Nesse, Randolph M. (2017). Evolutionary foundations for psychiatric research and practice. In B. J. Sadock, V. A. Sadock, & P. Ruiz (Eds.), Kaplan & Sadock's comprehensive textbook of psychiatry (Tenth edition, pp. 769–780). Philadelphia: Wolters Kluwer.



Contributions of the Social Sciences

▲ 4.1 Evolutionary Foundations for Psychiatric Research and Practice

RANDOLPH M. NESSE, M.D.

FIVE ADVANCES

Major advances in the evolutionary explanation of behavior and emotions from the second half of the 20th century have yet to be fully applied in psychiatry. This chapter summarizes those advances and how understanding them can make clinicians and researchers more effective. Some have direct applications, such as understanding the human mating system, how negative emotions are useful, and why there are no common alleles with large effects on highly heritable diseases such as schizophrenia. However, the big payoffs in the long run will come from the integrated framework evolution provided for understanding normal behavior and psychopathology. Evolutionary approaches are not an alternative to understanding mechanisms, they are the crucial complement that explains why mechanisms are the way they are, and why they are vulnerable to failure. Evolutionary biology provides a framework that can transform the bio-psycho-social model from a catch phrase into a solid working model. It provides, for psychiatry, what physiology provides for the rest of medicine—an understanding of normal functioning as the foundation for understanding pathology.

Five major advances in evolutionary biology are especially important for psychiatry. Each is described briefly below.

Proximate and Evolutionary Explanations Are Both Essential

Until the middle of the 20th century, the study of animal behavior was mostly descriptive. Meticulous observations by ethologists described

behavior in detail, but theory was absent. Everything changed in the mid-1960s, with recognition that all biological traits need evolutionary as well as proximate explanations. This insight came first from students of animal behavior, especially Nico Tinbergen. So-called "proximate questions" are about mechanisms; answers to such questions describe how mechanisms work, and how they develop. Other "evolutionary questions" are about how traits got to be the way they are; answers to such questions describe how and why the trait has changed over evolutionary time. For instance, a proximate explanation of anxiety describes the relevant brain and psychological mechanisms, how they develop, and how they are influenced by events and environmental influences. However, even describing every detail about the proximate mechanism does not explain why the capacity for anxiety exists at all. That requires an evolutionary explanation of how the capacity for anxiety increased fitness for our ancestors.

In a famous article published in 1963, Tinbergen outlined four questions that all must be answered to have a complete understanding of any trait. Two are evolutionary questions. The first is about phylogeny, the history of a trait. The other is about the adaptive significance of the trait and what forces of selection shaped it. There are also two proximate questions. One is about the mechanism and how it works at all levels, from molecules to social psychology. The other is about ontogeny, how the mechanism develops in an individual from a zygote to an adult (Table 4.1–1). Almost all research in psychiatry has been to describe mechanisms, their development, and their malfunctions. Only now is attention turning to also address evolutionary questions such as why emotions exist.

Evolutionary Explanations for Individual Behavior

The second core advance, closely related, was the application of evolutionary thinking to behavior. Initial approaches provided evolutionary explanations for specific behaviors, such as rams butting horns in the mating season, and birds removing broken shells from nests to avoid attention from predators. It was soon recognized, however,



Table 4.1–1.
Tinbergen's Four Questions

Tinbergen's Four Questions Adapted from Nesse, 2013		Two Objects of Explanation	
A.		Developmental/Historical A sequence that results in the trait	Single Form The trait at one slice in time
Two kinds of explanation	Proximate Describes the mechanism and its ontogeny	Ontogeny How does the trait develop in individuals?	Mechanism What is the structure of the trait; how does it work?
	Evolutionary Describes adaptive significance and phylogeny	Phylogeny What is the phylogeny of the trait?	Adaptive significance How have variations in the trait influenced fitness?

that it was not behaviors themselves that natural selection shaped, but behavior regulation mechanisms. That is, the brain.

A general core principle soon became clear: Brains are shaped by natural selection to give rise to behavior that maximizes Darwinian fitness. Instead of implying rigid behavior patterns, this principle recognizes the enormous fitness benefits of flexible behaviors that allow organisms to adapt to rapidly changing situations. Learning is not an alternative to an evolutionary explanation, it is a capacity shaped by natural selection. Textbooks of animal behavior are now all grounded in evolutionary biology.

Evolutionary Explanations for Social Behavior

The evolutionary analysis of social behavior was central to transforming animal behavior research. The old idea that organisms are shaped to behave in ways that benefit their groups and species was replaced by recognition that selection generally shapes traits that maximize individual fitness, even if that harms the group. Many have heard about lemmings jumping into the sea for the good of the group when food is too scarce for all to survive. This turns out to be a myth, one promulgated by a Disney film that seems to show lemmings flinging themselves off a cliff, when in fact they were swept off by workers with brooms. An allele that induces individuals to sacrifice themselves for the good of the group will be quickly selected out except in very special circumstances. Behaviors costly to individuals that benefit groups, such as parents sacrificing for their offspring, wolves sparing those who signal defeat, or crowded populations reducing reproduction, have other explanations.

Kin Selection

Recognition that costly individual sacrifices cannot routinely be explained by benefits to others was followed closely by William Hamilton's discovery of the main exception, kin selection. Close relatives share genes that are identical by descent; 50% of a child's genes are identical to each of its parents. Alleles that decrease an individual's number of offspring can be selected for if they sufficiently benefit identical alleles in kin. Hamilton's famous formula, $C < B \times r$, is a crucial foundation for understanding family relationships. An action that costs an amount C can nonetheless give inclusive fitness benefits if the cost to self is less than the benefit to a relative, B, times the percentage of genes identical by descent. The term "inclusive fitness" incorporates actions that increase the reproduction of an individual's relatives, as well as the individual. Kin selection offers a profound evolutionary explanation for basic human behaviors, such as parents making sacrifices that benefit their children.

This discovery led to thinking in terms of "selfish genes." The metaphor has been useful to combat naïve group-selection thinking, but it has been somewhat too potent for its own good. If genes are selfish, this seems to imply that organisms must be selfish. However, capacities for generosity and moral behavior exist because they increase inclusive fitness. Selfish genes make individuals who can be generous...selectively.

Evolutionary Medicine

Natural selection shapes traits that work well, so it would seem unable to explain diseases. That's correct—diseases are not shaped by natural selection. However, traits that leave individuals vulnerable to disease, such as the appendix, the narrow birth canal, and the capacity for low mood, have been shaped by natural selection. Evolutionary medicine tries to understand, for each disease, why selection has left

bodies vulnerable. Six main kinds of explanation help to organize the search. Notice that these are not explanations for why some individuals become ill while others do not. Instead, they are about why all humans share vulnerability to a disorder.

Six evolutionary explanations for vulnerability:

- 1. Mismatch with modern environments
- 2. Constraints-things selection cannot do
- 3. Coevolution with fast-evolving pathogens
- 4. Trade-offs
- 5. Reproduction at a cost to health
- 6. Defenses that are useful but costly and aversive

Mismatch of Environment to Body. The bulk of chronic disease results from the mismatch between the human body and the very pleasant environments humans have created for themselves. Atherosclerosis, breast cancer, and autoimmune diseases are vastly more common in technological societies. So are obesity, eating disorders, alcoholism, and drug abuse. Human behavior regulation mechanisms were never shaped to cope with the ready availability of hamburgers, candy bars, whiskey, and heroin. Our distant human ancestors also never had to cope with life in bureaucracies, 9-to-5 jobs, alarm clocks, and expectations of lifetime monogamous mating.

Many alleles that predispose to major disorders are not defects, they are merely genetic "quirks" that cause harm only in modern environments. For instance, nearsightedness is highly heritable, but nonetheless rare in hunter-gatherer populations not exposed to reading early in life. Other heritable tendencies may have vastly different significance in modern environments. For instance, attention deficit disorder may not have posed serious problems for hunter-gatherers (or it may have been uncommon). Some who advocate an evolutionary approach to mental disorders have attributed nearly all problems to a mismatch with modern environments. While such factors are significant, the five other factors are also important.

