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Sociobiology and Human Culture

Natural Selection and the Evolution of Behavioral Flexibility

Had I been born in central Papua New Guinea a century ago, odds are that I would have considered myself humiliated had I been an adult seen in public without my penis sheath, despite the fact that my penis sheath would have constituted essentially my only "clothing." I was born in Charlottesville, Virginia, however, and if I were to wander around my current neighborhood in Tempe, Arizona, outfitted in traditional New Guinean fashion, I would be arrested in short order. You do not need to be told that the difference in what constitutes appropriate attire varies enormously, and that is true even within Papua New Guinea today, where a great many men have traded in their penis sheaths for shorts and T-shirts.

The diversity of cultural traditions, the rapidity of cultural change, and the capacity of children transferred from one society to another to adopt the local customs and local language all demonstrate that human behavior is highly flexible and dependent upon the capacity to learn. As a result, many persons have accepted the non sequitur that the genes which have survived past episodes of natural selection have little or no role to play in the development of our behavior. However, as discussed in chapter 3, all behavioral traits, whether instinctive or learned, are the product of an interaction between genetic information and the "environment." Although the different traditions learned by a Papua New Guinean or a Tutsi or an Inuit or an Englishman obviously arise from differences in cultural environments, the capacity to learn and to acquire the trappings of a culture depends upon chemical events that take place in brain cells within the New Guinean, the Tutsi, the Inuit, and the Englishman. The brain cells in question are the developmental products of complex gene-environment interactions. Without the appropriate genetic information, there can be no development of the psychological mechanisms that support behavioral adaptability, including the learned acquisition of cultural traditions and mores.

Genetic differences in the past have surely affected vast numbers of gene-environment interactions that have occurred within ancestral hominids, generating ample variation in the kind of psychological mechanisms these individuals possessed. Therefore, selection was inevitable, with some genes becoming more frequent over time, namely, those whose information contributed to the development of the more adaptive learning mechanisms, which resided in bodies that reproduced more than other individuals with slightly different genes and slightly different psychological attributes.

Humans have not always had all the cultural accouterments of Hutus or Englishmen. At one time not so many million years ago, our ancestors could make only rudimentary tools while surely communicating in a far less sophisticated manner than we do currently. The immense increase in brain size over the last million or so years (fig. 8.1) must have had profound consequences for our capacity to learn and acquire our culture. If you accept the less-than-revolutionary assumption that brains are necessary for learned behavior, then past selection on hominids that varied in their capacity for culture is a certainty.

Thus, the real question is not whether the human brain and our ability to adopt cultural traditions have evolved. The real question is, What kind of brain and what kind of learning abilities have been produced by natural selection? For blank slate theorists, the answer to this question is that human brains have the capacity to learn almost any conceivable option while being "predisposed toward none." Those who wish to ignore evolution have adopted what John Tooby and Leda Cosmides call the Standard Social Science Model of the brain [314], which posits an all-purpose, content-free, hyper-impressionable organ that develops within infants and then awaits instruction from available culture bearers, instruction that the young brain faithfully absorbs. I join Tooby and Cosmides in acknowledging that different social scientists employ many different versions of the blank slate model; like Tooby and Cosmides, I will not expend space on "the qualifications and complexities by which positions are softened, pluralisms espoused, critical distinctions lost, and, for that matter, lip service paid" (p. 31 in [314]). It is fair to do so because no matter what variant of the blank slate model is advanced, it does not concern itself with selection's effects on brain design whereas the sociobiological alternative does.

For sociobiologists, the brain is essentially a reproductive organ, like every other evolved internal mechanism of living things. If selection has shaped the evolution of this device, as it must have, then the brain and the abilities this amazing structure controls should tend to increase the genetic success of individuals, at least in environments similar to those occupied by humans in the past. How might the brain achieve this goal? By having design features that help individuals overcome predictable obstacles to reproductive success, not completely blank, open-ended, and neutral attributes, but rather those that can facilitate the kind of behavioral flexibility that tends to result in successful reproduction. In contrast to the blank slate brain, the prepared or anticipatory brain is content-rich, loaded with specialized

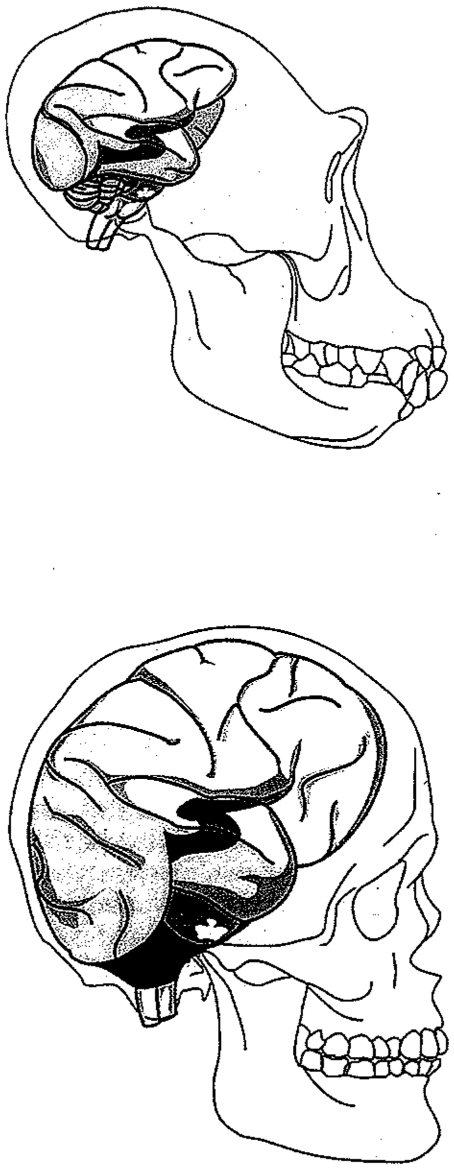

Figure 8.1. The extraordinary evolution of the human brain involved the expansion of an organ in an ancestral hominid that was about the same size as a modern chimpanzee's brain into one that is three times that size.

circuitry that can much more easily acquire from the environment information that is relevant to the reproductive competition that occurs in human populations. This is the kind of brain that will help individuals do a better job at those particular tasks relevant to genetic success.

How can we evaluate the plausibility of the two theories—the content-free, blank slate brain capable of learning all things equally well versus the information-rich, task-specific, prepared brain predisposed to learn certain things far more readily than others? We can judge the competing views in a host of ways, but first by asking whether our ancestors confronted certain obstacles to genetic success over and over again, generation after generation. If they did, selection surely favored individuals who happened to have brains with particular design features, neural modules if you will, that were well suited for overcoming these predictable obstacles. The physical and social features of the ancestral hominid environment were not random, arbitrary, or infinitely varied. For example, paleontological and anthropological evidence are usually interpreted to mean that our ancestors lived in small bands composed of a few family units [50, 199]. Band members foraged for a diverse set of foods, vegetable and animal, and these hunters and gatherers made and used tools for this purpose. Bands regularly came into contact with others, creating situations with the potential for competition or cooperation with respect to the control of resources and the acquisition of mates. Females almost certainly moved from their natal group to another cluster of people where they paired off with males. Adult males could and many did share resources with their mates, children, and others; women likewise shared foods they collected with other band members. The opportunities were vast for complex and dynamic social interactions on a whole range of fronts.

Given this kind of setting, those of our ancestors who were capable of learning certain things surely left more descendants than those who were less competent at the following tasks: acquiring information about who was related to whom by how much, learning about the reputation and personalities of potential mates and rivals, learning the identification, uses, and spatial location of resources, especially foods, within the foraging range of the band, learning how to make effective tools and how to utilize them efficiently, and so on. These are tasks that require very different abilities. The idea that one all-purpose learning mechanism could provide the cognitive basis for success in all these and many other different endeavors is about as plausible as the idea that a single piece of software can permit a computer user to engage in both word processing and the statistical analysis of data.

The inherent implausibility of the blank slate model also surfaces when one considers how easy it would be to learn things that reduce, rather than increase, one's genetic success. We will later examine some cases in which culturally supplied information currently has exactly that effect. For the moment, consider the

following thought experiment. Imagine a population of ancestral humans most of whom possessed genes that promoted the development of blank slate brains. Because of their open minds, these individuals absorbed whatever information other "culture bearers" in their groups provided them. Imagine that among these culture providers some possessed a hereditary predisposition to dish out information that made their companions amenable to exploitation in ways favorable to the exploiters. As Noam Chomsky notes, the blank slate brain is a dictator's dream (quoted in [300]).

In short order, the special genes of the manipulative "educators" would spread at the expense of the alternative forms of those genes in educable suckers. In this evolving population, other new alleles that in any way helped make persons resistant to exploitative education could be expected to spread, eventually creating a species whose members evaluate the "culture" to which they are exposed from a special perspective. The resultant decisions might be based on logical analysis or upon the individual's gut feelings, but the effect would be that persons would sometimes reject attempts to get them to accept certain kinds of culturally supplied advice, traditions, exhortations, or demands. Such persons sound very much like people all around us today, and indeed very much like ourselves! Most of us tend to be skeptical of a great deal of what we hear. Moreover, we are sometimes worried about being taken to the cleaners by others, we are always interested in the motivation and aims of our fellow man, and we feel mildly paranoid at times about our social life in general. Certain things, such as the idea of being enslaved, elicit strong negative reactions. Such attributes can prevent us from falling under the spell of others and marching along like automatons to the cultural tune sung by those who would take advantage of us.

My point is that blank slate mechanisms are inherently vulnerable to exploitation and therefore unlikely to persist for long, even if it were possible (and it probably isn't) for evolutionary processes to generate a truly blank slate neural apparatus of some sort. The kind of brain circuitry able to survive the genetic competition that has taken place during evolution ought to generate adaptive targeted flexibility of behavior, not undifferentiated equipotentiality of response. If behavioral flexibility is an evolved means to an end, namely, improved chances of genetic success, we can predict that in adaptable organisms, individuals will employ their ability to do X instead of Y or Z in ways that generally advance their chances of reproducing or those of their close relatives. We can check this prediction in many ways, including the examination of how behaviorally flexible organisms other than ourselves make use of their adaptability.

You might think it difficult to find nonhuman creatures that can do X, Y, or Z, depending upon their circumstances, if you have read such things as "In the vast majority of animal species, which are simple invertebrates, behavior is almost entirely genetically programmed" (p. 176 in [268]). Even if "rigidly determined" or "developmentally inflexible" is substituted for the patently misleading "genetically programmed," the claim does not stand up. Behavioral flexibility is definitely *not* a uniquely human attribute nor is it restricted to a few of the "higher" mammals. We have already mentioned, for example, the capacity of male red-winged blackbirds to calibrate their parental care in accordance with their mates' fidelity, and the ability of female red-winged blackbirds to make adaptive tactical decisions about which extra-pair males to accept as mates based on attributes correlated with male age. Likewise, young Seychelles warblers have options which they exercise, choosing between being a helper at the nest of their parents or leaving home to find a breeding territory of their own. Even among the much maligned insects, many species can skillfully adopt one or another tactic to deal with certain variable environmental conditions, as shown by the worker ants that treat their brothers and sisters differently, depending on how many males their queen mothers have mated (chap. 6).

