



CHAPTER 1

Conceptual Foundations of Evolutionary Psychology

JOHN TOOBY and LEDA COSMIDES

THE EMERGENCE OF EVOLUTIONARY PSYCHOLOGY: WHAT IS AT STAKE?

THE THEORY OF evolution by natural selection has revolutionary implications for understanding the design of the human mind and brain, as Darwin himself was the first to recognize (Darwin, 1859). Indeed, a principled understanding of the network of causation that built the functional architecture of the human species offers the possibility of transforming the study of humanity into a natural science capable of precision and rapid progress. Yet, nearly a century and a half after *The Origin of Species* was published, the psychological, social, and behavioral sciences remain largely untouched by these implications, and many of these disciplines continue to be founded on assumptions evolutionarily informed researchers know to be false (Pinker, 2002; Tooby & Cosmides, 1992). Evolutionary psychology is the long-forested scientific attempt to assemble out of the disjointed, fragmentary, and mutually contradictory human disciplines a single, logically integrated research framework for the psychological, social, and behavioral sciences—a framework that not only incorporates the evolutionary sciences on a full and equal basis, but that systematically works out all of the revisions in existing belief and research practice that such a synthesis requires (Tooby & Cosmides, 1992).

The long-term scientific goal toward which evolutionary psychologists are working is the mapping of our universal human nature. By this, we mean the construction of a set of empirically validated, high-resolution models of the evolved mechanisms that collectively constitute universal human nature. Because the evolved function of a psychological mechanism is computational—to regulate behavior and the body adaptively in response to informational inputs—such a model consists of a description of the functional circuit logic or information

We dedicate this chapter to Irven DeVore, professor emeritus, Department of Anthropology, Harvard University, on the occasion of his 70th birthday.

6 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

processing architecture of a mechanism (Cosmides & Tooby, 1987; Tooby & Cosmides, 1992). Eventually, these models should include the neural, developmental, and genetic bases of these mechanisms, and encompass the designs of other species as well.

A genuine, detailed specification of the circuit logic of human nature is expected to become the theoretical centerpiece of a newly reconstituted set of social sciences, because each model of an evolved psychological mechanism makes predictions about the psychological, behavioral, and social phenomena the circuits generate or influence. (For example, the evolutionarily specialized mechanisms underlying human alliance help to explain phenomena such as racism and group dynamics; Kurzban, Tooby, & Cosmides, 2001.) A growing inventory of such models will catalyze the transformation of the social sciences from fields that are predominantly descriptive, soft, and particularistic into theoretically principled scientific disciplines with genuine predictive and explanatory power. Evolutionary psychology in the narrow sense is the scientific project of mapping our evolved psychological mechanisms; in the broad sense, it includes the project of reformulating and expanding the social sciences (and medical sciences) in light of the progressive mapping of our species' evolved architecture.

The resulting changes to the social sciences are expected to be dramatic and far-reaching because the traditional conceptual framework for the social and behavioral sciences—what we have called the *Standard Social Science Model* (SSSM)—was built from defective assumptions about the nature of the human psychological architecture (for an analysis of the SSSM, see Tooby & Cosmides, 1992). The most consequential assumption is that the human psychological architecture consists predominantly of learning and reasoning mechanisms that are general-purpose, content-independent, and equipotential (Pinker, 2002; Tooby & Cosmides, 1992). That is, the mind is blank-slate like, and lacks specialized circuits that were designed by natural selection to respond differentially to inputs by virtue of their evolved significance. This presumed psychology justifies a crucial foundational claim: Just as a blank piece of paper plays no causal role in determining the content that is inscribed on it, the blank-slate view of the mind rationalizes the belief that the evolved organization of the mind plays little causal role in generating the content of human social and mental life. The mind with its learning capacity absorbs its content and organization almost entirely from external sources. Hence, according to the standard model, the social and cultural phenomena studied by the social sciences are autonomous and disconnected from any nontrivial causal patterning originating in our evolved psychological mechanisms. Organization flows inward to the mind, but does not flow outward (Geertz, 1973; Sahlin, 1976).

Yet if—as evolutionary psychologists have been demonstrating—the blank-slate view of the mind is wrong, then the social science project of the past century is not only wrong but radically misconceived. The blank-slate assumption removes the central causal organizers of social phenomena—evolved psychological mechanisms—from the analysis of social events, rendering the social sciences powerless to understand the animating logic of the social world. Evolutionary psychology provokes so much reflexive opposition because the stakes for many social scientists, behavioral scientists, and humanists are so high: If evolutionary psychology turns out to be well-founded, then the existing superstructure of the social and behavioral sciences—the Standard Social Science Model—will have to be disman-

tled. Instead, a new social science framework will need to be assembled in its place that recognizes that models of psychological mechanisms are essential constituents of social theories (Boyer, 2001; Sperber, 1994, 1996; Tooby & Cosmides, 1992). Within such a framework, the circuit logic of each evolved mechanism contributes to the explanation of every social or cultural phenomenon it influences or helps to generate. For example, the nature of the social interactions between the sexes are partly rooted in the design features of evolved mechanisms for mate preference and acquisition (Buss, 1994, 2000; Daly & Wilson, 1988; Symons, 1979); the patterned incidence of violence is partly explained by our species' psychology of aggression, parenting, and sexuality (Daly & Wilson, 1988); the foundations of trade can be located in evolved cognitive specializations for social exchange (Cosmides & Tooby, 1992, this volume); both incest avoidance and love for family members are rooted in evolved mechanisms for kin recognition (Lieberman, Tooby, & Cosmides, 2003, in press-a, in press-b). Indeed, even though the field is in its infancy, evolutionary psychologists have already identified a large set of examples that touch almost every aspect of human life (see, e.g., the chapters of this volume, as well as the chapters in Barkow, Cosmides, & Tooby, 1992).

For almost a century, adherence to the Standard Social Science Model has been strongly moralized within the scholarly world, immunizing key aspects from criticism and reform (Pinker, 2002; Tooby & Cosmides, 1992). As a result, in the international scholarly community, criteria for belief fixation have often strayed disturbingly far from the scientific merits of the issues involved, whenever research trajectories produce results that threaten to undermine the credibility of the Standard Social Science Model. Nevertheless, in recent decades, the strain of ignoring, exceptionalizing, or explaining away the growing weight of evidence contradicting traditional theories has become severe. Equally, reexaminations of the arguments advanced in favor of the moral necessity of the Standard Social Science Model suggest that they—at best—result from misplaced fears (Pinker, 2002; Tooby & Cosmides, 1992). Indeed, we may all have been complicit in the perpetuation of vast tides of human suffering—suffering that might have been prevented if the scientific community had not chosen to postpone or forgo a more veridical social and behavioral science.

THE INTELLECTUAL ORIGINS OF EVOLUTIONARY PSYCHOLOGY

Despite the marginalization of Darwinism within psychology during the twentieth century, a diverse minority of thinkers tried to think through how Darwinian insights could be applied to behavior. These efforts led to many valuable approaches, including: the instinct psychology of William James and William McDougall; the ethological approach of Tinbergen, Lorenz, and von Frisch, which integrated the careful observation of animal behavior in natural contexts with investigations of its adaptive significance and physiological basis; the sociobiological approach of Richard Alexander, William Hamilton, Robert Trivers, Edward O. Wilson, and many others, which tried to explain patterns of social behavior—differences as well as universals—in humans and other species in terms of their fitness consequences; nativist approaches to language pioneered by Chomsky (1959, 1966), Lenneberg (1967), and others, which brought to wider attention the question of whether one general-purpose learning system could

8 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

account for all learning; and even behaviorist psychology—quite orthodox with respect to the Standard Social Science Model—looked for phylogenetic continuities in the laws of learning that would apply across species. As valuable as each of these approaches turned out to be, conceptual handicaps internal to each program limited their scope of application and their capacity to usefully reorganize the human psychological, behavioral, and social sciences.

The way past these limitations involved isolating or deriving a core set of foundational concepts from the intersection of physics, biology, and information theory, elucidating their logical and causal interrelationships, and then building back upward from this groundwork. (A few representative concepts are *function*, *regulation*, *computational architecture*, *adaptation*, *organization*, *design*, *entropy*, *selection*, *replication*, *selection pressure*, *by-product*, *environment of evolutionary adaptedness*, and *task environment*.) These concepts could then be used to trace out the necessary interconnections among several previously distinct scientific programs, so that the previously independent (and inconsistent) disciplinary building blocks could be integrated into a single unified framework (Tooby & Cosmides, 1992). The building blocks from which evolutionary psychology was assembled include the modern revolution in theoretical evolutionary biology (Williams, 1966), the rise of the computational sciences (Shannon, 1948), the emergence of serious attempts to reconstruct the ancestral conditions and ways of life of humans and prehumans (e.g., Cheney et al., 1987; Lee & DeVore, 1968, 1976), and an adaptationist/computationalist resolution of the debate between environmentalists and nativists (e.g., Cosmides & Tooby, 1987; Tooby & Cosmides, 1990a, 1990b, 1992; Tooby, Cosmides, & Barrett, 2003).

