be superior). As predicted, men as a group are better in tasks involving mental rotations of objects, map reading, and maze learning, whereas women as a group show superiority in recalling objects and their locations. To take an ability where women show an advantage, a test for object memory, a group of 115 women correctly recalled on average 1.9 more objects from a diagram containing 27 objects than a group of 63 men (Silverman & Eals 1992, p. 539).

But in spite of this statistically significant difference favoring women (p < 0.01), the variability of individuals in each group (pooled standard deviation 4.03) resulted in a large enough overlap between men and women in this ability so that one cannot predict with confidence that a given woman will actually have a better memory for objects than a given man. Instead, since the mean difference between the groups is less than half the difference between a typical individual and his or her group's mean, a given man has close to a 7 out of 10 chance of being either above the woman's mean or not being more below that value than would be expected for a typical woman.

Even when group mean differences equivalent to one standard deviation are found (which is not common in psychological studies; an example would be a difference in means between two groups of 15 IQ points), it is still the case that a given individual in the lower group has an even chance of being either above the mean of the higher group or not farther below it than a typical individual of the higher group.

The lesson to take away from this is that a Darwinian approach to human behavior may lead to the discovery of interesting pancultural human universals and group differences, but such findings rarely if ever allow one to make accurate or useful predictions concerning the abilities or behavior of a given individual. So even if it is true, as Herrnstein and Murray claim, that American blacks score on the average 15 points below American whites on measures of general intelligence, such a group difference would be of virtually no use for making predictions about the intelligence of an individual white or black American. Evolutionary psychology, unlike behaviorism, also recognizes the central importance of desires and goals in explaining human behavior. But, curiously, its practitioners have yet to discover proximate psychological mechanisms that can explain how such goals and desires influence behavior. This is because the mechanisms they propose continue to be one-way cause-effect models in which sensory input is transformed (that is, cognitively processed) into behavioral outputs. To illustrate this perspective, here are Cosmides and Tooby stating their view of the proximate psychological mechanism (1987, p. 282):

Behavior is not randomly emitted; it is elicited by information which is gleaned from the organism's external environment, and, proprioceptively, from its internal states. Natural selection gave us information processing machinery to produce behavior, just as it gave us food processing machinery to produce digestion. . . . The evolutionary function of the human brain is to process information in ways that lead to adaptive behavior; the mind is a description of the operation of a brain that maps information input onto behavioral output. . . . Behavioral output differs with informational input; the information processing machinery that maps informational input onto behavioral output is a psychological mechanism.

But we saw in chapter 6 how such a one-way cause-effect mechanism is simply incapable of accounting for purposive behavior. If such a model cannot explain how a person can maintain the knot joining two rubber bands at a certain spot in spite of continuous disturbances, or keep a car centered in a highway lane despite curves and gusting winds, it certainly is inadequate to the task of accounting for how we are able to find food, procure mates, protect our children, defeat our enemies, and further our careers and reputations in complex, constantly changing, disturbancefilled environments.

This continued reliance on a one-way input-output mechanism of behavior leads to other problems. One is that evolutionary psychologists are susceptible to the behavioral illusion described in chapter 6 in which the covariation between some observable aspect of the environment and a person's behavior makes it appear as if a stimulus is causing behavior when in fact behavior is being used to control a perception that may not be apparent to the researcher. A second problem is that the one-way causeeffect model of behavior cannot distinguish between the intended consequences of human action and its unintended, accidental side effects. And a third problem is that an input-output view of behavior cannot account for the way in which certain desires or goals serve as subgoals, that is, as a means of achieving other goals, and how these subgoals are varied in response to disturbances to achieve the higher-level goals.

Perceptual control theory, with its hierarchy of perceptions and goals, provides an explicit, working model for these important characteristics of human behavior. But it is able to do so only by rejecting a one-way causeeffect view and replacing it with a hierarchy of closed loops, each involving the simultaneous functions of perception, comparison with a reference level, and action.

Whereas evolutionary psychologists recognize the Darwinian *origin* of many human desires and goals, as a group they have not yet escaped the grasp of one-way cause-effect reasoning in their attempts to understand the proximate *mechanisms* of behavior. Neither do they recognize the existence and importance of Darwinian processes occurring within the brain as humans constantly adapt their behaviors and desires to new environmental challenges for which our evolutionary past could not have prepared us. This application of Darwinian theory to adaptive processes occurring during the lifetime of organisms constitutes a veritable second Darwinian revolution that is the subject of the next chapter.