Pathogens Evolve Faster than Hosts. Infectious disease will always be present because pathogens evolve much faster than humans can. Also, every time selection shapes a host defense, pathogens evolve some way around it. The resulting arms race leaves us with costly defense mechanisms prone to cause disease.

For instance, streptococci have evolved immune markers similar to human tissues, making it risky for the immune system to attack them. Rheumatic fever, Sydenham's chorea, and some cases of obsessive-compulsive disorder are examples.

Constraints. There are many things that natural selection cannot do. It can never completely prevent mutations, although the extraordinary fidelity of DNA replication illustrates the power of selection. Evolution also cannot redesign a trait from scratch; it proceeds only by a process of small "tinkering" changes. So, while birth via the pelvis is painful and dangerous, no alternative route can evolve. Similarly, vertebrates are stuck with the blind spot where nerves and vessels enter an opening in the back of the eyeball, while cephalopods have nerves that traverse their eyeballs without causing a blind spot.

Trade-offs. No trait can be perfect. The vast majority of changes that could make a trait superior in one respect would make it inferior in other respects, or would compromise the effectiveness of other traits. Finches with larger beaks can crack tougher seeds. but they have less access to very fine seeds. Individuals with more

tendency to anxiety are able to avoid dangers, but at the cost of the inability to take advantage of many opportunities.

Reproduction at the Expense of Health. It is disturbing to recognize that natural selection does not shape organisms to maximize health, happiness, or longevity. It instead shapes organisms to maximize inclusive fitness. Usually health and long life are good for fitness, however, an allele that harms health will nonetheless spread if it increases reproduction.

The best example is the short lives of men compared to women. Male mortality rates in early adulthood are three times those for women because tendencies that lead to success in mating competition are selected for in males even if they harm health. Tendencies to tissue repair and sensible caution are relatively favored in females.

Much research has sought to understand the proximate mechanisms that account for women having more anxiety disorders than men. An evolutionary framework suggests that it is men who have the problem. Women have closer to the optimal amount of anxiety for their own health and well-being.

Some have speculated that tendencies to mania may have been selected for because they result in increased matings and increased reproductive success. If that were really the case, then the tendency would have spread and become universal. This provokes an interesting possible explanation for the high prevalence of mild bipolar tendencies. However, the rarity of manic depression suggests that the increased sexuality of individuals with tendencies to mania has not paid off with net increases in numbers of grandchildren.

Defenses. Most problems people bring to their physicians are not direct manifestations of disease; they are useful defensive responses, such as pain, fever, cough, nausea, and vomiting. These defenses, shaped by natural selection, are usually expressed only in the presence of some disease, but they are not diseases themselves. This knowledge is crucial for making good clinical decisions about when to block such defenses.

The smoke detector principle is also crucial for making such decisions well. Natural selection shapes mechanisms to regulate defenses so they are expressed in situations where their benefits are greater than their costs. However, information is often insufficient to be certain about the presence of a threat, so even an optimal system will have some false alarms, and some failures to respond when a response would be useful. This is particularly germane for understanding panic attacks. A fight-flight response will be potentially life-saving if the noise from behind a rock is made by a lion, but it will be wasted if the noise is coming from a monkey. Whether an individual should flee in a panic depends on how likely it is that the noise was from a lion. If the cost of flight is, for instance, 100 keal, and the cost of not fleeing if the lion is actually present is 100,000 keal. then the optimal system will set off the fight-flight response whenever the noise is loud enough to indicate a probability of a predator being present of greater than one in 1,000. This means that 999 responses of 1,000 will be false alarms, each useless, but completely normal. False alarms in the system are expected and normal. This has profound implications for understanding panic disorder, and explaining it to patients.

CORE PRINCIPLES OF EVOLUTIONARY BIOLOGY

Evolution has two major components, both discovered by Darwin. The first is the unity of all life; all individuals in all species are descendants of ancestors that go back in an unbroken chain to the

origins of life on earth. This is phylogeny, now traceable via genomics. It is relevant for tracing human origins, and for identifying the history of alleles related to mental disorders, but the focus here will be on Darwin's other discovery. Darwin's second discovery is natural selection and how it explains adaptations. It is the only viable explanation for why so many aspects of organisms are well-suited to coping with life's challenges. The rabbit's astute hearing, the woodpecker's barbed tongue, and the eagle's sharp eyes are products of natural selection. So are human empathy, emotions, cognition, and capacity for language and love. Or, more exactly, the brain, and its mechanisms for regulating thinking, emotions, and behavior.

Natural Selection

Natural selection is best understood in the context of selection in general. If members of a group differ in ways that influence their likelihood of being in the group in the future, the group will change over time. If you put all coins from your pocket into a jar each evening and select only the silver-colored coins in the morning, the jar will gradually take on a copper hue as the concentration of pennies increases. Television producers try out extraordinarily varied offerings. Those that get viewers and advertising dollars persist and are imitated, others are eliminated. Selection explains how groups change when variations among individuals influence their contributions to future groups.

Natural selection is the subtype of generic selection in which the variations are products of genetic variation that influence reproductive success. The principle is simple. If individuals in a population differ genetically in ways that influence how many surviving offspring they leave, the average characteristics of the population will change over the generations. This is not a theory, it is a theorem that is necessarily true. In the classic example, if previously light trees become covered with soot and moth color varies, light-colored moths are more likely to be eaten by birds, so the average moth will become darker over succeeding generations. VISTA is a useful mnemonic for the process of natural selection: Variation—Inheritance—Selection—Time—Adaptation.

Dogs offer a familiar example. From their common ancestors in wolves, artificial selection has produced dramatically diverse dog breeds in just a few thousand years. The process of natural selection is the same as breeding, except that differences in offspring numbers result not from decisions made by breeders, but from variations in ability to cope with life challenges that influence reproductive success. The products of natural selection look as if they were designed, and the sequence of species makes it seem as if there is something planned, or at least preordained, about the progression. However, there is no plan or endpoint, and traits that appear to be designed were shaped by mindless natural selection.

Standard examples usually describe how natural selection changes a trait, however natural selection mostly keeps traits the same. If individuals 7-ft tall had more children than others, the mean height would shift to that optimum. If individuals more aggressive or outgoing than others consistently had more children, the population mean would shift. However, at least over the past few tens of thousands of years, individuals at the extremes of height, aggressiveness, and extroversion almost certainly had fewer offspring than those closer to the mean. The persisting wide variation in these traits suggests that fitness is similar across a wide range.

Whether a trait or a gene is advantageous or deleterious depends on the environment. In equatorial climates, dark skin protects against sun damage, in cloudy environments it can result in rickets from insufficient sunlight-induced vitamin D synthesis. A tendency to prefer fatty foods can be useful where fat is scarce, but in modern environments it can lead to disease.

Evolution

Evolution involves much more than natural selection. The three other main forces are mutation, migration, and genetic drift. Mutations happen despite being minimized to an astounding degree by natural selection; increasing evidence points to their importance for explaining sehizophrenia and bipolar disorder. Migration may strongly influence the prevalence of an allele in a population. Most northern Europeans can digest milk because migrants brought the relevant gene from rapidly expanding dairying populations further south. Huntington chorea is especially common near Lake Maracaibo in Venezuela because Antonio Justo Doria, a Spanish sailor, brought the mutation there in the late 1800s. Genetic drift refers to changes in gene frequency, more correctly allele frequency, that result from random factors. An allele that increases fitness may be lost from an entire population if the individuals carrying it all die in an accident. An allele that is mildly harmful can nonetheless become more common if those who carry it have more children than others just by chance. Alleles whose effects on fitness are close to neutral can drift to fixation or be eliminated, especially in small populations. There are good reasons why population genetics relies on the so-called "null model" in which frequency changes result only from drift. This is not, however, an alternative to natural selection or a reason to think that most traits are not well-suited to their functions.

What Selection Shapes

The usual textbook examples of selection are fixed physical traits such as bird beaks and moth wing color. Far more important for psychiatry, however, is selection for systems that regulate the body and behavior. Most regulation systems keep things stable. Selection shapes mechanisms to maintain homeostasis at every level. Regulation of glucose, oxygen tension, acid—base balance, and osmolality are the usual examples.