The first building block of evolutionary psychology was the strain of theoretical evolutionary biology that started in the late 1950s and early 1960s, especially with the work of George Williams (Williams, 1966; Williams & Williams, 1957); William D. Hamilton (1964); and John Maynard Smith (1982). By being placed on a more rigorous, formal foundation of replicator dynamics, evolutionary biology was transformed over the ensuing decades from a vaguely conceptualized and sometimes implicitly teleological field into a principled discipline that rivals physics in its theoretical beauty and explanatory power. One face of this transformation has been the derivation of a series of elegant selectionist theories—theories of how natural selection acts on altruism, kinship, cooperation, mating, foraging, reproduction, parenting, risk taking, aggression, senescence, host-parasite interactions, intragenomic conflict, life history, communication, and many other dimensions of life. Research in biology and the human sciences informed by these theories is called sociobiology, behavioral ecology, or evolutionary ecology.

The other face of this revolution in biology is modern adaptationism—a set of deductions that are still often misunderstood, even in biology (Dawkins, 1986; Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2003; Williams, 1966). Adaptationism is based on the recognition that selection is the only known natural physical process that builds highly ordered functional organization (adaptations) into the designs of species, in a world otherwise continuously assaulted by the ubiquitous entropic tendency of physical systems to become increasingly disordered with time. Thus, although not everything is functional, whenever complex functional organization is found in the architectures of species, its existence and form can be traced back to a previous history of selection. Moreover, for a given selection pressure to drive an allele systematically upward until it is

incorporated into the species-typical design, the same selective cause-and-effect relationship must recur across large areas and for many generations. Complex adaptations necessarily reflect the functional demands of the cross-generationally long-enduring structure of the organism's ancestral world, rather than modern, local, transient, or individual conditions. This is why evolutionary psychology as an adaptationist field concerns the functional design of mechanisms given a recurrently structured ancestral world, rather than the idea that behavior is the fitness striving of individuals tailored to unique circumstances (Symons, 1992; Tooby & Cosmides, 1990a).

Consequently, systems of complex, antientropic functional organization (adaptations) in organisms require explanation wherever they are found; their correct explanation (barring supernatural events or artificial intervention) always involves a specific history of selection in ancestral environments; and so the prediction, discovery, mapping, and understanding of the functional architecture of organisms can be greatly facilitated by analyzing the recurrent structure of a species' ancestral world, in conjunction with the selection pressures that operated ancestrally. The foundational recognition that psychological mechanisms are evolved adaptations connects evolutionary biology to psychology in the strongest possible fashion, allowing everything we know about the study of adaptations to be applied to the study of psychological mechanisms. Psychology and evolutionary biology can no longer be defensibly divorced.

George Williams's 1966 volume, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* was central to both the selectionist and adaptationist revolutions. In it, Williams provided the first fully modern statement of the relationship between selection and adaptive design; clarified that selection operates at the genic level; developed strict evidentiary standards for deciding what aspects of a species' phenotype were adaptations, by-products of adaptations, or noise, and usefully distinguished the present usefulness of traits from their evolved functions (if any).¹

The second building block of evolutionary psychology was the rise of the computational sciences and the recognition of the true character of mental phenomena. Boole (1848) and Frege (1879) formalized logic in such a way that it became possible to see how logical operations could be carried out mechanically, automatically, and hence through purely physical causation, without the need for an animate interpretive intelligence to carry out the steps. This raised the irresistible theoretical possibility that not only logic but other mental phenomena such as goals and learning also consisted of formal relationships embodied non-vitalistically in physical processes (Weiner, 1948). With the rise of information theory, the development of the first computers, and advances in neuroscience, it became widely understood that mental events consisted of transformations of

¹The arguments that not every trait is an adaptation, not all beneficial effects of a trait are its functions, that phenotypes are full of by-products, and that there are constraints on developing systems were all central to Williams's 1966 critique of evolutionary biology. Thus, many of us were surprised when, 13 years later, Stephen Jay Gould and Richard Lewontin (1979) began to repeat the same critique without attribution, writing as if it were unknown to the evolutionary community they were criticizing. One striking difference between the two critiques was Williams's development of strict standards of evidence to distinguish adaptations from nonadaptations, rendering the issue a matter of empirical research rather than post hoc rhetoric.

10 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

structured informational relationships embodied as aspects of organized physical systems in the brain. This spreading appreciation constituted the cognitive revolution. The mental world was no longer a mysterious, indefinable realm, but locatable in the physical world in terms of precisely describable, highly organized causal relations.

Evolutionary psychology can therefore be seen as the inevitable intersection of the computationalism of the cognitive revolution with the adaptationism of Williams's evolutionary biology: Because mental phenomena are the expression of complex functional organization in biological systems, and complex organic functionality is the downstream consequence of natural selection, then it must be the case that the sciences of the mind and brain are adaptationist sciences, and psychological mechanisms are computational adaptations. In this way, the marriage of computationalism with adaptationism marks a major turning point in the history of ideas, dissolving the intellectual tethers that had limited fundamental progress and opening the way forward. Like Dalton's wedding of atomic theory to chemistry, computationalism and adaptationism solve each other's deepest problems, and open up new continents of scientific possibility (Cosmides & Tooby, 1987; Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2003, 2005).

Sociologically speaking, the single most significant factor in triggering the renewed efforts to apply evolution to behavior was the selectionist revolution in evolutionary biology, which subsequently became known as sociobiology (Wilson, 1975). Across the world, biologists and allied researchers were electrified by the potential predictive and explanatory power of the new selectionist theories that were emerging, together with how elegantly and systematically they could be derived. Dynamic research communities formed at Oxford, Cambridge, Sussex, Michigan, Harvard, the University of California, and elsewhere. As a result of the flood of empirical and theoretical work coming out of these communities, the sociobiological revolution rapidly established itself in the biological journals as the dominant theoretical approach biologists apply to understanding the behavior of nonhumans—a position behavioral and social scientists are surprised to find that it occupies today.²

Under the sponsorship of Irven DeVore and E. O. Wilson, one of the most influential and dynamic of these communities gathered at Harvard. This research community fluoresced in DeVore's living room, where Harvard's Simian Seminar was held from the late 1960s through the mid-1980s. In this atmosphere of ongoing discovery, ideas and findings sparked each other in an endless chain reaction. A remarkable procession of figures in evolutionary biology, behavioral ecology, primatology, and ethology spoke at DeVore's Simian Seminar, participating in this chain reaction, and sometimes staying for protracted periods. These included George Williams, Bill Hamilton, John Maynard Smith, Ernst Mayr, Edward O.

²Intellectuals wedded to the blank slate generated an unslakable demand for seemingly authoritative dismissals of the new biology. As a result, the handful of biologists who were willing to ignore the data and supply these dismissals came to be seen as the authentic voices of scientific biology to the intellectual world at large (e.g., Gould & Lewontin, 1979). The decisive empirical success of the paradigm within biology itself—what Alcock (2001) calls “the triumph of sociobiology”—is largely unknown outside of the field, and the majority of nonbiologists labor under the misimpression that sociobiology was substantively discredited by “real” biologists.

Wilson, Richard Alexander, Richard Dawkins, Tim Clutton-Brock, Paul Harvey, Joseph Shepher, Lionel Tiger, Robin Fox, Diane Fosse, Jane Goodall, Richard Wrangham, Robert Hinde, Richard Leakey, Richard Lee, Stephen Jay Gould, Martin Daly, and Margo Wilson, and the editor of this *Handbook*, David Buss. Among the participating students who became transformed into active researchers in this environment were Bob Bailey, Peter Ellison, Steve Gaulin, Sarah Blaffer Hrdy, Melvin Konner, Jeff Kurland, Peter Rodman, Robert Sapolsky, John Seger, Barbara Smuts, Bob Trivers, and ourselves (John Tooby and Leda Cosmides).

While Wilson's contributions are deservedly famous through his books and publications, DeVore's intellectual impact is less well known because his ideas were realized through his students and colleagues. Deeply interested in human origins, DeVore pioneered three major research movements. He instigated and then championed the systematic study of primate social behavior under natural conditions (DeVore, 1965). With Chagnon, Irons, and others, he worked on applying the new selectionist biology to anthropological questions. He inaugurated the systematic, empirical investigation of living hunter-gatherers (Lee & DeVore, 1968, 1976).