Targeted Flexibility of Behavior in an Insect

That behavioral flexibility is widespread among the animal kingdom can be illustrated with another example of an insect whose behavior belies the claim that insects are rigidly programmed robots, incapable of behavioral flexibility. I learned about this case when studying a species of rove beetle called *Leistotrophus versicolor*, merely one of thousands of beetles in the family Staphylinidae. This insect is not much to look at (fig. 8.2); indeed my wife slandered it upon first encounter as one of the ugliest creatures she had ever seen. I grant that it is homely as befits a creature that apparently is designed to look like a small deposit of bird dung, less than an inch in length, lying on a green forest leaf, the typical perch of the beetle in its tropical forest home in the mountains of Costa Rica. If you were wandering through the beetle's habitat, odds are that you would ignore it completely, which is not surprising since its appearance has surely evolved to camouflage it from visually hunting predators. But should you happen to stumble across the beetle and recognize it as such, you would be struck by its low-slung mottled brown body and drastically shortened wing covers, a key characteristic of the Staphylinidae. As a result of its special wing covers, much of the beetle's sinuous abdomen protrudes uncovered, giving the insect a half-naked look.

A fellow biologist, Adrian Forsyth, convinced me to join him in examining the behavior of this beetle in the forest near the town of Monteverde, a popular destination for ecotourists these days. Although the dung-mimicking insect lacks the appeal of the quetzals and howler monkeys that attract most visitors to Monteverde, the beetle's life is moderately dramatic and full of interest for the sociobiologist. In order to conduct our research, Forsyth and I placed small amounts of mammalian dung in the subtropical mountain forest habitat occupied by the beetles. These none-too-appealing materials appeal strongly to *L. versicolor*, which quickly detect and fly upwind to the dung. There they join various species of blowflies, which also are quick to respond to dung, which offers the flies much food and good egg-laying substrate. The feeding flies sometimes fail to notice a beetle creeping up behind them. The predator then explodes forward to grasp the prey with its formidable jaws, which chop the captured victim to bits during its meal.

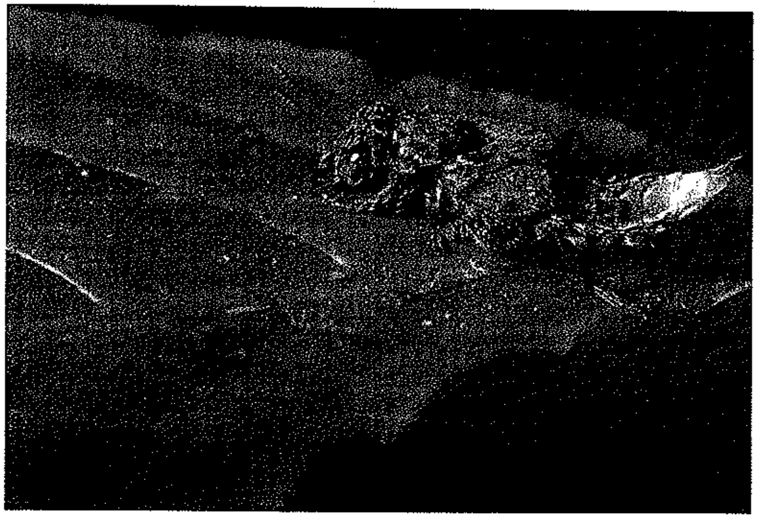

Figure 8.2. The rove beetle, *Leistotrophus versicolor*, is just one of a multitude of species with considerable behavioral flexibility thanks to a nervous system endowed with conditional strategies.

Good fly hunting attracts female beetles to the dung, which in part is why male rove beetles claim territories that encircle fly-attracting feces. The resident male approaches, chases, and expels all other males from "his" bit of dung. Winners get to monopolize incoming females, most of which are sexually receptive, with the result that a successful territory holder inseminates many partners, which zoom in one after another to feed heartily on prey and mate before cruising off to lay their eggs elsewhere [130].

The mating behavior of *L. versicolor* is rather more refined than you might imagine. Males do not simply mount and copulate with female visitors to their territory but instead engage in series of preliminaries that appear to promote female sexual receptivity. The key element in courtship is an abdomen-tapping routine in which the male approaches a female from behind and gently taps the tip of her upr[illegible] mobile abdomen with the underside of his head. An unreceptive female w[illegible] forward away from the courting male; a receptive female eventually stops mo[illegible] and lowers her abdomen, a signal to the courting male to twist his abdomen ab[illegible] so as to copulate with his partner.

By giving captured beetles distinctive paint marks after measuring them, [illegible] created a population of individuals of known sex and size, which facilitated o[illegible] attempts to determine whether large males had a reproductive advantage ov[illegible] smaller ones, as we expected they would. Forsyth and I noted that large males h[illegible] disproportionately large jaws, which they were not at all reluctant to use on smal[illegible] rivals, snapping at them as they chased them away from their dung-centered te[illegible]ritories. Large males converted their aggressive advantage into a territorial advan[illegible]tage, which gave them an edge in meeting and courting females.

But not long into our study, we observed large territorial males apparently cour[illegible]ing smaller marked beetles that our records indicated were males, since they ha[illegible] been captured and given their distinctive paint marks after they had copulated wit[illegible] females at other locations on previous days. Hmm. In these cases, the larger male approached the smaller one, which presented the tip of its abdomen, just as a female would. The larger male tapped the smaller male's abdomen, just as if this individual were a female. The smaller male walked forward at intervals, just as if it were an unreceptive female. But we knew that the object of the territorial male's courtship was a male, not a female.

Forsyth and I were delighted at this turn of events because we had found a Darwinian puzzle well worth resolving: Why should smaller males spend time and energy in an apparent attempt to pass as females? The first thing we learned was that female mimics fooled larger, territorial rivals into tolerating their presence, instead of attacking them violently, which is the usual response of territory holders confronted by male opponents. The nonaggressive mimics avoided disputes of this sort and instead took advantage of the territory holders' strong sex drive, which typically ensures that males do not miss chances to court and mate with females, but which on rare occasions can be exploited by rival males that behave like females. While being courted instead of assaulted, these mimics wandered around in another male's territory for some time before the duped male finally "figured out" what was going on and attacked. During this grace period, the mimics sometimes encountered and captured flies, and they even sometimes found true females, which they courted while being courted themselves. On occasion, a female impersonator copulated with the real McCoy while a large territorial male stood patiently behind waiting for an opportunity to resume courting the smaller male [130]. Thus, mimics can derive direct reproductive benefits from their deceptive behavior.

So two very different reproductive tactics coexist in the population of *L. versicolor*

What are the possible developmental (proximate) explanations for this state [illegible]rs? I suspect that most persons hearing about this sort of thing for the first [illegible] would guess that the two kinds of males differ genetically, with different gene-[illegible]nment interactions underlying the development of their different nervous [illegible]ms, which eventually causes the adults to behave differently. One could po[illegible]lly test this proximate hypothesis in many different ways but Forsyth and I [illegible]sed on one key prediction from the genetic differences hypothesis, which is that [illegible] differences between the two types should be stable. In other words, if the mimics [illegible] locked into their role by their heredity, we would expect to see them always [illegible]aving like females and not like territorial males.

In fact, however, at least some males of *L. versicolor* can switch back and forth [illegible]ween these roles with no difficulty, a point that was brought home to me force[illegible]y while watching a large male court a medium-sized one that had adopted the [illegible]male tactic. However, the medium-sized male abruptly abandoned his mimicry [illegible] females when he came across a smaller male while leading the duped larger [illegible]etle on a pseudo-courtship wander. The transformed mimic charged at the [illegible]aller male, snapping at his opponent, forcing him to retreat hastily. But when [illegible] larger male relocated him, the medium-sized beetle resumed his deceptive pat[illegible]rn of female mimicry.

In other words, it is entirely possible, indeed likely, that all the males of this species of staphylinid beetle differ very little in the key genes that affect the de[illegible]elopment of their nervous systems, so that their gene-environment interactions produce much the same neural mechanisms. But included in their armory of neural mechanisms is at least one that makes it possible for individuals to employ different reproductive tactics in different settings. Confronted with a substantially larger territorial rival, smaller males are able to finesse the situation by turning around and providing the signals that trigger courtship as opposed to eliciting a jaw-snapping attack. This tactic may buy the mimic some time at a dung pile where food and mates are relatively abundant, so that he has some chance of acquiring these reproduction-enhancing resources. Were he instead to engage the larger male in combat, odds are that he would immediately be forced to retreat because body size is so important in determining winners and losers in this insect, as it is in most other animals.

In the jargon of sociobiology, the beetle owes its behavioral flexibility to a *conditional strategy*, an inherited neural mechanism that switches on different responses in reaction to different conditions that males are likely to encounter. Up against a big bruiser? Activate the seductive female mimicry response. Run across a little guy? Damn the torpedoes. Full speed ahead. Attack the rival, if he dare stay around. It goes without saying, although I am going to say it, that the rove beetle male need not be consciously aware of its strategic condition-dependent responses. We do not know what, if anything, is going on in the beetle's "mind." It is sufficient that the male beetle possess internal mechanisms that confer a certain amount of flexibility in his responses to rivals.

Note that genes must underlie the behavioral flexibility of *L. versicolor*. Flexible decision making in this beetle and all other adaptable species depends on well-designed neural units, which could not have developed without the key enzymes needed for the chemical assembly of those structures. The critical enzymes require specific genetic information for their production. Of course, the environment is also essential in providing the materials needed for enzyme building and for neuron construction. In addition, certain experiences with rival rove beetles early in a male's adult life could conceivably help refine the development of the neural systems that are the foundation for the male's ability to switch back and forth between hyperaggressive territoriality and nonaggressive female mimicry. But all the raw materials and experiences in the world could have no developmental effect without the kind of genetic information capable of responding to particular chemicals and experiential stimuli.

Having considered the proximate basis for the rove beetle's conditional strategy, what about the ultimate reasons for the spread of the genes in the past that enable today's beetles to develop the key strategic mechanisms? One possibility is that in the past flexible males with their particular genes were up against more rigidly programmed individuals with some different forms of those genes. One can readily imagine that a strategically flexible male capable of female mimicry under some carefully prescribed circumstances might well have done better at leaving descendants than a male committed to a "damn the torpedoes" approach 100 percent of the time. Males that happen to be relatively small (because they were unlucky in finding food when they were larvae) will encounter larger males when they are adults. Smaller individuals that could only attack when a large rival loomed on the horizon might fare more poorly in the mating sweepstakes than genetically different types capable of slipping seductively into the female mimicry mode when facing a particular kind of opponent.

This scenario is testable. If the rove beetle's conditional strategy is an evolved adaptation, then the decisions that individuals make about which tactic to select in response to the conditions they confront should promote their genetic success. In other words, male beetles should adopt the tactic that yields the higher reproductive payoff for a particular set of conditions. If a male is capable of being a *successful* territorial aggressor, then he should exploit that tactic, because successful territory holders mate more often than males that behave in some other manner. Thus, if a female-mimicking male happens to encounter opponents he can defeat (i.e., smaller ones), he ought to switch over quickly to the aggressive role. As noted above, mimics do make this switch, which makes reproductive and evolutionary sense. Males rank their options in accordance with their reproductive payoffs, making the best of a bad situation via the female mimicry tactic, if they have to, but otherwise controlling a mating territory [130].