The association of natural selection with fixed traits and systems that maintain homeostasis fosters the misperception that an evolutionary explanation somehow implies rigidity, especially rigidity of behavior. Nothing could be further from the truth. Natural selection has shaped hundreds of mechanisms that adjust organisms to changing situations. The traits vary in scale from the molecular to largescale behavior, and across time from instantaneous changes to those that play out over a lifetime. The term plasticity often refers to longerterm changes, especially those that shape an individual in relatively irreversible ways as function of early experience, such as the barrelshaped chest of humans living at high altitudes. In the medium term, high altitude increases hemoglobin concentration, and exposure to sunlight induces skin tanning. In the short term, cold induces shivering, infection causes fever, and threat arouses fear. Some responses, such as blinking, are nearly instantaneous. All are facultative adaptations, mechanisms shaped by selection that adjust individuals to changing aspects of environments.

The brain is obviously responsible for many such responses. It monitors internal and external cues as input to mechanisms that adjust physiology, expression, behavior, cognition, and more. These responses vary across individuals, and some of the variation results from genetic variation. To make a long story short, the brain was, like every other organ, shaped by natural selection. It's function is to regulate behavior and other responses in ways that maximize inclusive fitness. Capacities for learning and relationships are especially

valuable ways to accomplish that. Humans have, perhaps uniquely among all animals, capacities for abstract representation that make language and causal thinking possible. Humans also have distinctive capacities for enduring relationships that go beyond merely trading favors. These capacities, in turn, make possible social complexities and cultures that create new selection forces, that further shape brains, in a feedback process that has shaped humans' astounding social and cognitive abilities. An evolutionary approach to human nature emphasizes the remarkable plasticity and adaptability of behavior to different circumstances.

Genotypes and Phenotypes

Natural selection changes gene frequencies, more accurately, allele frequencies. Population genetics describes how selection, migration, and genetic drift increase and decrease allele frequencies in different specific situations. This sometimes gives the impression that evolutionary explanations are genetic explanations, and that gives the impression that an evolutionary approach to behavior somehow implies a commitment to genetic explanations for variations in personality and behavior. These are misconceptions. It is instructive to realize that Darwin knew nothing about genes. The principles of natural selection were discovered by observing variations in phenotypes.

Genes carry the information that is acted on by natural selection, but that action is almost entirely via interactions of phenotypes and environments. Just as there is no such thing as a trait that is adaptive in general, there is no such thing as an allele that is useful in general; the adaptive significance of a genetic variation depends on interactions with other genes (epistasis) and interactions with environments.

Sexual Selection

The interests of an individual and his or her genes are generally the same. An allele that makes healthy long-lived phenotypes is more likely to be passed on. There is, however, an exception. Mutations that decrease health, happiness, longevity, or cooperativeness will spread nonetheless if they increase the number of offspring.

Sexual selection is the best example. It is the subtype of natural selection in which individuals compete for mates, either by displaying extreme traits that lead to being chosen by the other sex, or by traits that lead to success competing with others of the same sex. Gigantic colorful tails are a costly drag for peacocks, but the responsible genes spread because peahens prefer peacocks with big tails. The process can set up a positive feedback loop in which the advantages of extreme male traits give advantages to female preferences for those traits, because sons with extreme traits will have an advantage. The trait becomes more extreme until the costs it imposes are as large as the reproductive benefits.

The relevance of sexual selection to humans is illustrated by the excess mortality rates experienced by men compared to women. In the early reproductive years in modern societies, men are three times more likely to die than females. Much of the excess is from fights and accidents, but almost all causes of death are greater for males because they allocate effort to competitive ability at the expense of tissue repair. Even early childhood mortality rates are 50% higher for boys than girls.

Sexual selection is a subtype of social selection, the more general category of evolutionary change resulting from social choices and competitions. In sexual selection the resource at stake is mates, with its obvious connection to reproductive success. However, especially for humans, competition for status, friends and group memberships also influences reproductive success. Individuals preferred as

relationship partners or group members get advantages substantial enough to shape extreme human capacities for altruism and empathy unmatched by any other species. These advantages also help to account for extraordinary social sensitivity and the prevalence of social anxiety in humans.

Many people experience extreme concern about what others think about them. The explanation is that other people's opinions can help or harm reproductive success. There are good evolutionary reasons why many psychiatric disorders are associated with internalizing or externalizing personality extremes. There are good evolutionary reasons to expect constant conflicts between (id) impulses to get short-term advantages and (superego) constraints that sacrifice personal short-term gain for longer-term benefits of being a preferred social partner. Rigidity that emphasizes one over the other is disadvantageous and is recognized as sociopathy and neurosis. Most people benefit from mechanisms shaped by selection that allow them to shift their social strategies as a function of subtle shifts in social circumstances.

Levels of Selection

Recognition that selection works mainly at the level of the gene and the individual has profound implications for psychiatry. While few evolutionary biologists now support the idea that traits are routinely selected to benefit the group or the species, consensus about levels of selection remains elusive, and the idea of group selection remains attractive to many nonbiologists. This may be, in part, because it is so often framed as an explanation for "the mystery of altruism." In an evolutionary framework, tendencies that benefit the genes of unrelated individuals more than those of the actor will be selected against, while genes that benefit kin more than the actor can be selected for only if the cost/benefit ratio is greater than the percentage of genes in common.

What about cooperation between those who do not share genes in common by descent? Many are "mutualisms" that give benefits to both parties with no opportunity for defection, such as two people moving a heavy rock to get food. Often, however, exchanges are not immediate, leaving the possibility that one partner will fail to reciprocate a favor. Such "reciprocity" exchanges have been subject to exhaustive modeling using the prisoner's dilemma schema. In this model, the largest payoff comes if the actor defects and the other person cooperates. If both cooperate, they both get a modest benefit. If both defect, neither gets any benefit.

Because the cells in an individual's body are all genetically identical, their interests are almost always aligned with the welfare of the individual. However, some exceptions are particularly important for psychiatry. In particular, the interests of maternal and paternal genomes differ. Female mammals invest a proportion of their available resources in a pregnancy, reserving some for future offspring. The male parent may or may not be the parent of those future offspring, so the paternal genome gets an advantage if the fetus extracts a bit more nutrition from the mother. It may seem preposterous that maternal and paternal genomes should compete over relatively small differences of investment in an infant, yet intriguing genetic evidence suggests this is exactly what is happening.

IGF-II alleles tend to make offspring bigger. When they are passed on via an egg, they are imprinted, that is, methylated in a way that inhibits expression of the gene, thus making the baby smaller. IGF-IIr alleles counteract the actions of IGF-II, yielding larger offspring. IGF-IIr alleles are imprinted if they come through the paternal line. The balance between these opposing forces yields babies of normal size, but if imprinting is missing for either gene, offspring will be especially small or large.

Bernard Crespi has suggested that this phenomenon may be related to schizophrenia and autism. They can be viewed as flip sides of the same coin, with autism reflecting unbridled influences of the paternal genome, and schizophrenia reflects excess influences of the maternal genome. Genes that increase the risk of schizophrenia and autism are imprinted in ways remarkably congruent with this theory. A recent study found, as predicted, that babies lighter than average were especially likely to develop schizophrenia, while those born heavier than average were more likely to develop autism. These findings do not confirm the theory, but they do illustrate how to test a creative idea inspired by evolutionary thinking.

A more mundane but nonetheless fascinating example is the weaning conflict. There is a period when mammal mothers try to stop nursing but infants protest vigorously and try to continue. This conflict is predictable from evolutionary principles. The mother and infant share 50% of their genes, but the infant shares 100% of its genes with itself. A mother that fails to nurse her infant loses a huge investment, so providing whatever her baby needs early in life is in the mother's genes interests. As the baby grows, it is increasingly able to get nutrition from other sources. At some point this means that the mother's reproductive success would best be served by another pregnancy. The baby's interests, however, are best served by continuing to nurse until the point when the benefits via kin selection to a younger sibling (who shares 50% of genes) are as great as the benefits from continuing to nurse. At this point cessation of nursing is in the child's interest, so the weaning conflict ceases. An extensive literature in psychoanalysis and child development investigates nursing and weaning, but much remains to be done to put it in an evolutionary context.