DeVore and his colleague Richard Lee eschewed the "lone anthropologist" model (with its typological baggage), in which a single individual spends time documenting "the" culture of a people. In its place, they innovated a team-based approach like that found in other sciences. Their Kalahari San project brought scientists and scholars from a broad array of disciplines—anthropologists, demographers, physicians, linguists, folklorists, psychologists, ethologists, archeologists—in an attempt to document as completely as possible the behavior and lives of the !Kung San people in Botswana's Kalahari desert, before hunting and gathering as a way of life vanished forever from the planet. His goal in studying the San was to provide a detailed database that, when triangulated with other similarly detailed databases drawn from other hunter-gatherer groups, would allow new and powerful inferences to be made about the selection pressures that operated on hunter-gatherers to shape human design. Behavioral ecologists would be able to test optimal foraging models by matching foraging patterns to ecological conditions. Archaeologists could better interpret patterns found at ancestral sites by seeing patterns of campfires, animal remains, tool-making debris, and midden heaps produced by the social life of living hunter-gatherers. Physicians could gain insight into diseases of civilization by comparing diets and conditions in industrialized countries to the diets and stressors produced by a way of life that more closely resembles the conditions in which our species evolved. Developmental psychologists could gain insights into the mother-infant bond and human attachment by seeing the demands placed on infants and mothers in foraging contexts. Anthropologists could learn what social conditions foster risk pooling and food sharing; what kinds of knowledge hunter-gatherers have about animal behavior and plant life; how they use this knowledge in foraging; and how people negotiate the problems and opportunities of social life in a tiny community of interdependent, extended families (see, e.g., Lee & DeVore, 1976; Shostak, 1981). While commonplace now, these ideas were pathbreaking at the time. After all, if the human mind consists primarily of a general capacity to learn, then the particulars of the ancestral hunter-gatherer world and our prehuman history as Miocene apes left no interesting imprint on our design. In contrast, if our minds are collections of mechanisms designed to solve the adaptive problems posed by the ancestral world,

12 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

then hunter-gatherer studies and primatology become indispensable sources of knowledge about modern human nature. DeVore's insistence on situating the operation of natural selection within the detailed contexts of hunter-gatherer and nonhuman primate life was a signal contribution to the application of the evolutionary sciences to humans.

Many members of the evolutionary research communities believed that the new selectionist theories straightforwardly applied to humans, although others continued to welcome the Standard Social Science Model arguments that learning had insulated human life from evolutionary patterning. Human behavior exhibited many patterns that offered ready selectionist interpretations (e.g., sex differences in the psychology of mating), but many other phenomena resisted easy interpretation and seemed to lack clear nonhuman analogues (e.g., morality, the arts, language, culture). The result was a rich and contradictory pluralism of ideas about how evolution relates to human affairs—a pluralism that is still with us.

One of the most widespread approaches to emerge is what might be called fitness teleology. Teleological explanations are found in Aristotle, and arguably constitute an evolved mode of interpretation built into the human mind. Humans find explaining things in terms of the ends they lead to intuitive and often sufficient (Baron-Cohen, 1995; Dennett, 1987; Leslie, 1987, 1994). Social science theories have regularly depended on explicitly or implicitly teleological thinking. Economics, for example, explains choice behavior not in terms of its antecedent physical or computational causes but in terms of how the behavior serves utility maximization. Of course, the scientific revolution originated in Renaissance mechanics, and seeks ultimately to explain everything (non-quantum mechanical) using forward physical causality—a very different explanatory system in which teleology is not admissible. Darwin outlined a physical process—natural selection—that produces biological outcomes that had once been attributed to natural teleological processes (Darwin, 1859). Williams (1966) mounted a systematic critique of the myriad ways teleology had nonetheless implicitly infected evolutionary biology (where it persists in Darwinian disguises). Computationalism assimilated the other notable class of apparently teleological behavior in the universe—the seeming goal directedness of living systems—to physical causation by showing how informational structures in a regulatory system can operate in a forward causal way (Weiner, 1948). The teleological end that seems to exist in the future as the point toward which things tend is in reality a regulatory process or representation in the organism in the present. The modern scientific claim would be that adaptationism and computationalism in combination can explain by forward physical causation all events that once would have been explained teleologically.

Yet, the implicit or explicit substrate underlying many attempts to apply Darwinism to human behavior was a return to the sense that human behavior was explained by the ends it serves. For a Darwinian, it was argued, choices, practices, culture, and institutions were explained to the extent that they could be interpreted as contributing to individual (or sometimes group) reproduction: That is, the explanation for human behavior is that it naturally tends toward the end of maximizing reproduction in the present and future. This theory—Darwinism transmuted into fitness teleology—parallels the economic view of individuals as selfish utility maximizers, except that Hamilton's (1964) concept of inclusive fitness is substituted for the economists' concept of utility. Both approaches assume

that unbounded rationality is possible and that the mind is a general-purpose computer that can figure out, in any situation, what will maximize a given quantity over the long term (whether utility or children). Indeed, the concept of “learning” within the Standard Social Science Model itself tacitly invokes unbounded rationality, in that learning is the tendency of the general-purpose, equipotential mind to grow—by an unspecified and undiscovered computational means—whatever functional information-processing abilities it needs to serve its purposes, given time and experience in the task environment.

Evolutionary psychologists depart from fitness teleologists, traditional economists (but not neuroeconomists), and blank-slate learning theorists by arguing that neither human engineers nor evolution can build a computational device that exhibits these forms of unbounded rationality, because such architectures are impossible, even in principle (for arguments, see Cosmides & Tooby, 1987; Symons 1989, 1992; Tooby & Cosmides, 1990a, 1992). In any case, observed human behavior dramatically and systematically departs from the sociobiological predictions of generalized fitness striving (as well as the predictions of economic rationality and blank-slate learning abilities). To take one simple contrast, men will pay to have nonreproductive sex with prostitutes they believe and hope are contracepting, yet they have to be paid to contribute to sperm banks. More generally, across a range of wealthy nations, those able to afford more children choose to have fewer children—a striking disconfirmation of the prediction that humans teleologically seek to maximize reproduction or fitness (Vining, 1986). Human life is permeated with systematic deviations away from rationally maximized child-production and kin assistance.

For those eager to leap directly from theories of selection pressures to predictions of fitness maximization, there remains a missing level of causation and explanation: the informational or computational level. This level cannot be avoided if the application of Darwin’s theory to humans is ever to achieve the necessary level of scientific precision. Natural selection does not operate on behavior per se; it operates on a systematically caused *relationship* between information and behavior. Running—a behavior—is neither good nor bad. Running away from a lion can promote survival and reproduction; running toward a lion will curtail both. To be adaptive, behavioral regulation needs to be functionally contingent on information; for example, *flee when you see a stalking lion*. But a systematic relationship between information and a behavioral response cannot occur unless some reliably developing piece of organic machinery causes it. These causal relations between information and behavior are created by neural circuits in the brain, which function as programs that process information. By altering the neural circuitry that develops, mutations can alter the information processing properties of these programs, creating alternative information-behavior relationships. Selection should retain or discard alternative circuit designs from a species’ neural architecture on the basis of how well the information-behavior relationships they produce promote the propagation of the genetic bases of their designs. Those circuit designs that promote their own proliferation will be retained and spread, eventually becoming species-typical (or stably frequency-dependent); those that do not will eventually disappear from the population. The idea that the evolutionary causation of behavior would lead to rigid, inflexible behavior is the opposite of the truth: Evolved neural architectures are specifications of richly contingent systems for generating responses to informational inputs.

14 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

As a result of selection acting on information-behavior relationships, the human brain is predicted to be densely packed with programs that cause intricate relationships between information and behavior, including functionally specialized learning systems, domain-specialized rules of inference, default preferences that are adjusted by experience, complex decision rules, concepts that organize our experiences and databases of knowledge, and vast databases of acquired information stored in specialized memory systems—remembered episodes from our lives, encyclopedias of plant life and animal behavior, banks of information about other people’s proclivities and preferences, and so on. All of these programs and the databases they create can be called on in different combinations to elicit a dazzling variety of behavioral responses. These responses are themselves information, subsequently ingested by the same evolved programs, in endless cycles that produce complex eddies, currents, and even singularities in cultural life. To get a genuine purchase on human behavior and society, researchers need to know the architecture of these evolved programs. Knowing the selection pressures will not be enough. Our behavior is not a direct response to selection pressures or to a “need” to increase our reproduction.