Conditional strategies are extremely common in the animal kingdom, with the typical pattern being one in which individuals that are competitively disadvantaged for some reason possess the ability to salvage some genetic success by adopting an alternative tactic [94, 160]. Flexibility in decision making, especially when dealing with social competition, is not even remotely the sole province of human beings, despite widespread belief to this effect. Moreover, the beetle example also teaches us that the neural mechanisms underlying behavioral flexibility will spread over evolutionary time only if they generate adaptive consequences. Systems that yielded truly open-ended results in the past must have been reproductively inferior to more tightly designed ones. Think about it. Indiscriminate flexibility for flexibility's sake is not likely to generate genetic payoffs for male rove beetles. Reproductive success for males of *L. versicolor* depends on mechanisms that bias decision-making toward adaptive outcomes. Beetles not predisposed to treat large rivals one way and small rivals another are beetles whose unique genes have disappeared.

The concept of conditional strategies has every bit as much potential utility in helping explain human behavior as it does for beetles, ants, red-winged blackbirds, and Seychelles warblers. Just as is true for ants and warblers, human beings can vary in their behavior even when they share exactly the same hereditary information for brain development. If people have brains equipped with the same conditional strategy, then individuals can make different decisions in response to the special environmental conditions they experience. Remember that when sociobiologists study behavioral variation of this sort, it is to explore the adaptive properties of the conditional strategies involved and not to investigate the operation of brain circuitry or the means by which genes influence brain development.

Consider how sociobiologists deal with one much discussed aspect of our reproductive behavior, namely the willingness of men and women to engage in extra-pair matings (chap. 4). We can safely assume that our male and female ancestors over the past million years or more formed long-term pair bonds in order to rear offspring together. And we can also assume that some members of some pairs had short-term sexual relationships with other individuals as well. Persons unfamiliar with conditional strategy theory might be tempted to treat individuals who focused heavily on long-term pairing and those who favored short-term sex as if they differed in their hereditary makeup. But it is far more likely that selection favored ancestral hominids who happened to possess a conditional strategy with two tactics, the "faithful mate" and the "adulterous mate" options.

Individuals with this conditional strategy could make decisions about whether to pursue short-term matings *in addition to a long-term relationship* based on the nature of their own attributes and the social environment in which they lived. Just as with the Costa Rican rove beetle, we can predict that the flexibility such a strategy conferred on individuals had to have been targeted and judicious in order to have been adaptive. Short-term matings expose the male to attack from the social partners of the women he has inseminated as well as disrupting any mutually advantageous social ties he has established with these men. Moreover, the probability of success in mating with someone else's long-term partner surely varies, depending on such things as the male's appearance and wealth, factors carefully evaluated by modern women willing to engage in short-term sexual relationships [136, 250].

Given these elements, males should possess the kinds of emotional and rational mechanisms that encourage them to attempt extra-pair matings only when the behavior would have increased their genetic success in the ancestral environment of hominids and even today. Because the mix of costs and benefits from attempted adultery will differ among different men, the result should be variation among individuals in their fidelity to a single partner, a variation that need have nothing to do with genetic variation among the men in question and everything to do with the evolved operating rules of their psychological mechanisms (i.e., the male conditional strategy) in relation to their social environment and relative attractiveness [136].

Incidentally, an understanding of the conditional tactics underlying male reproductive behavior would have prevented Natalie Angier from claiming that because the probability of fertilizing an egg is low for any given copulation with any given woman, selection could not favor male promiscuity over male fidelity [19]. Angier notes that a male who copulates with his social partner every night for a month has the same chances of generating an offspring as one who copulates with a different female every night for a month, given the very low probability of conception per copulation. She therefore concludes that in the ancestral environment of humans, faithful males would have left as many descendants as promiscuous ones, so that any distinctive genes promoting the development of promiscuous psychologies could not have spread through ancestral populations. Angier is clearly under the impression than promiscuity and fidelity represent two different strategies, that is, two hereditarily distinct psychological mechanisms such that faithful males in the past were incapable of short-term matings at times when the genetic payoff was likely to be high from such activity. Given that in the environment of our ancestors, "wives" were likely to have been pregnant for much of their adulthood, inflexibly faithful men almost certainly left fewer descendants than *conditionally* faithful men. Men whose wives were pregnant almost certainly could have gained genetic success if they possessed the conditional capacity to engage in highly discrete extra-pair matings with nonpregnant women whose social partners then cared for any offspring arising from these liaisons.

The Evolution of Learning

We can apply the conditional strategy concept to the phenomenon of learning to make the point that learning mechanisms can and indeed must specify the various options that can result from the acquisition of information from experience. In order for an animal to learn something, its brain must be capable of changing as a result of experience, leading to a change in the decisions made by the educated individual. In effect what is required is a conditional strategy, a proximate mechanism, with the capacity to generate decision X under certain conditions or decision Y under different ones. To do so requires a prepared brain.

Thus, for example, the reproductive tactics adopted by men are surely affected by learning in a host of ways: individuals could learn from observation of others or from the traditions of their group about the consequences of ill-considered attempts at adultery, they could learn from the interactions with women about the degree to which they were considered attractive, they could learn from personal experience about which women in their band would be likely to respond to their advances, and so on. In order to assimilate this information and make adaptive use of it, however, men must possess specialized circuitry with all sorts of complex design specifications. Systems of this sort do not arise spontaneously out of the blue; they are the developmental product of what happens when particular genes operate within particular chemical environments. Alter the relevant genes and the developmental patterns will change, affecting the design features of the developing mechanisms. These design features determine how neuronal mechanisms respond to sensory information and then change the way they work so as to generate an adaptive modification of behavior.

We can perhaps better see just how tightly structured learning really is by leaving humans behind for the moment and turning our attention to some of the many creatures other than ourselves that learn from experience. For example, insect-eating birds quickly learn what is tasty and what is not. In some cases, a single unhappy experience, namely, vomiting after ingestion of a brightly colored toxic prey, does the trick with the bird thereafter giving the nauseating species X a wide berth. To learn to avoid all members of species X can happen *if and only if* the educable bird possesses neural mechanisms with special properties. These mechanisms include those cells that provide the punishing sensations associated with nausea and vomiting, while other cells store information about the visual stimuli of food items consumed shortly before the unpleasant experiences occurred. In addition, the bird's brain must be capable of making the association between the digestive distress induced by the food and the control center that regulates feeding responses to potential prey items. When these relationships are in place, the bird can modify its behavior with the happy proximate result that it avoids an additional punishing experience. At the ultimate level, the educated bird reduces its intake of toxic poisonous prey while retaining the useful calories and nutrients already contained in its stomach.

Consider how easy it would be for learning mechanisms to reduce rather than increase a learner's reproductive chances. For example, imagine a bird whose circuitry caused it to avoid members of every caterpillar species, including edible ones, that it had eaten in the fifteen minutes or hour before a single punishing experience with a particular toxic prey item. Or imagine a bird that responded to the experience of vomiting by seeking out more of the toxic prey in question in order to vomit again and again. The caterpillar itself provides nothing that guarantees an adaptive change in the bird's behavior. Therefore, consistently adaptive learned dietary choices must be the product of past selection for those physiological systems that bias, guide, steer, and direct individuals toward learning what is right in terms of individual genetic success. That most learned modifications of behavior are in fact advantageous must reflect the highly engineered design of neurons and their connections. As John Tooby and Leda Cosmides put it, neuronal "designs that produce 'plasticity' can be retained by selection only if they have features that guide behavior into the infinitesimally small regions of relatively successful performance with sufficient frequency" (p. 101 in [314]).

Evidence in support of this claim has been around for decades. For example, in the 1960s and 1970s John Garcia and other psychologists of like mind realized that the ruling behaviorist dogma at the time simply could not account for certain observations [138, 139]. The Skinnerian position, popular at that time, was that any action would become more frequently performed if it were positively reinforced (i.e., rewarded) and less frequently performed if coupled with aversive stimuli (i.e., punished). According to this view, all learning in all species occurred in accordance with this simple and supposedly universal law. However, Garcia devised tests of the "law" that showed its interesting limitations. For example, although white rats, a favorite subject of laboratory psychologists, can be easily conditioned to avoid fluids that are associated with internal distress such as nausea, they cannot learn to avoid the same materials if they are experimentally linked to a shock applied to the animal's skin. Provide a rat with a distinctively flavored liquid and then later, even hours later, expose it to X rays that make the animal sick to its stomach, and it will have nothing to do with the flavored liquid when it encounters it again. Run the procedure with another animal that is shocked shortly after it sips the flavored drink, and the rat simply does not get it. Instead the rat goes back for another drink and is shocked again, only to make the same error again.

Although this odd feature of rat learning puzzled some and irritated others within psychological circles, it delighted persons aware of selectionist theory. White rats are the domesticated relatives of wild Norway rats and they carry the genes of their ancestors in their bodies. In the past these genes helped in the development of learning mechanisms relevant to the real world problems confronted by free-living Norway rats. In the real world, the consumption of liquids and foods does not cause external skin pain but some ingested substances can have damaging *internal* effects. In the past, animals capable of detecting internal damage and linking these cues with foods or fluids recently consumed would have been able to modify their diet adaptively. No such benefit comes from circuitry that enables rats to associate specific foods or fluids with skin pain since ingested substances have no way of acting on external sensors.

The critical idea here is that learning abilities evolve in response to selection acting on individual differences in the ability to solve real world problems, not every conceivable problem. If true, learning abilities should have peculiarities, specializations, and oddities that make adaptive sense once one figures out the evolved purpose of the underlying learning mechanisms. Song learning by small passerine birds offers a superb example of just this kind of system [62].