Misunderstandings about Natural Selection

Some common misunderstandings about evolution deserve mention. Is evolution over for humans? This idea that lower death rates end evolution reflects a deep misunderstanding of natural selection. Natural selection depends on differential reproductive success, not survival. If a heritable trait results in some individuals having fewer offspring than others, then natural selection occurs. Individuals with two different versions of a gene may have the same lifespan, but if one has more offspring, selection will take place. So long as heritable traits influence numbers of offspring, selection will continue to change the average characteristics of the human species. This does not meet that future traits can be predicted with certainty. Death from drunk driving is now a powerful selection force, but it is hard to say whether it will select for disliking alcohol or better driving while drunk.

Can selection have any impact after menopause? Many people think not, but this is because they have not recognized the role of kin selection. Postmenopausal women can have a major influence on the proportion of their genes in future generations if they do things that help their grandchildren. Erickson's generative phase of life has an easy evolutionary explanation. Some have hypothesized that menopause is an adaptation shaped by the advantages of taking care of existing children instead of undergoing the risks of reproduction at advanced age that might jeopardize the welfare of older children.

Do all humans have Stone Age bodies and minds, unchanged for the past 10,000 years? No. Substantial changes have been documented; examples include changes in skin color, ability to digest lactose, and the ability of certain human subpopulations to cope with high altitudes. Increasingly complex social structures may also have imposed strong selection forces that have shaped social and emotional traits and language abilities. Selection for behavioral traits may

have sped up since the development of agriculture changed human social structures.

The opposite misconception, that selection changes traits in just a few generations, is also prevalent. However, selection is too slow to adjust the human body to environments that change drastically over just a few generations. Some people think that nearsightedness, a highly heritable trait, has become more common because the invention of eyeglasses has made it less of a disadvantage. However, a few hundred years is not nearly enough time for disadvantageous alleles to drift to a prevalence that would cause disability in about a third of the population. Myopia is a fine example of a "genetic quirk." The responsible alleles probably have disadvantageous consequences only when they interact with some modern environmental factor, possibly early reading, to cause pathology. One wonders how many alleles that predispose individuals to psychiatric disorders are also not defects, but quirks.

Does an evolutionary view of behavior imply some kind of rigidity or genetic determinism? Quite the opposite. Natural selection has shaped innumerable mechanisms that adapt bodies to current circumstances. Learning is not an alternative explanation for behavioral traits, it is but one of many behavioral regulation mechanisms shaped by natural selection to adjust behavior to different circumstances. Similarly, culture is not an alternative explanation for the existence of behavioral traits, although it is obvious that culture has massive effects on behavior. The emergence of complex cultures has created new selection forces that have given humans capacities for culture unmatched by any other species. Gene-culture coevolution escalates human capacities for culture, which in turn makes more complex culture possible, in a positive feedback cycle whose end is not yet in sight.

Much difficulty incorporating evolutionary biology as a basic science for psychiatry arises because of perceptions that it is associated with atheism. While belief in God is less common among scientists compared to the general public, the fact that humans have been shaped by natural selection does not directly imply anything about the existence of God. It does contradict some myths that are interpreted literally by some religious traditions, however many religions, including the Catholic Church, now officially recognize that humans are products of natural selection.

BEHAVIORAL ECOLOGY

The synthesis of ethology with evolutionary biology produced the field now known as behavioral ecology. It analyzes how behavior patterns influence fitness. Aside from the core principle that behavior tends to maximize inclusive fitness, behavioral ecology focuses on trade-offs between the different kinds of efforts individuals exert to get different kinds of resources. It routinely distinguishes several categories of effort. Somatic effort is to get calories and other resources to grow, sustain, and protect the body. Reproductive effort is to get mates, and to take care of offspring. Social effort is to recruit allies and to achieve status in the group.

This framework offers a powerful tool clinicians can use to unpack the sources of stress. Most stress comes from inability to get a secure, sufficient supply of some resource, threat of loss of a resource, or because efforts to get one resource interfere with efforts to get another. Examples abound in the clinic. One person may be working 70 hours a week, and feeling, correctly, that this makes searching for a romantic partner unrealistic. Another may be stressed because a commitment to full-time childcare makes it hard to allocate effort to anything else. Many people are distressed because of inability to find a mate, insecurity of a marriage, or wanting to leave a relationship.

Many others are unable to find a satisfactory job, worried about losing a job, or feeling stuck in a position that provides little respect.

Other problems arise from unbalanced allocations of effort. For some people money is the overwhelming goal, others are dedicated to being good, getting famous, having friends, or taking care of children. The task of balancing efforts to get these various resources is constant, and imbalances create pathology. Narcissism can be viewed as investing all life effort in the pursuit of self and status to the exclusion of all else. Conversely, some patients invest all effort into trying to please others. Some are preoccupied with their appearance, others with their wealth. Stress often arises from health problems that make it impossible to pursue other resources.

To identify the specific source of life stress, one can ask, for each area, whether the person's life strategy is providing sufficient and secure sources of the resource. Few people ever have everything they want, securely and to full measure, but it is nonetheless useful to distinguish patients who have generally adequate sources for most of life's core resources, from those who are unable to get something crucial, from those who lack sources of most main life resources.

Other animals face the same challenges. A grazing white-tailed deer looks up from the grass every few minutes to see if enemies might be present. Each time the animal looks up, it takes time away from eating. The allocation of effort between foraging and defense is regulated according to the level of nutritional supplies and the danger from predators. Risk-taking is also adjusted according to circumstances. Birds given a choice between a feeder that provides one seed every visit, and one that provides six seeds every sixth visit, generally prefer the steady payoff. If, however, the temperature is lowered to a point where the steady payoff provides too few calories to survive through the night, they switch to the risky payoff because that at least offers some chance of survival.

Studies of foraging also have important implications for psychiatry. Food for most animals is distributed in patches, such as different fruit trees. Starting in a new patch often provides many calories per minute, but as the patch is depleted, payoffs slow. How quickly should the animal move to the next patch? It depends on how long it will take to find a new one. Staying too long will waste time, resulting in very few calories per minute. Moving too quickly to a new patch will waste time looking for food when it could be spent gathering food. The optimum strategy is to continue in the current patch until the rate of return declines to that averaged over many patches. This is Charnov's marginal value theorem. Animals do not have to do calculus to figure out the optimum moving time; their brains have been shaped by selection to optimize such choices to a remarkable degree. This is relevant for attention disorders and for mood. Consider the enthusiasm experienced upon first beginning to pick berries from a new bush, starting a new job, or engaging in a new relationship. Inevitably, payoffs decline with time. Deciding when to make a change is a difficult decision that often is the focus for psychotherapy.

Reproductive Effort

Brains result in behaviors that maximize inclusive fitness, a term that combines the reproductive success of an individual and his or her relatives. The simplest rule of thumb is that natural selection shapes brains that result in behavior that tended, in ancestral environments, to maximize the number of grandchildren, nieces, and nephews.

This makes it seem as if everything depends on mating often and with many partners. Differences in reproduction are evolution's engine, but the notion that reproductive success is maximized by maximizing mating success is simplistic. Compared to chimpanzees, humans have a remarkable ability to selectively inhibit sexual

impulses. This ability must have given a selective advantage in the context of the mating patterns that developed during human evolution

Sex and mating behaviors have been a natural focus for behavioral ecological study. There is no room here to expand on this topic, but it is important to recognize that the very existence of sex poses an evolutionary mystery because parthenogenetic populations grow twice as fast as sexual ones. Also important are the forces that shape many small gametes in one sex (e.g., sperm) and fewer larger ones in the other sex (e.g., ova). This is the essence of the difference between males and females. It means that different mating strategies maximize fitness for males as compared to females. Compared to males, female mammals invest much more in each offspring-many calories, and the time and effort of pregnancy-so the total number of possible offspring is quite limited. The investment of a male can be as little as a few sperm and a few minutes, so one man can have hundreds of children, an outcome uncommon in technological cultures, but reported in cultures where agricultural surpluses made it possible for one man to have many mates. Variation in reproductive success is therefore potentially much larger for men; while some have many offspring, others have none.

However, the human mating system is quite different from that of most other primates. In particular, men make major investments in rearing children. In this respect, humans are more like birds than most other mammals in that rearing offspring takes two parents. Chicks left alone in the nest without protection are likely to quickly be eaten by a predator, so a partnership is required for successfully rearing young. Human babies are so helpless, and their rearing takes so many years, that just having sex is rarely enough to successfully reproduce.