Hence, one of several reasons why evolutionary psychology is distinct from human sociobiology and other similar approaches lies in its rejection of fitness maximization as an explanation for behavior (Cosmides & Tooby, 1987; Daly & Wilson, 1988; Symons, 1987, 1989, 1992; Tooby & Cosmides, 1990a, 1992). The relative degree of fitness promotion under ancestral conditions is simply the design criterion by which alternative mutant designs were sorted in the evolutionary past. (The causal role fitness plays in the present is in glacially changing the relative frequencies of alternative designs with respect to future generations.) Although organisms sometimes appear to be pursuing fitness on behalf of their genes, in reality they are executing the evolved circuit logic built into their neural programs, whether this corresponds to current fitness maximization or not. Organisms are adaptation executors, not fitness pursuers. Mapping the computational architecture of the mechanisms will give a precise theory of behavior, while relying on predictions derived from fitness maximization will give a very impoverished and unreliable set of predictions about behavioral dynamics.

To summarize, evolutionary psychology’s focus on psychological mechanisms as evolved programs was motivated by new developments from a series of different fields:

Advance 1: The cognitive revolution was providing, for the first time in human history, a precise language for describing mental mechanisms as programs that process information. Galileo’s discovery that mathematics provided a precise language for expressing the mechanical and physical relationships enabled the birth of modern physics. Analogously, cognitive scientists’ discovery that computational-informational formalisms provide a precise language for describing the design, properties, regulatory architecture, and operation of psychological mechanisms enables a modern science of mind (and its physical basis). Computational language is not just a convenience for modeling anything with complex dynamics. The brain’s evolved function is computational—to use information to adaptively regulate the body and behavior—so computational and informational formalisms are by their nature the most appropriate to capture the functional design of behavior regulation.

Advance 2: Advances in paleoanthropology, hunter-gatherer studies, and primatology were providing data about the adaptive problems our ancestors had to solve to survive and reproduce and the environments in which they did so.

Advance 3: Research in animal behavior, linguistics, and neuropsychology was showing that the mind is not a blank slate, passively recording the world. Organisms come “factory-equipped” with knowledge about the world, which allows them to learn some relationships easily and others only with great effort, if at all. Skinner’s hypothesis—that there is one simple learning process governed by reward and punishment—was wrong.

Advance 4: Evolutionary biology was revolutionized by being placed on a more rigorous, formal foundation of replicator dynamics, leading to the derivation of a diversity of powerful selectionist theories, and the analytic tools to recognize and differentiate adaptations, from by-products and stochastically generated evolutionary noise (Williams, 1966).

Ethology had brought together advances 2 and 3, sociobiology had connected advances 2 and 4, sometimes with 3; nativist cognitive science connected advances 1 and 3, but neglected and still shrinks from advances 2 and 4. Cognitive neuroscience partially and erratically accepts 1 and 3, but omits 2 and 4. Outside of cognitive approaches, the rest of psychology lacks much of advance 1, most of advance 3, and all of advances 2 and 4. Evolutionary anthropology appreciates advances 2 and 4, but neglects 1 and 3. Social anthropology and sociology lack all four. So it goes. If one counts the adaptationist/computationalist resolution of the nature-nurture issue as a critical advance, the situation is even bleaker.

We thought these new developments could be pieced together into an integrated framework that successfully addressed the difficulties that had plagued evolutionary and nonevolutionary approaches alike. The reason why the synthesis had not emerged earlier in the century was because the connections between the key concepts ran between fields rather than cleanly within them. Consequently, relatively few were in the fortunate position of being professionally equipped to see all the connections at once. This limited the field’s initial appeal, because what seems self-evident from the synoptic vantage point seems esoteric, pedantic, or cultish from other vantage points. Nevertheless, we and those working along similar lines were confident that by bringing all four advances together, the evolutionary sciences could be united with the cognitive revolution in a way that provided a framework not only for psychology but for all of the social and behavioral sciences. To signal its distinctiveness from other approaches, the field was named *evolutionary psychology*.³

³We sometimes read that evolutionary psychology is simply sociobiology, with the name changed to avoid the bad political press that sociobiology had received. Although it is amusing (given the record) to be accused of ducking controversy, these claims are historically and substantively wrong. In the first place, evolutionary psychologists are generally admirers and defenders of sociobiology (or behavioral ecology, or evolutionary ecology). It has been the most useful and most sophisticated branch of modern evolutionary biology, and several have made contributions to this literature. Nonetheless, the lengthy and intense debates about how to apply evolution to behavior made it increasingly clear that markedly opposed views needed different labels if any theoretical and empirical project was to be clearly understood. In the 1980s, Martin Daly, Margo Wilson, Don Symons, John Tooby, Leda Cosmides, and David Buss had many discussions about what to call this new field, some at Daly and Wilson’s kangaroo rat field site in Palm Desert, some in Santa Barbara,

EVOLUTIONARY PSYCHOLOGY

Like cognitive scientists, when evolutionary psychologists refer to the *mind*, they mean the set of information processing devices, embodied in neural tissue, that is responsible for all conscious and nonconscious mental activity, that generates all behavior, and that regulates the body. Like other psychologists, evolutionary psychologists test hypotheses about the design of these computational devices using methods from, for example, cognitive psychology, social psychology, developmental psychology, experimental economics, cognitive neuroscience, genetics, physiological psychology, and cross-cultural field work.

The primary tool that allows evolutionary psychologists to go beyond traditional psychologists in studying the mind is that they take full advantage in their research of an overlooked reality: The programs comprising the human mind were designed by natural selection to solve the adaptive problems regularly faced by our hunter-gatherer ancestors—problems such as finding a mate, cooperating with others, hunting, gathering, protecting children, navigating, avoiding predators, avoiding exploitation, and so on. Knowing this allows evolutionary psychologists to approach the study of the mind like an engineer. You start by carefully specifying an adaptive information processing problem; then you do a task analysis of that problem. A task analysis consists of identifying what properties a program would have to have to solve that problem well. This approach allows you to generate hypotheses about the structure of the programs that comprise the mind, which can then be tested.

From this point of view, there are precise causal connections that link the four developments discussed earlier into a coherent framework for thinking about human nature and society (Tooby & Cosmides, 1992):

C-1: Each organ in the body evolved to serve a function: The intestines digest, the heart pumps blood, and the liver detoxifies poisons. The brain's evolved function is to extract information from the environment and use that information to generate behavior and regulate physiology. Hence, the brain is not just like a computer. It is a computer—that is, a physical system that was designed to process information (Advance 1). Its programs were designed not by an engineer, but by natural selection, a causal process that retains and discards design features based on how well they solved adaptive problems in past environments (Advance 4).

The fact that the brain processes information is not an accidental side effect of some metabolic process. The brain was designed by natural selection *to be* a computer. Therefore, if you want to describe its operation in a way that captures its evolved function, you need to think of it as composed of programs that

and some at the Center for Advanced Study in the Behavioral Sciences. Politics and the press did not enter these discussions, and we anticipated (correctly) that the same content-free ad hominem attacks would pursue us throughout our careers. What we *did* discuss was that this new field focused on psychology—on characterizing the adaptations comprising the psychological architecture—whereas sociobiology had not. Sociobiology had focused mostly on selectionist theories, with no consideration of the computational level and little interest in mapping psychological mechanisms. Both the subject matter of evolutionary psychology and the theoretical commitments were simply different from that of sociobiology, in the same way that sociobiology was quite different from the ethology that preceded it and cognitive psychology was different from behaviorist psychology—necessitating a new name in each case.

process information. The question then becomes: What programs are to be found in the human brain? What are the reliably developing, species-typical programs that, taken together, comprise the human mind?

C-2: Individual behavior is generated by this evolved computer, in response to information that it extracts from the internal and external environment (including the social environment, Advance 1). To understand an individual's behavior, therefore, you need to know both the information that the person registered *and* the structure of the programs that generated his or her behavior.

C-3: The programs that comprise the human brain were sculpted over evolutionary time by the ancestral environments and selection pressures experienced by the hunter-gatherers from whom we are descended (Advances 2 and 4). Each evolved program exists because it produced behavior that promoted the survival and reproduction of our ancestors better than alternative programs that arose during human evolutionary history. Evolutionary psychologists emphasize hunter-gatherer life because the evolutionary process is slow—it takes thousands of generations to build a program of any complexity. The industrial revolution—even the agricultural revolution—is too brief a period to have selected for complex new cognitive programs.⁴

C-4: Although the behavior our evolved programs generate would, on average, have been adaptive (reproduction promoting) in ancestral environments, there is no guarantee that it will be so now. Modern environments differ importantly from ancestral ones, particularly when it comes to social behavior. We no longer live in small, face-to-face societies, in seminomadic bands of 20 to 100 people, many of whom were close relatives. Yet, our cognitive programs were designed for that social world.