Adaptive Design in the Song Learning of Songbirds

Many songbirds must learn to sing their species's distinctive song, which is a unique territorial and mate-attracting communication signal (fig. 8.3). Young male white-crowned sparrows, for example, cannot sing the normal complex song of white-crowned sparrows if they have been experimentally reared in acoustical isolation from others of their species. These experimental subjects will eventually produce a song that has only a vague similarity to the typical territorial song of adult male white-crowned sparrows. However, if a researcher plays taped songs of a

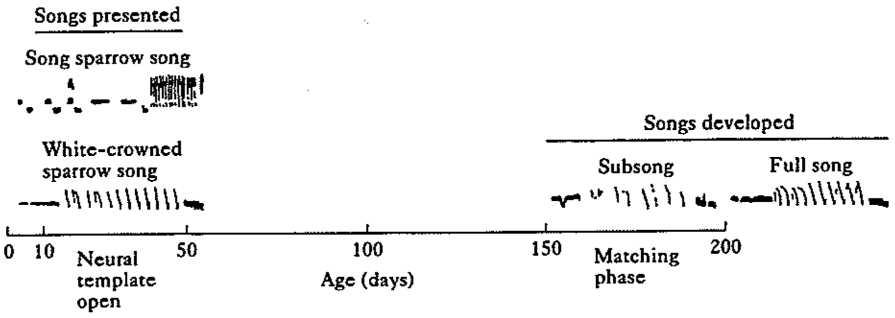

Figure 8.3. Song learning in the white-crowned sparrow. A young bird exposed to the songs of two species between age ten to fifty days will later match the song of its own species, while ignoring that of a different species, the song sparrow. During the matching phase, the young male produces increasingly more complete copies of the tutor white-crown song until it eventually sings a full song that closely resembles that of its tutor. Courtesy of Peter Marler.

white-crowned male to youngsters reared in complete social isolation from other birds, these sparrows will in due course produce a fully elaborated adult song, one that carefully duplicates the song the isolates have heard. Moreover, a young experimental male that is tape-tutored when it is a mere stripling, just ten to fifty days old, will copy and reproduce the song accurately when it is nine or ten months old. Because white-crowned males do not even begin to sing until they are five months old, they clearly can store memories of songs for months before beginning the process of shaping their vocalizations. If the young male cannot hear what it is singing, as a result of being deafened, song development stops in its tracks. The bird has to be able to hear its own song in order to alter it to match the song memories stored in its brain [222, 223].

Now here's another special feature of the song acquisition process, which depends on a neural structure located within the forebrain of the white-crowned sparrow [48]. If you give the ten- to fifty-day-old male white-crown a chance to listen to two tapes, one that plays white-crowned songs and another with the songs of another sparrow, the youngster will only learn the white-crowned sparrow song (fig. 8.3) [222].

Other factors, especially social interactions with adult male companions, also influence song learning in the white-crowned sparrow and other songbirds. If a young white-crowned male is housed experimentally only with a male of another species of sparrow, it may come to sing this species's song [28]. Thus, it is possible to override the predisposition of the young male to learn white-crown song, but only under restrictive experimental conditions that rarely, if ever, occur in nature. Young white-crowns growing up under natural conditions almost always have a chance to hear and interact with members of their own species, and therefore they almost always acquire their own species' song, thanks to the special features of their neuronal song system.

Needless to say, this creative constraint, this learning bias, makes all sorts of adaptive sense because white-crowned sparrows that sang another sparrow's song would often fail to defend their territories effectively against rival white-crowns and they would also fail to attract females of their species. At best, a white-crown that sang the wrong species song might acquire a mate of the other species, but their hybrid offspring would almost certainly operate under a huge handicap, developing many compromised hybrid abilities unlikely to be as good as the attributes of either parent. To avoid this outcome, white-crowned sparrows have brain components dedicated to the task of detecting and storing a very specific kind of acoustic information, holding the information until the young male can match his own song output with his memory of the sounds produced by his natural tutors.

The high degree of specificity exhibited by the white-crown's song-learning mechanism is not unique to these birds. For example, the zebra finch, another small songbird, possesses a special song memory system designed to provide the adult bird, not the juvenile, with a special learning ability relevant for the adult phase of life, namely, the ability to tell the difference between songs it has heard before and those it has not [68]. This ability is valuable because in the real world, zebra finches interact repeatedly with several neighboring zebra finches, male and female, each one of which produces calls and songs that can be recognized as different, provided one has the neural equipment to do so. A zebra finch able to distinguish between familiar and unfamiliar individuals by their songs can presumably make a host of adaptive decisions more efficiently than one unable to do so. Thus, a male that recognizes a familiar territorial neighbor need not challenge him at their territorial border, after having already reached an accommodation with him over the nature of their respective properties. In contrast, a newly arrived intruder represents a different kind of challenge for which a more aggressive response is adaptive.

The learned ability to differentiate between old neighbor and newcomer involves the caudomedial neostriatum in the finch brain. Cells in this well-defined structural unit of the forebrain fire frequently the first time a novel zebra finch song is played, but as the song is played again and again, the response amplitude of these cells steadily falls (fig. 8.4). The learned *habituation* to familiar songs is highly persistent, so that even after having been exposed to a long series of novel songs (eight in the experiment shown in fig. 8.4), the key brain cells remain relatively unresponsive when the first song type in the series is played back to them again. In contrast, any novel song will activate cells in the memory banks, providing a physiological foundation for the bird's ability to discriminate between new and familiar songs.

This reproductively relevant learning ability has additional design features that illustrate its naturally selected history [68]. The system works best with zebra finch song and calls. The bird can hear all sorts of sounds and the memory bank habituates to repeated presentation of a spoken phrase or a recording of another bird species' song. But habituation to these non–zebra finch sounds lasts for a shorter period than habituation to familiar zebra finch song stimuli. Which is exactly what one would predict if the caudomedial neostriatum has been shaped by natural selection to do something reproductively useful for zebra finches. Zebra finches are not in competition to see who can remember the largest number of previously heard sounds; they are in competition to see who can interact most effectively with their fellow zebra finches, the better to leave copies of their genes to subsequent generations. Learning that is biased toward zebra finch sounds will have a far greater impact on the social and genetic success of zebra finches than an all-purpose memory system that gives equal weight to the sounds associated with human speech, zebra finch songs, or any other bird song.

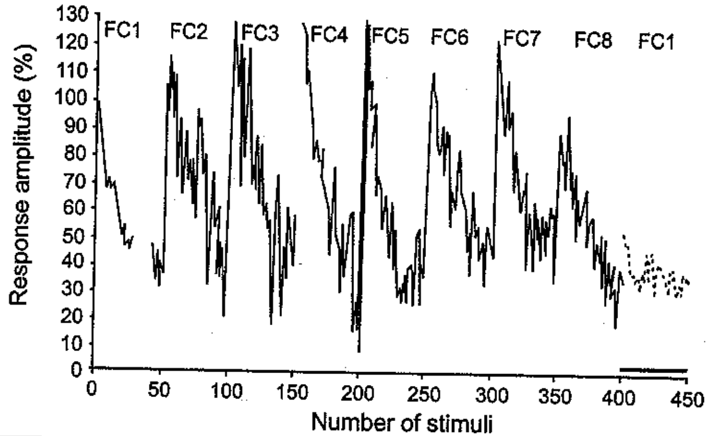

Figure 8.4. Sophisticated learned habituation of zebra finches to familiar calls of particular individuals appears to be based on the response of neurons in one region of the bird's brain. Here are the changes in responsiveness in one individual's brain cells to repeated playbacks of eight different calls presented in sequence (labeled FC1 through FC 8). After completing the sequence, the first call type (FC1) was played again. The bird's neurons responded at a very low level, demonstrating recognition of a stimulus to which the bird had been previously exposed. From [68].

The Adaptive Design of Human Learning Mechanisms

The same kind of specialized design must also be true for the neural systems that make learning possible in the human species. Humans are merely one of many animal species with exceedingly complex brains composed of many functional units, rather like the song system of birds, which are designed to do some things more easily and efficiently than others. Few people dispute this point when it comes to the sensory capabilities of animals, ourselves included. We all know that the family dog can detect a host of olfactory stimuli that are lost on us. Likewise, we do not detect every possible acoustical stimulus in our environment because our auditory system has been designed by natural selection to focus on stimuli of biological relevance for us. Sounds above 20,000 hertz convey little information of significance to us and we cannot hear them. The same stimuli are hugely important to the little brown bat, which employs ultrasonic calls to locate prey, and its auditory system is correspondingly sensitive to ultrasound. In addition, ultraviolet radiation and polarized light make no impression on our visual system, yet many other animals, such as honey bees, have evolved visual mechanisms that enable them to respond to these sensory cues because of their informational value to them as navigational and foraging guides.

All the perceptual equipment with which we are endowed comes with sensible restrictions and special design features. For example, the taste receptors most sensitive to potentially toxic substances are concentrated near the back of the tongue; when these "bitter" receptors are sufficiently stimulated, a gag reflex is automatically activated, the better to prevent us from swallowing even marginally toxic foods. And neurons in the retina of the vertebrate eye actually anticipate the path taken by moving objects in the visual field, with certain cells firing *before* stimulation from the moving object reaches them [37]. In this way, the anticipatory retinal cells eliminate the inevitable neuronal processing delays that occur as signals are sent and processed throughout the visual system. If not eliminated, these delays would cause individuals to perceive rapidly traveling objects in places where they weren't, not an ideal arrangement for those who wished to sidestep an onrushing predator or strike a fleeing rabbit with a stone.

There are no blank slate theorists when it comes to sensory perception because it is so obvious that human sensory mechanisms, like those of all other animal species, are specialized, biased, and focused for perfectly good adaptive reasons. These mechanisms help us make informed decisions by providing us with the kinds of information needed to do useful things. But when it comes to our learning mechanisms, the lesson of perception is forgotten by the critics of sociobiology who argue that the batteries of nerve cells contributing to our learned responses are equally susceptible to all potential learning experiences. In contrast, an evolutionary perspective suggests that the neural subsystems that control the way in which we learn are no more likely to be truly open-ended than our visual or auditory abilities. Instead, an evolved learning mechanism ought to make it more likely that we will change our behavior in particular (adaptive) ways in response to specific (biologically relevant) experiences. These experiences provide the information needed if an improvement in behavioral response is to occur, as opposed to a random change or one that usually reduces the individual's behavioral effectiveness.

The channeled nature of learning is nowhere more apparent than in the ability of speechless infants to acquire a language, an obviously plastic trait that nevertheless is utterly dependent on neuronal mechanisms with well-defined properties. In fact, language learning by babies requires an entire battery of marvelously specialized devices. For example, units in the brain must filter the acoustical information in the infant's environment, retaining information relevant to speech sounds while discarding the rest (with respect to language formation). In addition, auditory systems enable babies to recognize what sounds constitute words in the string of sounds that make up each spoken phrase or sentence. Infants create memories of the relevant word sounds, listen carefully to their own initial babblings, compare their output with the memories of speech that they have acquired, try to produce good matches, associate word sounds with objects and verbs, derive abstract grammatical rules from the speech of others, take pleasure from effective communication with others, build up vast vocabularies (a task that begins even before they can speak or understand words [179]), generate entirely novel word sequences that make sense to others, and so on and on.

All of this happens because the juvenile human brain is capable of processing acoustical input in a very special manner. Some perceptual components of a "language acquisition system" do occur in other primates that are incapable of speech, as demonstrated by the tendency of cotton-top tamarin monkeys to turn toward the speaker upon hearing sentences spoken in Japanese after the monkeys had become used to hearing sentences spoken in Dutch [263]. Interestingly, the cotton-tops do not turn toward the speaker when tapes of these same sentences are played backward, just as preverbal human infants apparently can only tell there is a language difference if the tapes are played forward. Thus, the origin of certain perceptual systems now utilized in speech acquisition long antedates the evolution of languages, but even so, only our species has the structured ability to integrate an entire battery of perceptual and vocal mechanisms in the service of acquiring and then producing a spoken language. This adaptive outcome arises only because of the way in which the underlying brain mechanisms work together. As J. R. Saffran and colleagues put it, "Linguistic structure cannot be learned through undirected analyses of input sentences, no matter how complex or numerous these analyses may be" (p. 1181 in [273]). The infant's brain analyzes what it hears in a highly directed, as opposed to undirected, fashion and thereby derives basic rules of speech organization from sounds generated by persons around it. Seven-month-old infants habituated to sounds repeated in the pattern ABA (e.g., *la ni la*) show little interest in this familiar pattern even when new "words" are substituted for the training sequence (e.g., *da ko da*) but pay attention again if the pattern changes from ABA to ABB (as in, *ni la la*, or *ko da da*) [219]. This directed attentional system surely reflects the effects of past selection acting on the underlying genetic, developmental, and neuronal mechanisms needed to absorb the rhythm of speech. The special products of selection are a tiny subset of all those that are conceivable, yet they make it possible for three-year-olds everywhere to use and comprehend spoken language.