Large investments in child rearing make sense for a man only if he can be relatively certain that the children are his own. So, tendencies to jealousy and mate guarding are human universals, although the range of accepted behaviors varies enormously between cultures, from death by stoning for what would elsewhere be dismissed as mere flirtation, to extramarital sex being acceptable in some situations.

These distinctive aspects of the human niche are likely related to another human peculiarity—human ovulation is concealed instead of being advertised, as it is in many species. This may have increased paternity certainty by drastically lowering the benefits of any forced copulation by a man who is not the woman's mate.

These generalizations are too often pushed to an essentialized version that purports to be THE normal human mating pattern, despite massive evidence for huge cultural variations in mating and family structures. Nonetheless, understanding the evolutionary origins of the human niche can be helpful in understanding marital conflicts, jealousy, and the complications of affairs and divorce.

Life History Traits

Traits such as the duration of gestation, rate of growth, age at maturity, interbirth interval, duration of nursing, and rates of aging are all shaped by selection. One particularly important dimension has been called fast versus slow life strategy. In environments where life is short, reproductive success is maximized by taking risks and reproducing early and often, investing less in each offspring. In more secure environments, it is better to invest more in longer-term strategies and invest more in each offspring. The wide range of human variation on this dimension has been proposed to result from a facultative mechanism that responds to different environments by inducing a faster or slower life history strategy.

Attachment

John Bowlby's recognition of the adaptive value of mother—infant attachment marked the beginning of evolutionary approaches to psychiatry. However, he worked before the major advances that revolutionized the study of behavior, so it is not surprising that he and his followers have tended to see secure attachment as the norm, and other kinds as pathological. Secure attachment is best for mental health, but important recent work has suggested that anxious or avoidant attachment may give selective advantages in some situations.

EMOTIONS

Emotions are special modes of operation shaped by selection to cope with the challenges that arise in situations that have recurred for thousands of years. Like sweating, cough, and pain, they are facultative adaptations that are useful in certain situations. They evolve in concert with mechanisms that monitor for cues associated with the situations in which they are useful. Like all such responses, emotional responses can be pathologically excessive or deficient. Determining if an emotional response is abnormal requires knowing the situation it has been shaped to cope with, and whether or not that situation is present.

When a patient presents with pain, fever, or cough, clinicians search for what might be arousing the response, such as tissue damage, infection, or foreign material in the lungs. When a patient presents with a negative emotion, the same kind of investigation is needed, but the search is more difficult. Instead of being aroused by tissue pathology or infection, emotions are aroused by less tangible situations. Modern emotions theory emphasizes that the stimuli are not just cues; emotions arise from an individual's appraisal of what new information means for his or her ability to pursue personal goals. A thorough investigation of the context is essential to determine if an emotion is normal and useful, normal but useless, excessive, or deficient.

Low mood and anxiety are the emotions that most often cause problems. Almost all effort to understand these disorders has focused on what is different about people who experience intense anxiety or low mood, compared with other people. An evolutionary framework suggests different questions. Why do the capacities for anxiety and low mood exist at all? In what situations are they useful? Why are the mechanisms that regulate them so vulnerable to failure?

The most fundamental question is why emotions exist at all. Controversies about emotions distract from a growing consensus that they are special states shaped by natural selection along with regulation mechanisms that express a specific emotion in the situation where it gives a selective advantage. No one aspect of emotions is primary. Emotional states shift sensation, perception, cognition, behavior, physiology, motivation, and learning. Subjective experience is just one of many aspects of an emotion.

Controversy about emotion has focused on whether they are best viewed as distinct categories (the basic emotions view), or whether they are best understood as positions on dimensions, such as positive versus negative, and aroused versus calm. Neither perspective is consistent with the evolutionary origins of emotions. Emotions are neither fully separate nor fully dimensional; they are overlapping clusters of changes that have evolved from previous emotions. See Figure 4.1–1.

Some attempts to understand the utility of emotions have tried to map specific functions to specific emotions. However, most emotions serve multiple functions including motivation, communication, and changes in physiology and behavior. Emotions were not shaped to serve specific functions, they were shaped to increase the ability of



FIGURE 4.1-1. A phylogeny of emotions.

an individual to cope with the many challenges that arise in a situation that has recurred over evolutionary time. Being chased by a predator happened often enough that it reliably evokes a coordinated suite of physiological behavioral and emotional changes, the fight-flight response. Realizing one has broken a promise arouses guilt. Experiencing generous help arouses gratitude. The key to understanding an emotion is to understand the situation it was shaped for.

One profound implication for psychiatry is that negative emotions are useful. Their aversiveness is one aspect that contributes to their utility. Anxiety, low mood, jealousy, anger, and envy exist because our ancestors with a capacity for these emotions got a selective advantage compared with those who lacked them. Negative emotions seem pathological because they are usually associated with untoward circumstances, and because they are so painful and prone to interfere with important daily tasks. However, they exist only because they have been useful... for human genes, even if not always for human individuals.

Fear is useful in the face of threat. It mobilizes energy, cognition, and behavior to escape the danger. Like all adaptive responses, pathology can result from deficiencies as well as excesses. People with excessive anxiety crowd psychiatric clinics. People with deficiency of the fear response, hypophobia, cope poorly with dangerous situations, but they rarely come for treatment.

Anxiety is often distinguished from fear because it is aroused by less tangible dangers that are distant or social. It is especially prone to be aroused by situations where an individual is tempted to do something that might give a short-term advantage at a major social cost. Here too, pathology from excessive anxiety, especially social anxiety, is obvious, while the costs of anxiety deficiencies are far less obvious, even though sometimes more devastating. People with social

anxiety tend to seek treatment, those with deficient social sensitivity suffer major social losses.

The value of low mood is much less obvious. The term low mood allows description of states of low motivation, low self-esteem, and pessimism without the terminological tangles that accompany the word "depression." In what situation can sadness or low mood be useful? Sadness is aroused by a loss. It helps to recover, replace, or otherwise adjust to a loss. Low mood is aroused when efforts to reach a goal are proving fruitless. That situation has recurred millions of times for individuals in the course of human evolution. While simply persisting with a positive attitude seems intuitively attractive, that is not the best strategy when foraging in winter, trapped in pursuit of an uninterested partner, or trying for the fifth year in a row to get into medical school. In such situations it is best to pause, conserve energy, consider other strategies, and, if no route appears viable after all options have been explored, give up, and put energies toward a more achievable goal.

A 20-year-old community college student requested help for moderately severe depression that was interfering with his ability to pass his courses. He said he had to stay in school or his fabulous girlfriend would leave him. When asked about the girlfriend, he said she was still in high school but planning after graduation to attend a college called Vassar. He was dead set on persisting in school despite his failing grades in order to preserve the relationship. Medication and psychotherapy were only modestly helpful over a 2-month period, but he returned at 3 months to report that his symptoms were gone and he had stopped his medication weeks ago. When asked about the girlfriend he said, "Oh, you mean the old girlfriend. She was too uppity for me, my new girlfriend is much more down to earth."

Continued pursuit of an unreachable goal can escalate low mood into clinical depression. There are many possible reasons for inability to give up a goal. Few parents are able to give up trying to get a child off of drugs or alcohol. Many individuals have identities so grounded in their careers that they persist despite years of failure. And often, in the face of impending divorce, one partner persists in trying to preserve the relationship, even as demoralization turns into depression.

Other hypotheses about the origins of capacities for depression are also under consideration. One is that depressive rumination is useful for finding solutions to complex social problems. Another is that depression motivates looking inwardat what one can do to avoid being expelled from a group. Another is that depression symptoms give benefits by manipulating others. A particularly influential and plausible proposal is summarized in the phrase "involuntary yielding," After losing a status competition, persisting in challenging the winner will likely bring more attacks or expulsion from the group. Experiencing oneself as helpless and lower status than one actually is can prevent such attacks. The relevant situation is pursuing an unreachable goal in the domain of status competition. Subtypes of low mood have been shaped to cope with the pursuit of different kinds of goals.