C-5: Perhaps most importantly, natural selection will ensure that the brain is composed of many different programs, many (or all) of which will be specialized for solving their own corresponding adaptive problems. That is, the evolutionary process will not produce a predominantly general-purpose, equipotential, domain-general architecture (Advance 3).

In fact, this is a ubiquitous engineering outcome. The existence of recurrent computational problems leads to functionally specialized application software. For example, the demand for effective word processing and good digital music playback led to different application programs because many of the design features that make a program an effective word processing program are different from those that make a program a good digital music player. Indeed, the greater the number of functionally specialized programs (or subroutines) your computer has installed, the more intelligent your computer is, and the more things it can accomplish. The same is true for organisms. Armed with this insight, we can lay to rest the myth that the more evolved organization the human mind has, the more inflexible its response. Interpreting the emotional expressions of others, seeing beauty, learning language, loving your child—all these enhancements to human mental life are made possible by specialized neural programs built by natural selection.

⁴Unidimensional traits, caused by quantitative genetic variation (e.g., taller, shorter), can be adjusted in less time; see Tooby & Cosmides, 1990b.

18 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

To survive and reproduce reliably as a hunter-gatherer required the solution of a large and diverse array of adaptive information-processing problems. These ranged from predator vigilance and prey stalking to plant gathering, mate selection, childbirth, parental care, coalition formation, and disease avoidance. Design features that make a program good at choosing nutritious foods, for example, are ill suited for finding a fertile mate or recognizing free riders. Some sets of problems would have required differentiated computational solutions.

The demand for diverse computational designs can be clearly seen when results from evolutionary theory (Advance 4) are combined with data about ancestral environments (Advance 2) to model different ancestral computational problems. The design features necessary for solving one problem are usually markedly different from the features required to construct programs capable of solving another adaptive problem. For example, game theoretic analyses of conditional helping show that programs designed for logical reasoning would be poorly designed for detecting cheaters in social exchange and vice versa; this incommensurability selected for programs that are functionally specialized for reasoning about reciprocity or exchange (Cosmides & Tooby, Chapter 20, this volume).

C-6: Finally, descriptions of the computational architecture of our evolved mechanisms allows a systematic understanding of cultural and social phenomena. The mind is not like a video camera, passively recording the world but imparting no content of its own. Domain-specific programs organize our experiences, create our inferences, inject certain recurrent concepts and motivations into our mental life, give us our passions, and provide cross-culturally universal frames of meaning that allow us to understand the actions and intentions of others. They invite us to think certain kinds of thoughts; they make certain ideas, feelings, and reactions seem reasonable, interesting, and memorable. Consequently, they play a key role in determining which ideas and customs will easily spread from mind to mind and which will not (Boyer, 2001; Sperber, 1994, 1996; Tooby & Cosmides, 1992). That is, they play a crucial role in shaping human culture.

Instincts are often thought of as the opposite of reasoning, decision making, and learning. But the reasoning, decision-making, and learning programs that evolutionary psychologists have been discovering (1) are complexly specialized for solving an adaptive problem, (2) reliably develop in all normal human beings, (3) develop without any conscious effort and in the absence of formal instruction, (4) are applied without any awareness of their underlying logic, and (5) are distinct from more general abilities to process information or behave intelligently. In other words, they have all the hallmarks of what we usually think of as instinct (Pinker, 1994). In fact, we can think of these specialized circuits as instincts: *reasoning instincts*, *decision instincts*, *motivational instincts*, and *learning instincts*. They make certain kinds of inferences and decisions just as easy, effortless, and natural to us as humans as catching flies is to a frog or burrowing is to a mole.

Consider this example from the work of Simon Baron-Cohen (1995). Like adults, normal 4-year-olds easily and automatically note eye direction in others, and use it to make inferences about the mental states of the gazer. For example, 4-year-olds, like adults, infer that when presented with an array of candy, the gazer wants the particular candy he or she is looking at. Children with autism do not

make this inference. Although children with this developmental disorder can compute eye direction correctly, they cannot use that information to infer what someone wants. Normal individuals know, spontaneously and with no mental effort, that the person wants the candy he or she is looking at. This is so obvious to us that it hardly seems to require an inference at all. It is just common sense. But “common sense” is caused: It is produced by cognitive mechanisms. To infer a mental state (wanting) from information about eye direction requires a computation. There is an inference circuit—a reasoning instinct—that produces this inference. When the circuit that does this computation is broken or fails to develop, the inference cannot be made. Those with autism fail this task because they lack this reasoning instinct, even though they often acquire very sophisticated competences of other sorts. If the mind consisted of a domain-general knowledge acquisition system, narrow impairments of this kind would not be possible.

Instincts are invisible to our intuitions, even as they generate them. They are no more accessible to consciousness than our retinal cells and line detectors but are just as important in manufacturing our perceptions of the world. As a species, we have been blind to the existence of these instincts, not because we lack them but precisely because they work so well. Because they process information so effortlessly and automatically, their operation disappears unnoticed into the background. Moreover, these instincts structure our thought and experience so powerfully we mistake their products for features of the external world: Color, beauty, status, friendship, charm—all are computed by the mind and then experienced as if they were objective properties of the objects they are attributed to. These mechanisms limit our sense of behavioral possibility to choices people commonly make, shielding us from seeing how complex and regulated the mechanics of choice is. Indeed, these mechanisms make it difficult to imagine how things could be otherwise. As a result, we take normal behavior for granted: We do not realize that normal behavior needs to be explained at all.

As behavioral scientists, we need corrective lenses to overcome our instinct blindness. The brain is fantastically complex, packed with programs, most of which are currently unknown to science. Theories of adaptive function can serve as corrective lenses for psychologists, allowing us to see computational problems that are invisible to human intuition. When carefully thought out, these functional theories can lead us to look for programs in the brain that no one had previously suspected.

PRINCIPLES OF ORGANIC DESIGN

Biology is the study of organisms, and psychology is—in a fundamental sense—a branch of biology. It is the study of the evolved designs of the behavior-regulating tissues of organisms. To be effective researchers, psychologists will need to become at least minimally acquainted with the principles of organic design.

NATURAL SELECTION IS AN ENGINEER THAT DESIGNS ORGANIC MACHINES

The phenomenon that Darwin was trying to explain is the presence of functional organization in living systems—the kind of organization found in artifacts, such as clocks, spectacles, or carriages; indeed, the kind of organization that appeared to be designed by an intelligent engineer to solve a problem. Darwin realized that

20 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

organisms can be thought of as *self-reproducing machines*. What distinguishes living from nonliving machines is reproduction: the presence in a machine of devices (organized components) that cause it to produce new and similarly reproducing machines. Given a population of living machines, this property—self-reproduction—drives a system of positive and negative feedback—natural selection—that can explain the remarkable fit between the design of organisms and the problems they must solve to survive and reproduce.

In contrast to human-made machines, which are designed by inventors, living machines acquire their intricate functional design over immense lengths of time, as a consequence of the fact that they reproduce themselves. Indeed, modern Darwinism has an elegant deductive structure that logically follows from Darwin's initial insight that reproduction is the defining property of life:

When an organism reproduces, genes that cause the development of its design features are introduced into its offspring. But the replication of the design of the parental machine is not always error free. As a result, randomly modified designs (i.e., mutants) are introduced into populations of reproducers. Because living machines are already exactly organized so that they cause the otherwise improbable outcome of constructing offspring machines, random modifications will usually introduce disruptions into the complex sequence of actions necessary for self-reproduction. Consequently, most newly modified but now defective designs will remove themselves from the population: a case of negative feedback.

However, a small number of these random design modifications will, by chance, improve the system's machinery for causing its own reproduction. Such improved designs (by definition) cause their own increasing frequency in the population: a case of positive feedback.

This increase continues until (usually) such modified designs outreproduce and thereby replace the alternative designs in the population, leading to a new species-standard (or population-standard) design: a new retinal design, or blood cell, or reasoning circuit, or food preference ordering. After such an event, the population of reproducing machines is different from the ancestral population. The population has taken a step "uphill" toward a greater degree of functional organization for reproduction than it had previously. Over the long run, down chains of descent, this feedback cycle pushes designs through state-space toward increasingly well-engineered—and increasingly improbable—functional arrangements. These arrangements are *functional* in a specific sense: The elements are well organized to cause their own reproduction in the environment in which the species evolved.

For example, if a mutation appeared that caused individuals to find family members sexually repugnant, they would be less likely to conceive children incestuously. They would produce children with fewer genetic diseases, and more of these children would mature and reproduce than would the children of those who were not averse to incest. Such an incest-avoiding design would produce a larger set of healthy children every generation, down the generations. By promoting the reproduction of its bearers, the incest-avoiding circuit thereby promotes its own spread over the generations, until it eventually replaces the earlier-model sexual circuitry and becomes a universal feature of that species' design. This spontaneous feedback process—natural selection—causes functional organization to emerge naturally, without the intervention of an intelligent designer or supernatural forces.