The sophistication and careful design of our language-learning mechanisms can be illustrated by a look at another of the many developmental features involved in language acquisition. When human infants enter this world, they are born with the auditory capacity to discriminate between the complete battery of phonetic units of human speech, such as "da" versus "ba," including some word sounds that are *not* utilized by *every* language. For example, very young infants can tell the difference between different vowel sounds that are produced only by English-speaking and only by Swedish-speaking individuals, respectively. (Babies reveal that they have detected a difference when they increase the rate at which they suck on a pacifier upon exposure to acoustical stimuli that seem novel to them.)

But the infant's perception of the building blocks of language changes as a result of exposure to one language or another [194]. A child reared in an English-speaking household will at six months of age lump together slight variants of the basic phonemes that are characteristic of the English language (fig. 8.5). As a result, a sound that is actually structurally more similar to a vowel sound found in the Swedish language will be perceived by the now experienced infant as a familiar vowel in his native language. Remember that this capacity to generalize, that is, to lump together similar sounds into a shared distinctive category, takes place long before the infant can understand speech, let alone produce it.

What is the significance of this finding? The ability to categorize the acoustical stimuli provided by speakers into a complex set of word sounds must help the infant understand the meaning of spoken words when the child begins this task at about nine or ten months of age. The baby will be listening to a variety of speakers who will inevitably differ somewhat in the acoustical structure of the words they produce. But the listening child will be able to categorize the speech sounds in a manner appropriate for the language of its culture instead of making fine-scale discriminations between all possible speech sounds, which could actually hinder the eventual comprehension and production of one language in particular.

Second, the adaptive outcome of the process rests upon a highly nonrandom form of learning. The child's brain has the special ability to blur acoustical discriminations in light of the experience provided by listening to a spoken language. Alterations in the phonetic perception of infants could not occur without corresponding changes in neural biochemistry and function; the ability to make the "right" changes requires that the cells "anticipate" the relevant environmental cues, namely those sounds that are the building blocks for words that vary somewhat from speaker to speaker of a given language. Which is to say that learning to speak requires an innate, well-designed capacity for specific kinds of neural changes.

The existence of specialized circuitry that steers language acquisition in a particular direction is revealed in many ways, including the similarities that exist among all or most languages. For example, cross-linguistic analysis has shown that the grammatical category of those words labeled "adverbs" has the same standard relationship to other key elements of sentences in dozens of very different languages [69]. Likewise, the fact that "creole" languages converge on a similar, complex grammatical structure supports the hypothesis that the brain is prepared to learn language in a particular way, thanks to its evolved properties. Incidentally, creole languages are novel derivations based on elementary pidgins, which are employed for occasional and rudimentary communication between persons speaking two different languages; when many individuals begin to use pidgin English, pidgin Spanish, or pidgin Portuguese as their primary language for all social circumstances, they elaborate and modify it in generally similar ways no matter what the ethnic or linguistic origins of their parents [105]. The fundamental point is that learning a language is far too important for human social and genetic success to be left in the hands of an all-purpose learning device.

The many neuronal units that make language learning all but unavoidable are

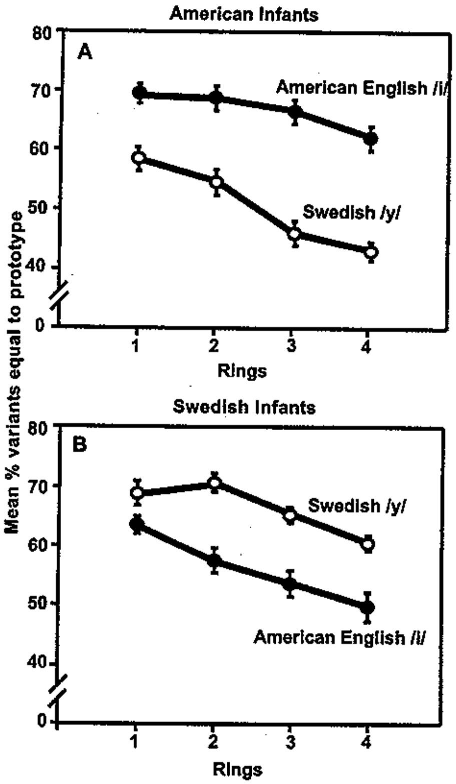

Figure 8.5. Sound classification in human infants changes as a result of listening to a particular language in the first months of life. (Above) When exposed to four categories ("rings") of artificial variant sounds increasingly unlike the American English vowel /i/, infants with several months' experience listening to American English usually reacted just as they did upon hearing the prototypical vowel. They were significantly more likely to respond differently to sound variants of the unfamiliar Swedish vowel /y/ compared to their response to the prototype's sound. (Below) The situation was exactly reversed for infants experienced in listening to Swedish, who tended to respond the same to sounds roughly similar to the prototypical Swedish /y/ vowel sound as they did to the prototype itself. These infants were more likely to react differently to sounds similar to the American English vowel /I/ as compared to the prototype. From [194].

merely part of much larger arsenal of learning mechanisms, each with its own distinctive developmental history and its own distinctive functional significance. Language is just one of the tools that humans possess to facilitate social interactions. In addition, our social effectiveness depends on learning to anticipate what others will do in certain situations, an ability that should also require special psychological mechanisms that steer us toward the most adaptive manifestations of this form of plasticity. If so, we can predict that we must possess a mechanism that directs our attention to what others are doing, the better to guess their intentions so that we can cooperate efficiently with helpful companions or thwart opponents by beating them to the punch.

Evidence that such mechanisms exist comes from several sources. For one thing, brain imaging studies reveal that when volunteer subjects are asked to infer the intentions of others as described in stories or shown in pictures, certain well-defined regions of the brain consistently "light up," including components of the posterior superior temporal sulcus. Moreover, single neurons from this part of the brain become especially active when the subject views another person or part of a person moving, a response that provides the brain with information about the actions of others [133].

Another line of evidence on the existence of a neuronal system dedicated to the analysis of the social goals of others comes from studies of infants. Some researchers have taken advantage of the fact that when people, babies included, are visually interested in something, they spend more time looking at the favored object or action than at alternatives. Therefore, by analyzing the gaze of infants, researchers can determine whether they are predisposed to take an interest specifically in the goal-oriented actions of others. Indeed, babies just nine months old spend more time observing an adult's hand as it moves toward and grasps a toy than they do when the human arm and hand moves in precisely the same path but does not take the toy. Likewise, a hand that reaches for and takes a toy stimulates more attention than a mechanical arm and claw that performs the same toy-grabbing action [349]. As Amanda Woodward points out, even at this early age, the infant's brain is preprogrammed to try to make sense of the intentions of other people. A baby could not learn social intent as effectively if it were equally interested, or equally uninterested, in all possible visual stimuli in its environment.

Selection and Remembering Faces

Another example of social learning that is dependent upon a "prepared" brain is provided by our ability to recognize faces, a skill we are so good at that we take it for granted. Nonetheless, face recognition is an astonishing human attribute [61]. We can make accurate identifications of familiar faces very rapidly; a half second will do. If we are given a pack of fifty photographs of faces we have not seen previously and are permitted to examine each photograph for just five seconds, we will later be able to pick out 90 percent or more of these faces from a large photo collection in which some previously observed images are intermingled with those of novel faces.

The development of this skill almost certainly has something to do with the young infant's drive to examine the visual stimuli associated specifically with faces. Babies are more likely to look at a moving schematic face in its normal position (eyes above mouth) as opposed to the identical image upside down [61]. Here then is another attentional bias and perceptual preference of infants that directs a flow of socially relevant information to regions of the developing brain designed to accommodate the input. These mechanisms nearly guarantee that the brain gathers inputs relevant to learning faces, making us all expert at this socially relevant task.

Evidence for the existence of specialized circuitry devoted primarily to face recognition comes from a variety of sources, but of special interest are those rare instances of brain trauma that eliminate a person's capacity to put identities with faces [118]. The most revealing cases involve people who have retained their intellect, can see perfectly well, and are able to identify objects without difficulty, but they draw a blank with human faces, even those of friends and family, even their own facial image [100]. (There are also some persons who have lost the ability to name objects—except for faces [237].) For persons with the face recognition deficit, training generally fails to restore the individual's capacity to recognize human faces. However, in at least one case a person with this disorder could identify individual sheep in his flock from their photographs [231].

In addition, injury-induced learning deficits with respect to faces include some types that do not involve failure to discriminate between familiar and unfamiliar faces. One of the most curious of these more subtle face recognition errors is exhibited by persons with Capgras syndrome [165]. The syndrome is characterized by the delusion that persons well known to the observer are actually impostors, doubles that are passing as familiar individuals. For example, a Brazilian man who had been in a coma after a car accident but who subsequently recovered and exhibited normal intelligence, said of his father, "He looks exactly like my father but he really isn't. He's a nice guy, but he isn't my father, Doctor." This same patient, upon viewing a series of photographs of the same woman's face shown gazing in different directions, concluded that these were "different women who looked just like each other."

The researchers working with this person suggest that his delusions were created because of a disconnect of some sort between the face recognition mechanisms in his visual cortex and his amygdala. Each time the patient met his father or was shown a different photograph of the same woman, he had no trouble perceiving the facial similarities in the visual stimuli confronting him. But these stimuli evidently failed to arouse the emotional sensations of familiarity, which would normally have been generated by neural activity in the amygdala, a structure in the brain that assigns emotional significance to particular faces [5]. When you and I see a parent, an offspring, or any other familiar person, our brains automatically endow this individual with an emotional aura of some sort, which then prompts the brain's memory management systems (some of which may be located in the frontal cortex) to open up a previously established "file" for this person.

But if the visual cortex-amygdala links have been disrupted, then every time a patient with Capgras syndrome sees a familiar individual, his or her brain permits the recognition of stimulus similarity but not the emotional context needed to access the existing file on that person. Instead, the brain opens a new file, producing the sensation that this individual is different from all others in the memory banks, despite his or her close physical resemblance to persons that the patient has met previously.