Jealousy is aroused by a threat of loss of a mate or the mate's fidelity. Responsible for vast interpersonal problems and millions of murders, sexual jealousy is a toxic emotion. However, the situation of a mating relationship being threatened by an outsider has occurred so often over human evolutionary history, with such extreme effects on reproductive success, that it has shaped a specialized pattern of responses. The actions characteristic of jealousy are often unreasonable in the extreme, but game theory tells us that unpredictability is essential to a successful strategy. Being predictable means being manipulable. Not being fully aware of one's motives or able to control one's behavior may well be advantageous. Once again, the benelits may be for one's gencs, not necessarily for oneself.



Table 4.1–2. Emotions Aroused by Situations That Emerge in Reciprocity Relationships

	Other Cooperates	Other Defects
lou cooperate	Triendship, trust	Suspicion (before) Anger (after)
You defect	Anxiety (before) Guilt (after)	Rejection, disgust

Positive emotions are equally useful, even if not, unfortunately, so common, In situations characterized by short-term opportunities, enhasiasm, risk-taking, and energetic initiative are all valuable. This suggests that short-term opportunities will give rise to more enthusiasm and effort than long-term opportunities. Excesses of positive mood rarely motivate treatment-seeking except when they go the extremes found in mania.

The resources that influence human reproductive success are overwhelmingly social, so specific emotions were shaped to cope with the situations that arise in relationships. The boxes of the prisoner's dilemma lend themselves well to understanding the origins of some social emotions. The game is named for situations in which the police offer leniency to whichever of two suspects first confesses the details of a crime. The dilemma arises because keeping quiet results in a modest punishment, but each prisoner knows that he will get a higher sentence if the other confesses first to avoid any punishment,

Repeated cooperation by both parties arouses friendship, loyalty, and trust. If you cooperate when the other defects, anger is the reliable result. It signals that apologies and reparations are required to preserve the relationship. It also may be accompanied by spite, motivations to harm the defector even when the costs are larger for the self. This apparently senseless emotion gives advantages by its powerful ability to keep others from defecting when they otherwise would. The game-theoretic best strategy of doing what the other person did on the previous move is called tit-for-tat. It accounts for the runs of cooperation and defection seen in relationships (Table 4.1–2).

RELATIONSHIPS

Views of human relationships as fully explained by kinship and reciprocity are grossly simplistic. A small research industry has grown up to try to explain apparent anomalies of human social behavior, including tendencies to cooperation even without guarantee of payback, willingness to punish defectors even when that will harm the actor, and eagerness for spiteful revenge that can have no direct payoff.

A key to such anomalies is found in a variation on the core principle. Just as selection shapes bodies to maximize reproductive success, even at a cost to health or longevity, it shapes minds and emotions to maximize reproductive success at the expense of rationality. As Robert Trivers pointed out in his preface to *The Selfish Gene*, the idea that selection shaped us for objective thought is naïve indeed. Often, especially in social situations, commitments beyond justification, and wishes for revenge beyond measure, are more useful.

This has an important implication for psychoanalysis and psychotherapy in general. While self-knowledge is desirable and can be enormously helpful, lack of conscious access to one's own motives and emotions may sometimes be adaptive. It has been suggested that the human capacity for psychodynamic defenses that maintain active repression of memories and motives may give selective advantages, not just by making life more bearable, but also by influencing others.

The field of sociobiology studies how natural selection shapes social behaviors and resulting group behaviors. There is no room here to explore its well-developed framework; however, when a relationship is at the root of a clinical problem, as is often the case, a formal analysis of how that relationship is or is not working offers a solid starting place. This is very different from trying to understand the personality traits of the participants or the early events that lead to distortions and rigid relationship strategies. Instead, it looks at the history and current state of exchanges and expectations in the relationship.

While this perspective is just beginning to be applied, some clinical phenomena are readily approached from this point of view. For instance, the classic borderline personality pattern of excessive immediate intimacy and adulation, followed by disappointment and distancing, reflects a rigid relationship strategy of intense personal commitment that, when not reciprocated, leads to rejection and anger. The pattern in neurosis is more one of trying always to please others, and being angry when they do not live up to expectations.

EXPLAINING VULNERABILITY TO SPECIFIC DISORDERS

Every medical disorder needs two kinds of explanation. First, a proximate explanation for what aspect of the body's mechanism has gone awry, and why. Second, an evolutionary explanation for why natural selection has left the body vulnerable to this kind of failure. The six categories from evolutionary medicine help to explain vulnerability to mental disorders, just as they do to other medical disorders.

Disorders of Emotions

As noted already for anxiety and mood disorders, emotional disorders result from dysregulation of otherwise useful responses. This means that determining whether a particular emotion is normal or abnormal requires understanding the situation in which that emotion is useful, the cues that usually regulate it, and the presence or absence of that situation. Current DSM diagnostic criteria ignore context and attend only to frequency, severity, and duration of emotional symptoms. This works well at the extremes and increases diagnostic reliability, but gives no guidance in the more common cases where it is hard to decide if an emotion is normal or not.

The tendency to automatically view negative emotions as pathological contributes greatly to this problem, as does the failure to recognize that emotional responses were shaped to benefit reproductive success, not individual welfare. The functional significance of negative emotions should in no way inhibit attempts to relieve them. The rest of medicine routinely provides relief from the suffering that accompanies normal pain, fever, cough, and other symptoms. Psychiatrists should not be inhibited about relieving anxiety, low mood, and jealousy, even when they are normal responses. Having an evolutionary perspective on the origins and functions of such emotions gives clinicians a framework for understanding the causes of such emotions, and when blocking a negative emotion might be unwise.

A professional motorcycle racer requested treatment because he was unable to sleep or keep food down the night before a race. The problem started when a friend died in a crash. It became worse after another crash caused another friend to become quadriplegic. He denied symptoms of other disorders and denied problems with anxiety before his friend's crashes. He had predictable difficulty recognizing the potentially life-saving nature of his anxiety.

The other categories of evolutionary explanation for vulnerability also apply for emotional disorders. Useless emotions can be aroused by aspects of modern environments, such as being trapped in a hierarchical bureaucracy. Emotions routinely involve trade-offs, with both costs and benefits from excessive or deficient expression. Finally, emotions all too often motivate behavior that is good for reproductive success, but bad for an individual's health and well-being. Examples include sexual desires that cannot be satisfied, jealousy, envy, wishes for revenge, and ambitions that result in constant dissatisfaction. There are, unfortunately, good evolutionary reasons why such emotions are prevalent, aversive, and hard to control.

Schizophrenia

Most of the variation in risk for schizophrenia results from genetic variation. Why did not natural selection eliminate the responsible alleles? Many have suggested possible advantages to those with the disorder, or, more plausibly, to their relatives. However, reproductive success for people with schizophrenia is a fraction of that for other people, and there is no documented advantage for relatives, so this hypothesis fails. Others have suggested that it is a disease of modern environments, but there is limited evidence for dramatically lower rates in nonindustrial societies. New genetic evidence finds that every identified common allele that increases schizophrenia risk has only a tiny effect. Larger effects are mostly due to rare copy-number variations. This pattern is exactly what one would expect if selection were continuously and efficiently purging vulnerability alleles from the genome. Increased rates of schizophrenia associated with older paternal age and runs of homozygosity further support the hypothesis that alleles predisposing to schizophrenia are in mutation-selection balance

This leaves open the question of why the cognitive system is so vulnerable to this particular kind of failure. One possibility is that some advantageous cognitive trait has been pushed close to a fitness "cliff edge" beyond which failure is likely, just as strong selection for speed in race horses has made their lower leg bones long, light, and thin, but vulnerable to breaking. The neural mechanism could involve neuron pruning, cortical folding, or any number of other traits that give major benefits up to some threshold beyond which failure becomes likely.

Substance Abuse

The devastation and early death resulting from substance abuse selects against the alleles that increase vulnerability. However, pure substances and means to administer them have been reliably and readily available for far too little time for selection to have a big effect. From this perspective, vulnerability to substance abuse is a product of mismatch with modern environments. Chemicals mediate the brain's motivation and learning systems, so it should be no surprise that exogenous chemicals can hijack those systems. The amazing thing is that so many people can use drugs and alcohol without major problems. Active efforts are underway to understand why some people have brain mechanisms that make them especially vulnerable. It would be most interesting to see how people with high and low levels of vulnerability behave in environments where substances of abuse are not readily available. Do they use different strategies when foraging for food? Are their interpersonal relationships different? Answering these questions could lead to new behavioral tests that estimate vulnerability.