Genes and Design Self-reproducing systems could not exist unless there were adaptations that conserved the functional design against entropy from one generation to the next. Genes are the means by which functional design features replicate themselves from parent to offspring. They can be thought of as particles of design. These elements are transmitted from parent to offspring and together with stable features of an environment, cause the organism to develop some design features and not others. Genes have two primary ways they can propagate themselves: by increasing the probability that offspring will be produced by the organism in which they are situated or by increasing reproduction in others who are more likely than random members of the population to carry the same gene.

An individual's genetic relatives carry some of the same genes, by virtue of having received some of the same genes from a recent common ancestor. Thus, a gene in an individual that causes an increase in the reproductive rate of that individual's kin will, by so doing, tend to increase its own frequency in the population. A circuit that motivates individuals to help feed their sisters and brothers, if they are in sufficiently greater need, is an example of a program that increases kin reproduction. As Hamilton (1964) pointed out, design features that promote both direct reproduction and kin reproduction and that make efficient trade-offs between the two will replace those that do not (a process called *kin selection*).

Reproduction and Function How well a design feature systematically promotes direct and kin reproduction is the bizarre but real engineering criterion determining whether a specific design feature will be added to or discarded from a species' design.

The concept of *adaptive behavior* can now be defined with precision. Adaptive behavior, in the evolutionary sense, is behavior that tended to promote the net lifetime reproduction of the individual or that individual's genetic relatives. By promoting the replication of the genes that built them, circuits that—systematically and over many generations—cause adaptive behavior become incorporated into a species' neural design. In contrast, behavior that undermines the reproduction of the individual or his or her genetic relatives removes the circuits causing those behaviors from the species. Such behavior is maladaptive.

Evolutionists analyze how design features are organized (in ancestral environments) to contribute to the propagation of their genetic basis because gene propagation was the final causal pathway through which a functionally improved design feature caused itself to increase in frequency until it became standard equipment in all ordinary members of the species.

Adaptive Problems Select for Adaptations Darwin's detailed studies of plants and animals revealed complex structures composed of parts that appeared to be organized to overcome reproductive obstacles (e.g., the presence of predators) or to take advantage of reproductive opportunities (e.g., the presence of fertile mates). Enduring conditions in the world that create reproductive opportunities or obstacles constitute *adaptive problems*, such as the presence of pathogens, variance in the food supply, the vulnerability of infants, or the presence of family in an individual's social group. Adaptive problems have two defining characteristics. First, they are conditions or cause-and-effect relationships that many or most individual ancestors encountered, reappearing again and again during the evolutionary history of the species, giving natural selection enough time to design

22 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

adaptations in response. Second, they are that subset of enduring relationships that could, in principle, be exploited by some property of an organism to increase its reproduction or the reproduction of its relatives. Alternative designs are retained or discarded by natural selection on the basis of how well they function as solutions to adaptive problems.

Over evolutionary time, more and more design features accumulate to form an integrated structure or device that is well engineered to solve its particular adaptive problem. Such a structure or device is called an *adaptation*. Indeed, an organism can be thought of as a collection of adaptations, together with the engineering by-products of adaptations, and evolutionary noise. The functional subcomponents of the ear, hand, intestines, uterus, or circulatory system are examples. Each of these adaptations exists in the human design now because it contributed to the process of direct and kin reproduction in the ancestral past. Adaptive problems are the only kind of problem that natural selection can design machinery for solving.

The Environment of Evolutionary Adaptedness One key to understanding the functional architecture of the mind is to remember that its programs were not selected for because they solved the problems faced by modern humans. Instead, they were shaped by how well they solved adaptive problems among our hunter-gatherer ancestors. The second key is to understand that the developmental processes that build each program, as well as each program in its mature state, evolved to use information and conditions that were reliably present in ancestral environments. The design of each adaptation assumes the presence of certain background conditions and operates as a successful problem solver only when those conditions are met. The *environment of evolutionary adaptedness* (EEA) refers jointly to the problems hunter-gatherers had to solve and the conditions under which they solved them (including their developmental environment).

Although the hominid line is thought to have originated on edges of the African savannahs, the EEA is not a particular place or time. The EEA for a given adaptation is the statistical composite of the enduring selection pressures or cause-and-effect relationships that pushed the alleles underlying an adaptation systematically upward in frequency until they became species-typical or reached a frequency-dependent equilibrium (most adaptations are species-typical; see Hagen, Chapter 5, this volume). Because the coordinated fixation of alleles at different loci takes time, complex adaptations reflect enduring features of the ancestral world. The adaptation is the consequence of the EEA, and so the structure of the adaptation reflects the structure of the EEA. The adaptation evolved so that when it interacted with the stable features of the ancestral task environment, their interaction systematically promoted fitness (i.e., solves an adaptive problem). The concept of the EEA is essential to Darwinism, but its formalization was prompted by the evolutionary analysis of humans because human environments have changed more dramatically than the environments most other species occupy. The research problems faced by most biologists do not require them to distinguish the modern environment from a species' ancestral environment. Because adaptations evolved and assumed their modern form at different times and because different aspects of the environment were relevant to the design of each, the EEA for one adaptation may be somewhat different from the EEA for another. Conditions of terrestrial illumination, which

form (part of) the EEA for the vertebrate eye, remained relatively constant for hundreds of millions of years—and can still be observed by turning off all artificial lights. In contrast, the social and foraging conditions that formed (part of) the EEA that selected for neural programs that cause human males to provision and care for their offspring (under certain conditions) is almost certainly less than two million years old.

When a program is operating outside the envelope of ancestral conditions that selected for its design, it may look like a poorly engineered problem solver. Efficient foraging, for example, requires good probability judgments, yet laboratory data suggested that people are poor intuitive statisticians, incapable of making simple inferences about conditional probabilities (Kahneman, Slovic, & Tversky, 1982). Evolutionary psychologists recognized that these findings were problematic, given that birds and insects solve similar problems with ease. The paradox evaporates when you consider the EEA for probability judgment. Behavioral ecologists presented birds and bees with information in ecologically valid formats; psychologists studying humans were not.

Being mindful of the EEA concept changes how research is designed and what is discovered. Giving people probability information in the form of absolute frequencies—an ecologically valid format for hunter-gatherers—reveals the presence of mechanisms that generate sound Bayesian inferences (Brase, Cosmides, & Tooby, 1998; Cosmides & Tooby, 1996; Gigerenzer, 1991; Gigerenzer, Todd, & the ABC Group, 1999). Indeed, EEA-minded research on judgment under uncertainty is now showing that the human mind is equipped with a toolbox of “fast-and-frugal heuristics,” each designed to make well-calibrated judgments quickly on the basis of limited information (Gigerenzer & Selten, 2002; Gigerenzer, Todd, & the ABC Group, 1999; Todd, Hertwig, & Hoffrage, Chapter 27, this volume). These procedures are *ecologically rational*, providing good solutions when operating in the task environments for which they evolved (Tooby & Cosmides, in press).

Knowing the Past It is often argued that we can know nothing about the past that is relevant to psychology because behavior doesn't fossilize. Thus, the whole field of evolutionary psychology is claimed to rest on uncertain speculation or conjecture. In reality, we know with certainty thousands of important things about our ancestors and the world they inhabited, many of which can be useful in guiding psychological research. Some of these should be obvious, although their implications may not be. For example, it is a certainty that our ancestors lived in a world in which certain principles of physics governed the motions of objects: facts that allowed Shepard (1984, 1987) to discover how the mind represents the motion of objects, both in perception and imagination. It is equally certain that hominids had eyes, looked at what interested them, and absorbed information about what they were looking at, making eye-gaze direction informative to onlookers: facts that helped Baron-Cohen (1995) to create a far-reaching research program on the cognitive basis of mind-reading, the ability to infer the mental states of others. It is certain that our ancestors, like other Old World primates, nursed; had two sexes; chose mates; had color vision calibrated to the spectral properties of sunlight; lived in a biotic environment with predatory cats, venomous snakes, and spiders; were predated on; bled when wounded; were incapacitated from injuries; were vulnerable to a large variety of parasites and pathogens; and had deleterious recessives rendering them subject to inbreeding depression if they mated

24 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

with siblings. All of these conditions are known, and all pose adaptive problems. By considering these selection pressures, a careful, intelligent thinker can develop plausible, testable theories of the adaptations that arose in response to them. Selection would not plausibly have built an equipotential cognitive architecture that had to encounter the world as if it were unprepared for functionally significant sets of evolutionarily recurrent relationships. It is remarkable that such a model is so vigorously defended.