This example shows that what we learn and how we learn it are utterly dependent upon the neural arrangement of our brains. Change (or damage) the amygdala or the ventromedial frontal cortex even slightly and things can go very wrong [4]. The existence of one neuronal system dedicated to the recognition of familiar faces and an allied unit that stores information on the emotional associations linked with particular visual facial images ought to make us skeptical that we have *any* truly undifferentiated learning mechanisms. Indeed, we have every reason to believe on theoretical grounds alone that a structured, task-oriented batch of neurons must contribute more to the genetic success of individuals than an amorphous, generalized system of equal size. Humans confront a large number of reasonably predictable tasks of biological significance. Recognizing the faces of our companions and feeling friendly toward some, less so toward others, ought to promote success in the environment of our species, which has a predictable social component with the great potential for productive cooperation among friends but not with strangers or enemies.

In addition, on empirical grounds, the more that is learned about the brain, the more detailed we can be about the location of units dedicated to particular functions. Technological advances now permit neurologists to record the site of brain activity in fully conscious, naturally behaving "subjects." Experiments of this sort reveal that information about faces is processed in a distinctive part of the visual cortex called the fusiform face area [181], which becomes active when persons are confronted with images of faces, especially unfamiliar ones (fig. 8.6). The same region can be employed for other tasks, such as bird or car identification by persons who choose to train themselves to be dedicated bird or car watchers, but these unusual abilities exploit a special neural substrate that almost certainly evolved for other reasons [140]. Almost everyone is a face identification expert, whereas only a tiny minority are truly proficient at bird identification.

Likewise, the ability to use a mental map demands its own specially designed brain units, as demonstrated by researchers who monitored brain activity in persons navigating their way on computer through a virtual reality town. This study re-

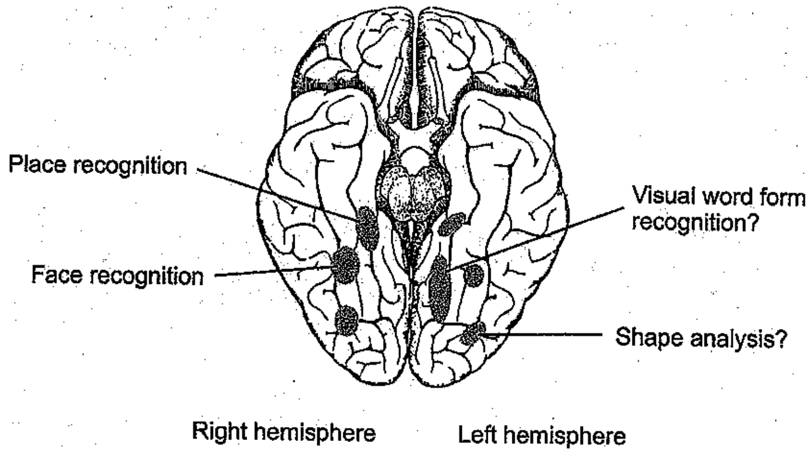

Figure 8.6. The human brain consistently analyzes different categories of visual stimuli in different parts of the visual cortex. Thus, when people observe faces, a particular region is invariably activated when the visual information provided by certain places stimulates different batteries of neurons. From [18].

vealed that the right hippocampus is hard at work when someone knows where different places are in town and can navigate from A to B accurately. The right caudate nucleus has another role to play, one that affects the speed with which the navigator gets from A to B, while still other brain regions facilitate navigation in other ways [212]. To the extent that you and I can learn faces or to find our way around in familiar terrain or imagine what is going on in someone else's mind [133], we can thank not just any old brain cells but particular subsystems of nerve cells in the brain whose role in our lives is to promote adaptively relevant learning.

The simple point is that our brain is not a bowl of porridge. Instead, this organ possesses great structural specificity both in terms of its gross anatomy as well as with respect to its individual cells. To think that such a complex and intricate piece of machinery would provide us with an undifferentiated ability to learn all things with equal ease not only fails the plausibility test but also fails to jibe with the available evidence. What we know about human learning mechanisms indicates that they are biased in reproductively significant ways, just as is true for all other animal species.

Learning, Cultural Change, and Genetic Success

"Okay," you may be saying, "but how can one talk about evolved specializations when our brains have permitted us to acquire a host of cultural innovations that

superficially at least appear to have nothing to do with whatever it w supposedly evolved brain was selected to accomplish? It is only in th ew thousand years that people have begun to write and read, extraordinary abilities indeed. We build and fly airplanes, we operate computers, we launch cruise missiles, some of us wear high heels, others don three-piece Brooks Brothers suits. We do so many things that even our relatively recent ancestors did not do, let alone our Pleistocene ancestors. Surely this tells us that with the advent of culture, we shed whatever limitations our evolutionary history imposed on our precultural ancestors."

However, it is one thing to note that cultures change rapidly, and another to argue that the nature of the changes means that cultural characteristics are essentially arbitrary. If cultures exist because of the evolved psychological systems of human beings, then human brains ought to be home to a bevy of adaptive conditional strategies, which in turn means that some cultural innovations are far more likely to have psychological appeal than others, particularly innovations that enhance our control of resources, our looks, and our status, as well as improving our capacity to manipulate others. To the extent that the past history of brain evolution shapes the evolution of cultures, the traditions that people favor ought to have some connection with overcoming obstacles to achieving the same proximate goals that motivated people in the past, such as the satisfaction of sexual desires and the formation of friendly alliances with others. To the extent that people achieve those proximate ends, they ought to also, albeit invariably unwittingly, increase the odds of transmitting their special genes to the next generation, at least if the environment of the altered culture bears moderate resemblance to the environments of our distant ancestors.

Some recent changes, however, such as the greatly increased density of humans, the development of agriculture and modern industry, and assorted technological advances may have so altered the human environment as to remove the link between achieving one's proximate goals and increasing one's genetic success (see below). Many evolved conditional strategies, including our battery of specialized learning mechanisms, can be exploited or coopted to some extent by novel innovations (just as the fusiform face area can be used by a dedicated bird-watcher to store information on the difference between the white-crowned sparrow and the golden-crowned sparrow). The result might sometimes be the production of novel maladaptive behaviors in highly altered environments. But even documented cases of this sort cannot be considered totally arbitrary products of an independent cultural entity if it can be shown that they arise as the *predictable* result of an interaction between psychological mechanisms that evolved for other purposes but that are now employed for novel ends in novel circumstances.

Thus, a large gulf separates what might be called "arbitrary culture" theory from the sociobiological theory of culture. For arbitrary culture theorists, innovations are the largely inexplicable inventions of human imagination that somehow become established as a cultural tradition, thereafter to be inscribed on the blank-slate brains of immature humans exposed to a given culture. For the sociobiologist, in contrast, understanding cultural innovation and change requires a search for the predicted underlying evolved conditional strategies that provide the proximate foundation for development and acceptance of a novel practice. And the really interesting cases are those Darwinian puzzles in which human cultures encourage people to behave in an apparently maladaptive fashion, which ought to lead to the eventual extinction of the maladaptive trait.

So let us apply the sociobiological approach to some recent cultural phenomena, starting with writing and reading. Here the evolved proximate foundation for the invention of written language and its use certainly involves the language centers of the brain and the brain's capacity for symbolic thinking. In addition, our skill in differentiating among written symbols depends on elements of our highly evolved visual system, which makes it possible for us to tell the difference between many very similar stimuli, the better to determine what is in our environment. Along these lines, I wonder if the visual analysis of hand gestures, which carry symbolic information, might also have provided a piece of the evolved foundation for analyzing written language symbols, given that sign language may have preceded spoken language in human evolution [73]. In all cultures, people employ gestures when speaking; even those who are blind and have been so since birth use their hands when they talk, demonstrating the close relationship between spoken and visual channels of communication in our species [171]. This relationship may have been tapped by the persons who invented writing.

And once invented, what contributed to the persistence of writing and reading? The primary function of the first written texts, which were Sumerian cuneiform tablets produced about 5,000 years ago, was to record economic information, such as data about the exchanges of goods between individuals [276]. Denise Schmandt-Besserat makes a persuasive case that the invention of small clay tokens of various shapes, at first plain, later incised, and later still impressed into clay containers and tablets, led to the eventual development of symbolic texts. The tokens represented quantities of cereal grains or livestock, enabling individuals to count material goods, the better to control their distribution. Given the importance of resource control for social status, political power, and ultimately reproductive success, it is only mildly speculative to suggest that the first token users, and later the first cuneiform writers and those who employed them, derived material benefits from their inventions, which may well have translated into reproductive gains for these persons at this time. As Schmandt-Besserat points out, "The fact that tokens occur only in rare occasions in [burials], and only in graves of prestigious individuals, points to their economic significance" (p. 36 in [276]). The early token users and writers (and their employers) need not have noticed the connection between wealth and reproductive

success; it was enough that they were motivated to seek wealth and could understand the economic value of accounting for goods they managed to accumulate.

One need not be a sociobiologist to guess why people everywhere are highly adept at figuring out which actions have rewarding economic payoffs. Surely it is no accident that cultures offer different but useful traditions, tailored to local conditions, that enable people to overcome obstacles associated with securing critical resources. For example, the hunting technology and knowledge of local natural history passed down across generations of Inuit and Bushmen are highly dissimilar but these cultural traditions obviously help hunters and gatherers acquire food in the high Arctic and the Kalahari Desert, respectively. Likewise, traditional agricultural groups in different parts of the world have transmitted different knowledge to their descendants but the particular plants grown and special techniques employed in a given region were clearly designed to increase the calories and nutrients available to the families of those persons doing the farming.

But the interesting problems for evolutionary analysis do not come from the kinds of traditions that promote obviously useful behavior in terms of survival and reproduction. The worthy challenges come from cultural practices that appear to vary arbitrarily from place to place and that lead people to do things that seem to reduce their fitness, rather than increase it. A case in point is the use of spices in food preparation. The spicy plant products that appear in traditional cuisines vary dramatically from culture to culture. And within historical times, major changes have occurred in the availability and desirability of certain spices as societies were exposed to the cultural practices of other groups. Thus, one could easily conclude that spice traditions are arbitrary matters that represent the more or less accidental result of untrammeled human imaginations at work in different parts of the globe.

But maybe not. The fact that many people have gone to considerable trouble and substantial expense to acquire even small amounts of certain spices suggested to Jennifer Billing and Paul Sherman that they had a Darwinian puzzle to explore [40]. Europeans in the Middle Ages paid extraordinary amounts for pepper, nutmeg, cloves, and the like, so much so that peppercorns were accepted as currency in England, where they could be used to pay rents and taxes. The Countess of Leicester did not flinch at the price of ten to twelve shillings for a pound of cloves in 1265, even though she could have purchased a cow for less [262]. Why pay so much for something that offers so little in the way of calories and nutrients? Remember that answers such as "people like the taste of spices"or "people use cloves because they are influenced by cultural tradition" are proximate explanations, which leave untouched the evolutionary basis for human taste perceptions or the capacity for cultural indoctrination.

After ruling out the possibility that spice use varies only because different parts of the world produce different spices, Billing and Sherman focused primarily on one ultimate explanation, which they termed the antimicrobial hypothesis, namely that spices are added to foods to make them safer to eat by destroying the bacteria and fungi that can make food inedible or poisonous. It is well known that many plants produce so-called secondary compounds as defense mechanisms against certain bacteria, fungi, or herbivores, which would otherwise consume the plant. Perhaps humans use certain plants in order to exploit their secondary chemicals to combat food-spoiling microorganisms. This hypothesis leads to the prediction that spices will indeed contain chemicals with antimicrobial action, which proves to be generally true. Nutmeg, for example, kills or blocks the growth of about half of the twenty-five species of bacteria with which it has been tested to date. And nutmeg is actually one of the least active spices in terms of bacterial inhibition with garlic, onion, cinnamon, allspice, and oregano blocking the growth of all of the admittedly relatively few bacterial species with which they have been tested.