Eating Disorders

Anorexia and bulimia have likely become more common in the past century. The predisposing alleles are almost certainly quirks without major effects on fitness until they interact with modern environments. Developmental and personality factors strongly influence who gets an eating disorder. However, the shared human vulnerability seems to result from evolved nutrition regulation mechanisms interacting with novel environmental exposures. Good candidates include the ready availability of every imaginable kind of food, a resulting epidemic of obesity, and media that portray slimmer-than-real bodies. Most serious eating disorders are initiated by a strict diet. The resulting binge eating would be life-saving in a famine, but it causes panic and guilt in dieters, and increased resolve to more strictly restrict intake, creating a vicious cycle.

Child Abuse

It makes no evolutionary sense for parents to harm their own children. This led evolutionary psychologists to investigate whether the risk of death of a child depends on how it is related to the parents. The finding is remarkable—death rates from child abuse are 80 times higher if there is a step-parent in the home. This research was inspired by studies of vervet monkeys that found infanticide to be routine when a new male takes over a harem. Eliminating nursing infants speeds return to estrus in the females, thus increasing the reproductive success of the new male during the relatively brief window until another male displaces him. The different human mating system means that infanticide in humans gives no such advantage and was not shaped by selection. However, not being with both parents from the start seems to interfere with the bonding that usually protects children from harm.

Extended early contact also seems to be the signal that makes parents and children uninterested in each other as sex partners. For instance, children raised together from their early years in a kib-butz experience embarrassment and disgust at the idea of marrying another member of the group. Over evolutionary time, this incest inhibition mechanism has increased reproductive success by reducing the risk of having children with many pairs of identical deleterious recessive genes. In this example, cultural prohibitions amplify already existing evolved inhibitions. The relevance to psychiatry all too obvious in cases where such inhibitions are weak because parent has little early contact with a child. It is interesting to consider if the development of such inhibitions is related to early Oedips wishes and their subsequent repression.

Sociopathy

The range of prosocial tendencies in humans is breathtaking. Some individuals lie awake nights wondering if some small oversight might have caused others inconvenience, while sociopaths take pleasure in deceiving others and sadistically causing them pain. In the case, selection seems not to have settled on a narrow optimal measure frequency-dependent selection has been proposed as a possible explanation.

If people with sociopathic tendencies do well in groups when there are many cooperators to exploit, but badly in groups when many others are also sociopathic, this could maintain a small proportion of sociopaths in the population. Their tendency toward sexual license and lack of commitment to families and children could give an advantage until the proportion of sociopathic individuals becomes

high enough that they must deal with each other, and until cooperative individuals have developed strong abilities to detect and avoid them. This hypothesis is supported by the high heritability for sociopathy, but it is undermined by evidence for minor neurologic abnormalities in many such individuals, and by the role of early abuse and neglect. From a longer-term perspective, the presumed relatively recent evolution of strong prosocial tendencies may turn out to be important. Note that these evolutionary explanations say little about why some people become sociopathic and others do not. They only explain how extreme prosocial traits may give selective advantages, and why not all individuals may have such traits.

Personality Disorders

Other personality disorders are also characterized by rigid extremes of social strategies. People with obsessive-compulsive personality traits do their duty to an extreme, expect others to be equally conscientious, and are constantly disappointed. Ordinary neurotics are not so rigid, but they also invest huge proportions of life effort into trying to please others, and they also often experience disappointment. Those with paranoid tendencies expect that others will deceive or harm them, and their lack of trust means they have difficulty finding relationship partners who can correct their misperception. Those with anxious, avoidant personalities invest vastly excessive proportions of life energy into protecting against possible harm in general. Dependent personality tendencies result in overwhelming investments in particular relationships, and in preserving those relationships. From an evolutionary point of view, personality disorders are not interpreted as adaptations, but as extremes of normal personality dimensions that reflect different social strategies.

FUTURE DIRECTIONS

The evolutionary foundations for psychiatry provide an invaluable framework for understanding behavior, relationships, and emotions. Clinicians who understand the evolutionary origins and functions of emotions have tools that allow them to better understand disorders of emotions. Those who understand the evolutionary origins of capacities for relationships are better able to deal with problematic relationships and the emotions they arouse. Those who understand how natural selection has shaped extreme prosocial tendencies in humans are better able to understand social anxiety and neurosis. Those who recognize personality characteristics as social strategies have a framework for understanding personality disorders. Most globally, clinicians who grasp the distinction between proximate and evolutionary explanations are well prepared to integrate their knowledge of factors increasing risks for individuals with their knowledge about the evolutionary reasons why all members of the species are vulnerable to a particular disorder.

The implications for research are perhaps even more important. Huge efforts to try to identify specific disorders based on specific brain abnormalities will eventually succeed for some disorders, but others will turn out to be, like epilepsy or congestive heart failure, failures in evolved systems that can have many causes. Severe brain disorders such as autism and schizophrenia may turn out to have a specific, consistent neuropathology, but an evolutionary view suggests that there should be openness to the possibility that they result from systems that have been pushed by selection close to some fitness cliff edge, or that they are otherwise intrinsically vulnerable to failure for other good evolutionary reasons.

Implications for studies of treatment are substantial. Studies of drugs to relieve emotional suffering are often framed as normalizing neurotransmitter abnormalities. However, recognizing that even negative emotions are useful suggests that drugs relieving aversive emotions are like drugs that relieve cough or fever by blocking normal mediating mechanisms. Studies of cognitive-behavioral interventions increasingly go beyond simple learning theory to also consider social factors that influence schemas, and the advantages as well as the disadvantages of distorted thinking. They also increasingly recognize the power of social groups and relationships to get people to carry out behavioral exercises that are difficult, but essential. Interpersonal therapy analyzes social roles and conflicts that almost invariably involve struggles to get important reproductive resources, and trade-offs among conflicting strategies, roles, and relationships.

This chapter provides only the briefest sketch of a basic science whose implications for psychiatric research and treatment are just beginning to be explored. Recognizing the opportunities will lead to increased support for research that should result in major advances.

REFERENCES

*Alcock J. The Triumph of Sociobiology. New York: Oxford University Press; 2001.

Alcock J. Animal Behavior: An Evolutionary Approach. 10th ed. Sunderland, MA: Sinauer Associates; 2013.

Baron-Cohen S, ed. *The Maladapted Mind*. East Sussex: Psychology Press, Erlbaum; 1997.
*Brüne M. *Textbook of Evolutionary Psychiatry: The Origins of Psychopathology.* 2nd ed. Oxford; New York: Oxford University Press; 2016.

Brüne M, Belsky J, Fabrega H, et al. The crisis of psychiatry—insights and prospects from evolutionary theory. World Psychiatry. 2012;11(1):55-57.

Crespi B. An evolutionary framework for psychological maladaptations. Psychological Inquiry, 2014;25(3-4):322–324.

Crespi B, Foster K, Úbeda F. First principles of Hamiltonian medicine. Philosophical Transactions of the Royal Society B: *Biological Sciences*, 2014;369(1642): 20130366–20130366.

Crespi B, Stead P, Elliot M. Evolution in health and medicine Sackler colloquium: Comparative genomics of autism and schizophrenia. *Pruc Natl Acad Sci US A*, 2010; 107(Suppl 1):1736–1741.

Del Giudice M, Ellis BJ, Cicchetti D. Evolutionary foundations of developmental psychopathology. Developmental Psychopathology. 2014;1.

Fried El, Nesse RM. Depression sum-scores don't add up: why analyzing specific depression symptoms is essential. BMC Medicine. 2015;1(1):72.

Gilbert P. Evolution and depression: issues and implications, *Psychol Med.* 2006;36(03): 287–297.

Gilbert P, Bailey KG. Genes on the Couch: Explorations in Evolutionary Psychotherapy. Philadelphia, PA: Taylor & Francis; 2000.

Horwitz AV, Wakefield JC. The Loss of Sadness: How Psychiatry Transformed Normal Sorrow into Depressive Disorder. New York: Oxford University Press; 2007.