By triangulating the work of researchers in many disciplines, many other sound inferences can be made. Evolutionary psychologists, behavioral ecologists, and evolutionary biologists have already created a library of sophisticated models of the selection pressures, strategies, and trade-offs that characterize fundamental adaptive problems (Advance 4), which they use in studying processes of attention, memory, decision making, and learning in nonhuman animals. Which model is applicable for a given species depends on certain key life-history parameters. Findings from paleoanthropology, hunter-gatherer archaeology, and studies of living hunter-gatherer populations locate humans in this theoretical landscape by filling in the critical parameter values (Advance 2). Ancestral hominids were ground-living primates; omnivores,⁵ exposed to a wide variety of plant toxins and meat-borne bacteria and fungi; they had a sexual division of labor involving differential rates of hunting and gathering. They were mammals with altricial young, long periods of biparental investment in offspring, enduring male-female mateships, and an extended period of physiologically obligatory female investment in pregnancy and lactation. They were a long-lived, low-fecundity species in which variance in male reproductive success was higher than variance in female reproductive success. They lived in small, nomadic, kin-based bands often of 20 to 100; they would rarely (if ever) have seen more than 1,000 people at one time; they had only modest opportunities to store provisions for the future; they engaged in cooperative hunting, defense, and aggressive coalitions; and they made tools and engaged in extensive amounts of cooperative reciprocity. When these parameters are combined with formal models from evolutionary biology and behavioral ecology, a reasonably consistent picture of ancestral life begins to appear (e.g., Tooby & DeVore, 1987). From this, researchers can refine theories of adaptive problems, develop models of their computational requirements, and test for the presence of mechanisms equipped with design features that satisfy these requirements. Most chapters in this volume provide examples of this process.

Many adaptive problems can be further illuminated by the application of evolutionary theory (see, e.g., Cosmides & Tooby, Chapter 20, this volume). For example, variance in the food supply can be buffered through food sharing, a method of pooling risk, which is stable only when the variance is primarily due to luck rather than effort. Studies of modern hunter-gatherers have allowed quantitative estimates of how much variance there is in successfully finding different kinds of foods; for example, among the Ache of Paraguay, meat and honey are high-variance foods even for skilled foragers, whereas the variance in gathering vegetable foods is low and comes from effort rather than luck. As might be pre-

⁵Fossil sites show extensive processing sites for animal products. Large East African woodland primates hunt and eat meat. Hunter-gatherers are observed to get a major fraction of their diet from hunting. Hunting is a disproportionately male activity not only in humans but in chimpanzees and baboons.

dicted from an analysis of the adaptive problems posed by variance in the food supply, Ache hunter-gatherers risk-pool with meat and honey by sharing widely at the band level, but they share gathered vegetable foods only within nuclear families (Kaplan & Hill, 1985). This analysis suggests that our minds house at least two different decision rules for sharing, each creating a different sense of what is appropriate or fair, and each triggered by a different experience of variance. This, in turn, led to the successful prediction that we have mechanisms designed to be effectively calibrated to variance and its causes (e.g., Rode, Cosmides, Hell, & Tooby, 1999; Wang, 2002).

Although behavioral scientists can be certain about a huge inventory of facts about the ancestral world that have not yet been harnessed to guide psychological research, certainty about the past is not necessary for building better hypotheses. We can derive valuable experimental hypotheses from possible rather than certain features of the ancestral world. At worst, such a hypothesis is no more likely to be falsified than the hypotheses advanced by nonevolutionary researchers, who have no principled source from which to derive their hypotheses. There are also many features of the ancestral world about which we are completely ignorant: These features simply do not form the basis for experiments.

PSYCHOLOGY IS REVERSE ENGINEERING

As engineers go, natural selection is superlative. It has produced exquisitely engineered biological machines—the vertebrate eye, the four-chambered heart, the liver, and the immune system—whose performance at solving problems is unrivaled by any machine yet designed by humans. (Consider the poor quality of machine vision compared to evolved vision, artificial pacemakers compared to the evolved system regulating the heart, pharmaceuticals with their negative side effects compared to the body's immune and detoxification systems.)

Psychologists—evolutionary or otherwise—are engineers working in reverse. The human neural architecture is a complex functional system, composed of programs whose design was engineered by natural selection to solve specific adaptive problems. Our job is to reverse-engineer its components: to dissect its computational architecture into functionally isolable information processing units—programs—and to determine how these units operate, both computationally and physically. To arrive at the appropriate construal, the cognitive architecture must be conceptualized as a set of parts designed to interact in such a way that they solve adaptive problems. This conceptualization requires theories of adaptive function—engineering specifications that provide analyses of what would count as good design for a particular problem. In so doing, they also provide the criteria necessary to decide whether a property of an organism is a design feature, a functionless by-product, or noise.

Many Properties of Organisms Are Not Adaptations The cross-generationally recurrent design of an organism can be partitioned into (1) adaptations, which are present because they were selected for, (2) by-products of adaptations, which were not themselves targets of selection but are present because they are causally coupled to or produced by traits that were, and (3) noise, which was injected by the stochastic components of evolution. Consider, for example, that all brain-intact persons learn to speak (or sign) the language of their surrounding community

26 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

without explicit instruction, whereas reading and writing require explicit schooling, are not mastered by every individual, and are entirely absent from some cultures. The neural programs that allow humans to acquire and use spoken language are adaptations, specialized by selection for that task (Pinker, 1994; Pinker & Bloom, 1990). But once an information processing mechanism exists, it can be deployed in activities that are unrelated to its original function. Because we have evolved learning mechanisms that cause language acquisition, we can, through laborious study and schooling, learn to write and read. But the learning mechanisms that enable these activities were not selected for *because* they caused reading and writing. The ability to read and write are by-products of adaptations for spoken language, enabled by their causal structure. Random evolutionary noise exists as well, for example, the gene variants that cause dyslexia (difficulties with learning to read).

Adaptations are present because of a prior history of selection. They are not defined as any ability or trait, however rare or modern, that is beneficial by virtue of enabling a particular individual to have more children. Suppose, for example, that a computer programmer were to become wealthy through writing code and used that wealth to have many children. This would not make computer programming, which is a very recent cultural invention, an adaptation, nor would it mean that the cognitive mechanisms that enable computer programming are adaptations designed for producing computer programs. The ability to write code is a beneficial side effect of cognitive adaptations that arose to solve entirely different problems, ones that promoted reproduction in an ancestral past.⁶

Thus, although selection creates functional organization, not all traits of organisms are functional. In fact, most “parts” of an organism are not functional for a simple reason: Most ways of conceptually dissecting a species’ phenotype into parts will fail to capture functional components.⁷ To see the organization that exists in a complex system, researchers need to be able to distinguish its functional components from the by-products and noise.

With a well-specified theory of an adaptive problem, researchers can identify functional and nonfunctional parts of an organism. Of the three kinds of properties, adaptations are the most important and illuminating because they explain why a system has certain parts, why these participate in certain cause-and-effect relationships with one another, and why they interact with the world in the way that they do. Adaptations are problem-solving machines and can be identified using design evidence. This entails probability judgments about the degree to

⁶In the case of computer programming, these adaptations might include the numerical abilities that underwrite foraging (Wynn, 1998), recursion for producing metarepresentations (Leslie, 1987), grammatical mechanisms (Pinker, 1994), certain deductive capacities (Rips, 1994), and so on. To determine which adaptations underwrite the ability to program computers would require cognitive experimentation aimed at discovering which information processing mechanisms are activated when someone is engaged in this evolutionarily novel activity. Moreover, different constellations of mechanisms might be activated when different individuals program, precisely because there has not been enough time for natural selection to produce an integrated design specifically for this purpose.

⁷Imagine you are looking inside a television and considering ways to conceptually divide its innards into parts. A random parsing is unlikely to isolate the functional units that allow a TV to transduce electromagnetic radiation into a color bitmap (its function). Indeed, most ways of dividing its insides will fail to capture *any* functional components, and any such nonfunctional “parts” will be by-products of the functional ones (Hagen, Chapter 5, this volume).

which a set of design features nonrandomly solve an independently defined ancestral adaptive problem.

DESIGN EVIDENCE

To determine a system's adaptive function, researchers need to produce evidence of a fit between its design and the proposed function. This requires the application of engineering standards. As an analogy, consider the relation between design and function in human-made artifacts. A ceramic mug is made of an insulating material that does not dissolve or melt when it contacts hot drinks; its shape stably contains about 8 ounces of liquid while allowing a mouth access to it; and it has a heat-dissipating handle. These properties of a mug are *design features*: properties that exist *because* they are good solutions to the problem of drinking hot beverages without burning your hands.