In addition, the antimicrobial hypothesis can be checked by taking advantage of the cross-cultural diversity in the uses of spices. If it is true that spices serve an antibacterial function, then the fitness benefits of spice use will vary depending upon the risk that available foods will be contaminated by bacteria. This risk in turn is largely a function of climate. In tropical regions where temperatures are higher, rapid bacterial growth is more likely, and therefore the functional value of spices should be greater. Based on this premise, Billing and Sherman produced an array of predictions about the relationship between a country's mean annual temperature and the local culture's use of spices. They expected that the higher the mean temperature, (1) the greater the proportion of recipes calling for spice use in traditional cookbooks (which feature a culture's distinctive cuisine), (2) the greater the number of spices required per recipe, (3) the greater the total number of spices used overall, and (4) the greater the likelihood that the most potent antibacterial spices would be used. Billing and Sherman tracked down at least one traditional cookbook for thirty-six countries ranging from Norway to Indonesia and examined 4,241 meat-based recipes. The data taken from these sources supported all four predictions. So, for example, the highly antimicrobial chiles, garlic, and onion are far more likely to appear in meals prepared in hot tropical cultures than in cool, temperate countries (fig. 8.7).

The story is far from complete; it would be good, for example, to have data on the efficacy of the various spices in combating bacteria in cooked foods themselves rather than relying on the often limited data derived from exposing bacterial colonies to solutions of different spices [230]. But Billing and Sherman have demonstrated why evolutionary biologists do not throw in the towel when it comes to culturally variable traits. Indeed, Billing and Sherman are not the only persons who have checked evolutionary hypotheses on dietary additives. For example, Timothy Johns and his coworkers have examined why the Maasai and Batemi of East Africa add certain plant products to the milk they drink. Members of these traditional herding societies rely very heavily on milk and other fatty products of the cattle they manage, and so they survive on diets with exceptional levels of animal fats and cholesterol. Johns and his colleagues predicted that the plant additives consumed by the Maasai and Batemi would therefore be high in saponins and phenolics, which are known to have antioxidant properties and the capacity to lower cholesterol levels in the blood. In fact, about 80 percent of the plant additives traditionally employed by these peoples contained saponins or phenolics, supporting the hypothesis that the food supplements chosen by the Maasai and Batemi have

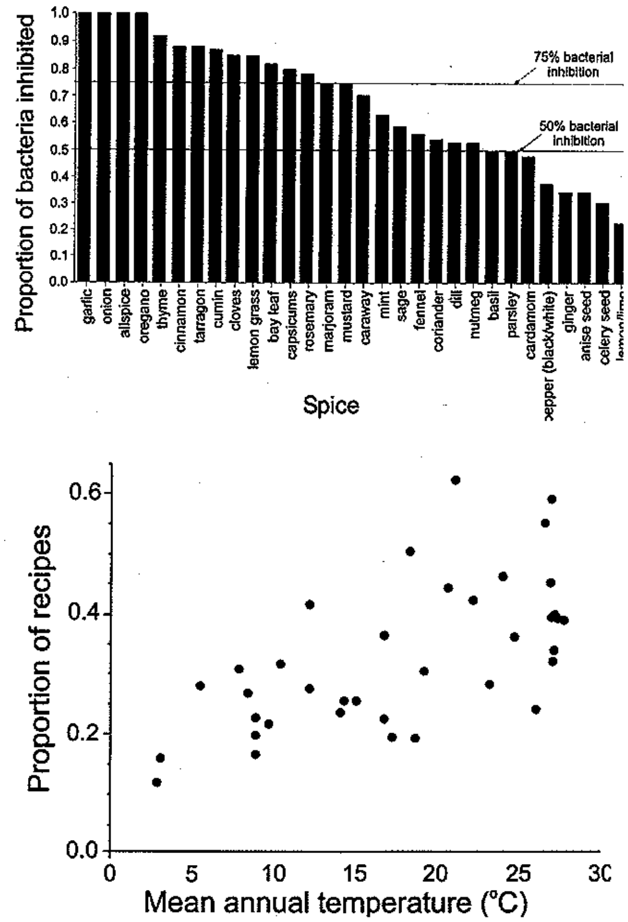

Figure 8.7. (Above) The bacterial inhibitory properties of spices varies but most kill a large proportion of the bacteria they have been tested against. (Below) A strong correlation exists between the mean annual temperature in a country and the proportion of recipes that call for spices that strongly inhibit bacteria. From [40].

alue in fighting the potentially harmful effects of a high cholesterol diet, notably by reducing heart disease [174].

The general point is that differences in cultural practices can arise from culturally universal abilities. In fact, several basic attributes of humans may have "encouraged" people in various societies and different eras to use dietary additives differently but adaptively, including taste perception mechanisms that attach positive value to foods of high nutritional quality and low toxicity, an interest in the medicinal effects of certain foodplants, psychological mechanisms that consciously or unconsciously associate a reduction in food poisoning or gastrointestinal distress or other illnesses with the addition of certain distinctively tasting substances to meals, the predisposition to accept long-standing traditions of one's own culture (such traditions are likely to have long-established positive functional consequences), and the willingness to adopt novel practices that are well established in other cultural groups (i.e., traits that have been thoroughly tested by these other peoples), especially if they have been adopted by individuals of high status within one's own group (since adoption of such practices may raise one's own social standing).

If we take the spice example seriously, we may be less eager to accept the view that cultural practices are whimsical, arbitrary novelties made strictly for the sake of inventiveness, without at least first attempting to test the alternative hypothesis that a given practice has or recently had positive effects on the genetic success of its practitioners. To the extent that a culturally promoted activity has adaptive value, natural selection will favor the maintenance of the underlying genetic, developmental, and psychological mechanisms that help individuals do what is right for their genes, whatever these mechanisms may be.

Sociobiology and Apparently Maladaptive Behavior

The effect of inheriting naturally selected proximate mechanisms ought to make individuals behave in ways that generally advance their genetic success. Contrary to this Darwinian expectation, however, some humans do things that appear to *reduce* their fitness. For example, some people are willing to help others despite the fact that they are unlikely to receive any payback from those they help. Thus, the charity of Mother Theresa, the donations made by many to the Salvation Army, the chastity of the parish priest who dedicates his life to others, the vasectomy that Tom had recently because he said he wanted to help prevent world overpopulation, and so on. Actions of this sort, which fall into the category of seemingly unreciprocated cooperation, are among the most difficult to explain in sociobiological terms, much more so than examples of mutual cooperation, in which individuals reap benefits through their combined endeavors, *or* reciprocity, in which helpers are eventually repaid by those whom they have assisted.

However, before we embrace the conclusion that acts of charity are i
in evolutionary terms, it would be wise to consider ultimate hypotheses based on the notion that hidden benefits accrue to the altruist. One explanation of this sort was developed independently by two prominent sociobiologists, Robert Trivers [320] and Richard Alexander [15], both of whom were attracted to the puzzle of unreciprocated charity precisely because it is a hard nut to crack. Their argument was that any evolved tendencies for unrepaid do-goodery might have positive fitness consequences for the do-gooders, if their kind acts were observed by others and if the observers therefore felt more inclined to join the do-gooders later on in mutually advantageous cooperative or reciprocal endeavors. According to this view, one way to build a positive reputation, and thereby attract the assistance of third parties, is to engage in small but highly visible acts of "selfless" charity.

When some persons encounter the idea that charitable individuals may actually gain genetic success from their actions, even those that seem utterly free of self-interest, they may react with the same dismay as the anthropologist William Arens who writes, "Acts of 'altruism,' commonly viewed by others as indicators of the highest moral intentions of our species, become in the hands of sociobiologists, a mere reproductive strategy" (p. 407 in [25]). However, evolutionary theory demands an analysis of *every* costly attribute in terms of its contribution to genetic success. Sociobiologists are evenhanded in this regard; they examine the full spectrum of behavioral actions in every species to determine whether these traits, helpful or selfish, moral or immoral, are components of "mere" reproductive strategies which can be analyzed in terms of their possible contributions to the genetic success of individuals.

That such an approach bothers Arens and others stems largely from their inability to distinguish between proximate and ultimate explanations of behavior (chap. 1). To say that an act of altruism arises from our proximate capacity for intentional morality in no way eliminates the complementary ultimate explanation that our morally motivated behavior, or the psychological mechanism that underlies the behavior, tends to advance the genetic success of individuals, or did so in environments of the past. To propose that moral behavior is actually *genetically* self-benefiting (an evolutionary hypothesis) as opposed to motivated by the desire to do good (a proximate hypothesis) is confusing only when the listener does not grasp the distinction between the two levels of analysis.

In any event, for the sociobiologist, the issue is to test the indirect reciprocity hypothesis by examining the predictions it generates, such as, people will have an intense interest in the reputations of others, they will be strongly concerned about their own reputation for generosity, individuals will almost always make their small acts of kindness known to others, and acts of charity will typically be of low cost. Modest amounts of evidence exist on these matters; for example, social psychologists have documented the superficial, low-cost nature of purely empathy-driven assistance [239].

A formal test of the hypothesis has been provided by Claus Wedekind and Manfred Milinski, who enlisted seventy-nine Swiss undergraduates to participate in a game of charity [333]. In the game, students were given a starting pot of money (seven Swiss francs) and then permitted to donate either one or two francs to individuals whose record of donations was known to them. The recipients received four francs with each donation from a fellow player, with the researchers adding the extra amount to the one- or two-franc gift supplied by a player. Thus, it was possible for the students to build on their starting amount, provided they attracted the assistance of others.

But players could not simply help others who helped them because the game's design prevented them from knowing if a potential receiver had helped them in an earlier round; they only knew the "charity score" of each recipient, a score that increased by one point when that player gave money to another and decreased by one point if he did not contribute when he had a chance to do so. Players with higher charity scores were more likely to receive donations from other players, whether or not they had helped their helpers before. In other words, persons with an established reputation for generosity did enjoy an economic benefit as a result, thanks to the attentiveness of the players to the social image of others, as predicted by the indirect reciprocity hypothesis. In real life, as opposed to laboratory games, being viewed positively by others could have significant fitness advantages in both the present and past.