Horwitz AV, Wakefield JC. All we have to fear: Psychiatry's transformation of natural anxieties into mental disorders. New York, NY: Oxford University Press; 2012.

*Krebs JR, Davies NB. Behavioural Ecology: An Evolutionary Approach. 4th ed. Cambridge, MA: Blackwell Science; 1997.

McGuire MT, Troisi A. *Darwinian Psychiatry*. Cambridge, MA: Harvard University Press; 1998.

Nesse RM. Explaining depression: neuroscience is not enough, evolution is essential. In: Pariente CM, Nesse RM, Nutt DJ, Wolpert L, eds. *Understanding Depression: A Translational Approach*. Oxford; 2009:17–35.

*Nesse RM. Ten questions for evolutionary studies of disease vulnerability, Evol Appl. 2011;4(2):264–277.

Nesse RM. Evolutionary Psychology and Mental Health. In D. Buss (Ed.), The Evolutionary Psychology Handbook. 2nd ed., Vol. 2: Integrations, pp. 1007–1026. New York, NY: John Wiley and Sons; 2015.

Nesse RM, Bergstrom CT, Ellison PT, et al. Making evolutionary biology a basic science for medicine. Pruc Nat. Acad Sci U S A. 2010;107:1800–1807.

Nesse RM, Berridge KC. Psychoactive drug use in evolutionary perspective. Science, 1997;278:63–66.

Nesse RM, Ellsworth PC. Evolution, emotions, and emotional disorders. Am Psychol. 2009;64(2):129–139.
 Nesse RM, Stein DJ. Towards a genuinely medical model for psychiatric nosology. BMC

Med. 2012;10(1):5.

*Nesse RM, Williams GC. Why We Get Sick—The New Science of Darwinian Medicine, New York: Times Books: 1994.

Price J, Sloman L, Gardner R, Gilbert P, Rohde P. The social competition hypothesis of depression. Br J Psychiatry. 1994;164;309–315.

Stearns SC, Koella JC, eds. Evolution in Health and Disease. 2nd ed. New York: Oxford University Press; 2008. Troisi A. Mental health and well-being: clinical applications of Darwinian psychiatry. Applied Evolutionary Psychology. 2012:276.

van Dongen J, Boomsma DI. The evolutionary paradox and the missing heritability of schizophrenia. Am J Med Genet B Neuropsychiatr Genet. 2013;162(2):122-136.
Wenegrat B. Sociobiological Psychiatry: A New Conceptual Framework. Lexington, MS: Lexington; 1990.

▲ 4.2 Neurocentrism: Implications for Addiction and the Courtroom

SALLY L. SATEL, M.D., AND SCOTT O. LILIENFELD, Ph.D.

In the early 21st century, neuroscience has captured the public imagination like never before. Understanding the brain is helpful, perhaps essential, to developing treatments for devastating illnesses like schizophrenia and Parkinson's. More abstract but no less compelling, the functioning of the brain is intimately tied to one's identity, memories, and aspirations. But the excitement to explore the brain has spawned a new fixation that one might call *neurocentrism*—the view that human behavior can be best explained by looking solely or primarily at the brain.

In the view of some critics neurocentrism poses a threat to psychiatry because it risks oversimplifying a number of complex issues. In its extreme form, it devalues the importance of psychological explanations and environmental factors, such as familial chaos and stressors, understanding disturbances of mood, thought, and overt behavior. In turn, neurocentrism may pose a distraction from seeking effective and perhaps more enduring solutions, including psychotherapies, and may imply that pharmaceutical approaches should be first-line intervention for addictions and other behavioral problems.

The prime impetus behind this enthusiasm is functional magnetic resonance imaging (fMRI) and the now-iconic, vibrant brain images that grace the science pages of the daily newspaper. Author Tom Wolfe was characteristically prescient when he wrote of fMRI in 1996, just a few years after its introduction, "Anyone who cares to get up early and catch a truly blinding twenty-first century dawn will want to keep an eye on it." Why the fixation? First, there is the very subject of the scans: the brain itself. More complex than any structure in the known cosmos, the brain is a masterwork of nature endowed with cognitive powers that far outstrip the capacity of any silicon machine built to emulate it. Containing roughly 85 billion brain cells, or neurons, each of which communicates with thousands of other neurons, this 3-lb universe cradled between the ears has more connections than there are stars in the Milky Way. How this enormous neural edifice gives rise to subjective feelings, a question often called the "hard problem" of consciousness, is one of the greatest mysteries of science and philosophy. Combine this mystique with the simple fact that multicolored pictures—in this case, brain scans—can be powerful. Of all the human senses, vision is the most developed and occupies the largest share of cortical space.

There are good evolutionary reasons for this arrangement: The major threats to primate ancestors were apprehended visually, as were their sources of food. Plausibly, the survival advantage of vision gave rise to man's reflexive bias for believing that the world is as he or she perceive it to be, an error that psychologists and philosophers call naive realism. This misplaced faith in the trustworthiness of

one's perceptions is the wellspring of two of history's most famously misguided theories: that the world is flat and that the sun revolves around the earth. For thousands of years, people trusted their raw impressions of the heavens. Yet, as Galileo understood all too well, the eyes can deceive. He wrote in his *Dialogues* of 1632 that the Copernican model of the heliocentric universe commits a "rape upon the senses"—it violates everything the eyes reveal.

Trusting the patterns on brain scans to reveal nuanced mental contents is a form of neurorealism, a term coined by University of Montreal researcher Eric Racine. A first cousin of naive realism, neurorealism denotes the fallacious but tempting propensity to regard brain images as inherently more "real" or valid than other types of behavioral data. As Stanford neuroeconomist Paul Zak has described his work on the neurobiology of trust, a brain scan "lets me embrace words like 'morality' or 'love' or 'compassion' in a non-squishy way. These are real things." Or take the psychological impact of combat. A researcher at the Minneapolis VA tells TIME magazine that claimed that brain imaging confirms that posttraumatic stress disorder (PTSD) is a "real disorder." In both quotes, it is not clear that brain images provide with novel information; such images are not required to conclude that love or PTSD is genuine.

As a tool for exploring the biology of the mind, neuroimaging has given neuroscience not merely a huge scientific boost but a strong cultural presence. As one scientist remarked, brain images are now "replacing Bohr's planetary atom as the symbol of science." With its implied promise of decoding the brain, it is easy to see why brain imaging would beguile almost anyone interested in pulling back the curtain on the mental lives of others: politicians hoping to manipulate voter attitudes, marketers tapping the brain to learn what consumers really want to buy, agents of the law seeking an infallible lie deteror, addiction researchers trying to gauge the pull of temptation psychologists and psychiatrists seeking the causes of mental illneand defense attorneys fighting to prove that their clients lack malintent or even free will. At the same time, this fascination is a doubledged sword, as it may lead eager audiences to accept dubious new science claims without adequate scrutiny.

Some misapplications of neuroscience are merely amusing a may be essentially harmless. Take, for instance, the new trend neuro-management books, such as one entitled *Your Brain as Business: The Neuroscience of Great Leader.* The latter advis nervous CEOs "to be aware that anxiety centers in the brain conect to thinking centers, including the PFC [prefrontal cortex] as ACC [anterior cingulate cortex]." The fad has, perhaps not surpringly, infiltrated the parenting and education markets, too. Parel and teachers are easy marks for "brain gyms," "brain-compatibe education," and "brain-based parenting," not to mention dozens other unsubstantiated techniques. Although these methods may be dangerous *per se*, they may incur both direct financial costs as opportunity costs arising from a failure to seek out more efficacion interventions.

For the most part, these enterprises merely dress up or repackage good advice with neuroscientific findings that add little or nothing to the overall program. As one cognitive psychologist quipped, "Unable to persuade others about your viewpoint? Take a Neuro-Prefix—influence grows or your money back." But reading too much into brain scans can be a problem when real-world concerns hang in the balance. Consider the law. When a person commits a crime, who is at fault: the perpetrator or his or her brain? This is a false choice. If biology teaches anything, it is that "my brain" versus "me" is a false distinction. Still, if biological roots can be identified—and better yet, captured on a brain scan as juicy blotches of color—it is too easy for nonprofessionals to assume that the behavior under scrutiny