The Demographic Transition

The case we have just reviewed tells us again not to jump to conclusions when evaluating human behavior. Actions that superficially seem disadvantageous to individuals may actually contribute to their economic and reproductive welfare. Nevertheless, some behaviors cannot plausibly be interpreted as having positive adaptive value, and sociobiologists regularly acknowledge this point as we have seen in our discussions of pet love and alcoholism. One possible cause of fitness-damaging behavior, like alcoholism, is that the trait occurs more often under novel current conditions than it would in environments of the past. The novel environment hypothesis has been called upon to help explain the current willingness of a great many people to reduce, rather than increase, their production of surviving offspring, a classic example of a maladaptive response. In many parts of the world today, people voluntarily limit the size of their families, despite the fact that they are capable of rearing more children to adulthood. In fact, so many people fall into the subreproductive category as to change the age structure of entire countries. In Europe, the demographic transition began in the late 1800s, resulting in massive declines in fertility in the space of a few decades (fig. 8.8). The drop in the number of babies that couples produced took place at a time when average family wealth was increasing rapidly thanks to industrialization, directly violating the evolutionary expectation that access to increased resources enables parents to produce more offspring, not fewer.

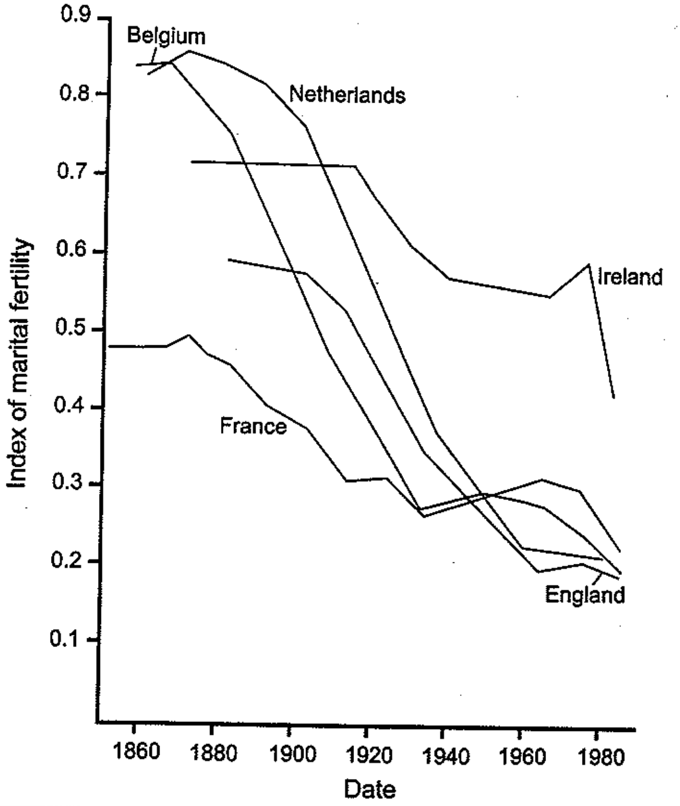

Figure 8.8. The demographic transition in human populations occurred at different times and rates in different European countries, but all have undergone a marked reduction in the fertility of married women. From [70].

More than one observer has argued that the reproductive behavior of people in places where the demographic transition has occurred or is occurring constitutes key evidence against sociobiological analyses. Thus, D. R. Vining states that "social and reproductive success must be positively correlated if sociobiology is to be successful as a general model of modern human populations" (p. 168 in [326]). Given that social and reproductive success are not positively correlated in some modern human populations, Vining and others would have us abandon evolutionary theory when it comes to analyzing our own behavior. Should we take their advice and concede that modern human reproductive activities are purely arbitrary, a phenomenon with only cultural causes?

In a word, no [44, 92]. For starters, even if we were to accept a proximate sociological explanation for reductions in family size, we would still have plenty of ultimate evolutionary questions to answer. Imagine, for example, that the demographic transition gets underway when a certain threshold number of wealthy, influential individuals adopt the "cultural concept" of low fertility, and others then emulate their behavior. What is there about the evolved human brain that made it possible for the first "pioneers" to choose to have fewer offspring than they could support? Why, in evolutionary terms, did others imitate them? Is there something about modern environments that interacts with brain circuitry designed for other conditions that tends to generate maladaptive decisions? Evolutionary theory is far from irrelevant if we really wish to answer these questions.

For example, perhaps the willingness of richer people to have fewer offspring occurs because our evolved brain is operating in a novel environment, one created by the very recent development of powerful birth control technology. We, unlike 99.9 percent of our ancestors, have access to highly effective birth control pills, condoms, diaphragms, and spermicides that permit copulation with greatly reduced likelihood of conception. Under these novel circumstances, many individuals do something that would have been essentially impossible in the past, which is to copulate regularly yet have relatively few babies, and thus experience reduced genetic success. This argument is similar to that used to explain why sea turtles eat plastic bags, which they do even though the plastic often blocks the turtles' digestive tract and leads to their premature death. Clearly the unfortunate turtles that currently consume these objects in their environment are behaving maladaptively, but plastic bags are such a recent novelty that selection has not had time to select for avoidance of these items, which happen to share some stimulus properties in common with the turtle's favored and entirely edible prey, jellyfish.

The evolutionary novelty hypothesis for the demographic transition has to account for why humans often want to use birth control devices, just as we want to know why sea turtles have evolved a neuronal mechanism that causes them to approach and consume plastic bags. One possible argument is that during human evolution, our ancestors were subject to selection that favored those with an interest in controlling the timing of the production of the first child and the duration of the interval between births. These variables have a profound effect on the total lifetime reproductive success of parents; for example, women who gave birth to children before having secured paternal support almost certainly had fewer *surviving* offspring than those who had a partner committed to parental assistance before the first baby arrived on the scene. If past selection has shaped the evolution of the human brain so that it possesses attentional, motivational, and learning mechanisms focused on reproductive control, then these systems could be partly responsible for the speed and enthusiasm with which birth control technology has been adopted by modern human populations.

The adaptive value of reproductive control can hardly be disputed. Note, for example, that women currently control their reproduction via abortion in a highly selective fashion, with age and marital status having great effect on the likelihood of terminating the pregnancy. The fact that young, unmarried women are most likely to have an abortion is consistent with theoretical evolutionary expectation [209]. Such women generally lack paternal support for any current offspring, which would have greatly compromised the chances of survival of any such children in the ancestral environment of human beings. Yet these women have a reasonable chance of reproducing successfully in the future, if they can acquire a helpful social partner. The prospects for eventual marriage are increased if the woman lacks dependent children who have been fathered by someone other than prospective husbands. In other words, human psychology surely has been shaped by the reality that there are times and places when having children is maladaptive, which favors psyches with the capacity to avoid pregnancy under some circumstances. Strategic avoidance of pregnancy is made more possible than ever before with modern abortion and birth control technology.

One way to test the novel environment hypothesis for reductions in family size would be to predict that declines in fertility will vary from place to place, depending on the availability of modern birth control devices. Contrary to the prediction, however, the demographic transition began in Europe well after the invention and widespread distribution of the means for reasonably effective birth control (e.g., condoms) [49, 92]; moreover, the oral contraceptive pill, the most efficient method of birth control, was not invented until the late 1950s [26], by which time the demographic transition had long been under way in Europe. In addition, the novel environment hypothesis does not mesh with the fact that the demographic transition is only barely beginning in Africa, despite some access to anticonception technology there as well as widespread awareness of the importance of condoms in combating HIV transmission. Note that this case illustrates again that an evolutionary speculation, when translated into a formal hypothesis, can be tested and rejected, despite claims to the contrary.

Moreover, the rejection of one evolutionary hypothesis does not demonstrate that human behavior simply cannot be analyzed from a sociobiological perspective. Many alternative evolutionary hypotheses have been developed for the demographic transition [44, 92, 211]. Here is one example. Over the course of most of human history, a strong drive to acquire material resources, especially food and superior tools, would almost certainly have been adaptive for obvious reasons, even if successful individuals gave away much of their "wealth" in order to gain a positive reputation and to secure socially indebted companions who would return these favors in times of need. With the rise of agriculture and more sedentary lifestyles, however, this same materialistic drive could have motivated some people to accumulate considerable durable wealth. Wealth that lasts is something of an evolutionary novelty (hunter-gatherers obviously did not have cash and could not transport large quantities of food from one campsite to the next). Once durable wealth existed, however, parents with the right stuff could use it as a form of parental investment to be transferred to their offspring. These transfers could affect their children's competitive success in the economic and social status arenas, which would surely affect their children's likelihood of acquiring mates and producing offspring. Moreover, once some parents began to employ this tactic, others might be drawn along in a kind of arms race revolving around social, as opposed to military, competition.

Thus, it is possible that in the early human cultural environments where wealth could be accumulated, individuals who attempted to maximize their ownership of durable goods may have had more grandchildren than those who attempted to maximize the number of children they personally produced. The point is that fewer but richer children may generate more surviving grandchildren in total than a mob of poverty-stricken offspring, none of whom has the resources to sustain a large family. Borgerhoff Mulder tested her hypothesis by examining the marriage strategy in a traditional herding culture, the Kipsigis of Kenya. In this polygynous society, men pay a bride-price for each wife; the more land owned, the more cows a man can herd; the more cows owned, the more wives one can purchase; the more wives, the more offspring. But rather than expend all their wealth in the acquisition of wives, Kipsigis males regularly forgo such expenditures in order to retain large cattle herds. Kipsigis men, like men in many other societies, have a deep and abiding interest in getting rich and staying rich. In so doing, they are able to provide their male offspring with cattle, enabling them to acquire wives sooner than otherwise, generating more grandchildren for the strategic parent [208].

Therefore, in cultures where it is possible to become rich, an evolved desire for cultural success can lead to competition among men for wealth and the high social status that goes with it. This attribute might then act in conjunction with discriminating parental investment to promote the genetic success of grandparents in some situations. Others who imitate the culturally successful members of their group can also improve their genetic success to the extent that their efforts at imitation are successful. However, although these elements of human psychology may have advanced individual genetic success in some preindustrial societies, they most assuredly do not have that effect in modern cultures that have undergone the demographic transition. What's going on here?

The average North American controls an extraordinary amount of wealth compared to a hunter-gatherer or even a well-off Kipsigis herdsman. The evolved drive to acquire goods in an environment with so many different and desirable things

available for purchase could conceivably lead individuals to devote themselves to the accumulation of wealth at the expense of maximizing the number of grandchildren. Such an outcome is made more likely given two other evolutionary novelties, excellent birth control technology and culturally enforced monogamy, both of which tend to reduce the number of offspring a married man, even a very wealthy one, is likely to produce.

This hypothesis remains largely untested but it brings a totally different and absolutely necessary dimension to the table for future research on the demographic transition. This work will examine the possibility that our reproductive behavior has been shaped by at least four major psychological mechanisms that could have been adaptive in the past: (1) an interest in controlling the timing and spacing of offspring, (2) a drive to secure material resources, (3) a willingness to manipulate investments in offspring in particular ways, and (4) a desire to imitate the practices of culturally successful members of their group.

Although we do not yet fully understand the evolutionary reasons why so many people have so few offspring, this does not mean that our current reproductive behavior (and our capacity to be culturally influenced with respect to reproductive matters) lacks evolutionary causes. Even if certain tabula rasa academics refuse to explore the ultimate basis of our behavior, the rest of us need not follow their example. As the cases reviewed in this chapter demonstrate, cultural practices are adopted by living, breathing people whose brains give every indication of having been shaped by natural selection. Understanding this simple but profound point is the key to understanding why evolutionary theory has something important to say about human behavior.

↳ BUT DOES IT
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