These properties are unlikely to occur together by chance. Moreover, other uses to which mugs are put (e.g., paperweights, pencil holders) neither predict nor explain these features (paperweights need only be heavy; pencil holders must have a containing shape, but many materials will do and no handle is needed). A mug can produce many beneficial effects, but only one of these is its function, that is, the explanation for its design. We can tell which design explanation is correct by analyzing the fit between the mug's design and a proposed function. Mugs have many interlocking properties that are good solutions to the problem of drinking hot drinks, and their properties are poorly explained by alternative theories of their function; that is how we know that they were designed for that function. The more complex the architecture, the more powerful design evidence can be. For example, there are many design features that can decide whether a toaster was intended to be a vehicle, a nutrient, a cleaner, a geological accident, or a means for toasting slices of bread.

In the same way, design evidence is critical for claiming that a property of an organism is an adaptation, whether that property is a knee, a heart, or a neural circuit that processes information. Does the organic machinery in question have properties that cause it to solve an adaptive problem precisely, reliably, and economically? If not, then its ability to solve the problem at issue may be incidental, a side effect of a system that is well designed to perform some alternative adaptive function (Williams, 1966). For example, zoologists found that nocturnal bats have a sonar system with many of the same intricate and interlocking features of human-engineered sonar and radar systems, including features that make bat sonar a good design for finding insects and avoiding obstacles at night (e.g., higher pulse rates when hunting small moving targets than when cruising; for discussion, see Dawkins, 1986). At the same time, bat sonar is poorly suited for solving most other problems (e.g., judging the relative ripeness of fruit during the day). And there is no physical law or general metabolic process that produces bat sonar as a side effect.

Finding and pursuing small flying food items in the dark without crashing into things pose intricate computational problems, which very few arrangements of matter can solve. The bat's sonar solves these problems well. There is a tight fit between the problems' requirements and the evolved solution. It is by virtue of this excellence in design that we recognize finding insects and avoiding obstacles at night as the adaptive function of bat sonar.

28 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

Researchers can identify an aspect of an organism's physical, developmental, or psychological structure—its phenotype—as an adaptation by showing that (1) it has many design features that are improbably well suited to solving an ancestral adaptive problem, (2) these phenotypic properties are unlikely to have arisen by chance alone, and (3) they are not better explained as the by-product of mechanisms designed to solve some alternative adaptive problem or some more inclusive class of adaptive problem. Finding that a reliably developing feature of the species' architecture solves an adaptive problem with reliability, precision, efficiency, and economy is *prima facie* evidence that an adaptation has been located. This is like showing that an oddly shaped piece of metal easily opens the lock on your front door. It is almost certainly a key designed for your door because door locks are not easily opened by random bits of metal, by can openers or candlesticks, or even by keys designed for other doors.

To show that something is a by-product, researchers must first establish that something else is an adaptation (e.g., blood as an oxygen transport system) and then show how the feature is a side effect of the adaptation (e.g., the redness of blood is a side effect of the oxygen-carrying iron in hemoglobin). Features that are uncoordinated with functional demands are evolutionary noise (e.g., the locations of flecks of color in the eye).

THEORIES OF GOOD DESIGN ARE A HEURISTIC FOR DISCOVERY

If design evidence were important only for explaining why known properties of organisms have the form that they do (i.e., why the lens of the eye is transparent rather than opaque), its use in psychology would be limited. After all, most properties of the human mind are currently unknown. The concept of good design for solving an adaptive problem is important because it allows researchers to discover new mechanisms within the human mind. There is a systematic method for using theories of adaptive function and principles of good design for discovering new programs.

One starts with an adaptive problem encountered by human ancestors, including what information would potentially have been present in past environments for solving that problem. From the model of an adaptive problem, the researcher develops a task analysis of the kinds of computations necessary for solving that problem, concentrating on what would count as a well-designed program given the adaptive function under consideration. Based on this task analysis, hypotheses can be formulated about what kinds of programs might actually have evolved. Next, their presence can be tested for experimentally, using methods from cognitive, social, and developmental psychology, cognitive neuroscience/neuropsychology, experimental economics, cross-cultural studies—whatever methods are most appropriate for illuminating programs with the hypothesized properties. If the predicted design features are found, tests can be conducted to make sure they are not better explained by alternative hypotheses about the programs responsible. Testing includes making sure the program in question is distributed cross-culturally in the way predicted by the theory, which may predict universality, different expressions triggered by different environmental or social conditions, or local calibration by specific circumstances.

Research on the architecture of kin detection in humans provides an example of how this process of discovery can work (Lieberman et al., 2003, in press-a, in

press-b, in press-c). Avoiding the deleterious effects of inbreeding was an important adaptive problem faced by our hominid ancestors. The best way to avoid the costs of inbreeding is to avoid having sex with close genetic relatives. This, in turn, requires a system for distinguishing close genetic relatives from other individuals: a kin detection system, which computes a kinship estimate for each individual with whom one lives in close association. Because genetic relatedness cannot be directly observed, it is important to consider what information relevant to estimating degrees of kinship would have been available to an ancestral hunter-gatherer. To be useful, kinship estimates would have to be based on cues that reliably predicted genetic relatedness in the social conditions under which our ancestors lived. We are looking for cues that would have been stably present across a broad variety of ancestral social conditions and habitats. For example, hunter-gatherers often live and forage in groups that fuse and fission along nuclear family lines, such that parents more frequently stay together with children, adult siblings and their families maintain association, but to a lesser degree, and so on. This would allow the cumulative duration of childhood coresidence to function as a cue to genetic relatedness. An individual who observed his or her mother caring for another infant (what we call maternal perinatal association) would be a more direct cue that the infant was a sibling. A third cue might be an olfactory signature indicating similarity of the major histocompatibility complex. Based on the stable information structure of the ancestral world, the kin detection system is expected to evolve to monitor ancestrally valid cues, and use them to compute a relatedness index for everyone in the individual's social world. This internal regulatory variable should serve as input to systems that compute the sexual value of another individual to himself or herself: All else equal, close genetic relatives should be assigned a lower sexual value than unrelated people. This sexual value estimate—another internal regulatory variable—should regulate the motivational system that generates sexual attraction. A low kinship estimate should upregulate sexual attraction whereas a high kinship estimate should downregulate sexual attraction, perhaps by activating disgust in response to the prospect of sex with that person. These and other theoretically derived predictions about the existence and architecture of the human kin detection system were empirically confirmed, along with a parallel set of predictions about kin-directed altruism. The two predicted cues—maternal perinatal association and duration of childhood coresidence—regulate sexual disgust toward genetic relatives and kin-directed altruism as well (as predicted by Hamilton, 1964). The cues used by older siblings in detecting younger ones differ from those used by younger siblings detecting older ones. The results are incompatible with a variety of alternative theories that could be put forth to explain the results (e.g., Lieberman, Tooby, & Cosmides, 2003, in press-a, in press-b). So far, the pattern found holds in a variety of different cultural settings, consistent with the hypothesis that the kin detection system develops cross-culturally as a universal mechanism of the human mind (Lieberman et al., in press-c).

Note that by starting with an adaptive problem—inbreeding avoidance—and analyzing the computational requirements of a system that solves this problem, a significant neurocomputational system was predicted, tested for, and discovered—a system that was previously unknown and uninvestigated by traditional psychologists and cognitive scientists.

It may not seem so at first glance, but notice that the kin detection system is a *learning mechanism*. Its function is to learn which individuals in a person's

30 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

environment are kin and which are not, and it is designed to make this categorization on the basis of certain cues present during development, while ignoring others. For example, an individual's consciously held beliefs about who is a sibling do not predict degree of sexual aversion, once duration of childhood coresidence is controlled for (but coresidence does predict sexual aversion, controlling for beliefs about who is a sibling; Lieberman et al., 2003, in press-a). The kin detection system is not, however, a *general-purpose* learning mechanism. It is highly specialized for a narrow task and has nothing in common with mechanisms of classical and operant conditioning, the way facts are learned in school, or any other more general-purpose method of learning.⁸

NATURE AND NURTURE: AN ADAPTATIONIST PERSPECTIVE

To fully understand the concept of design evidence, we need to consider how evolutionary psychologists think about nature and nurture. Debates about the relative contribution (as it is misleadingly put) of genes and environment during development have been among the most contentious in psychology. The premises that underlie these debates are flawed, yet they are so deeply entrenched that many people, scientists and nonscientists alike, have difficulty seeing that there are better ways to think about these issues.

Rather than there being one nature-nurture issue, there are many independent issues. Unfortunately, they have become so tangled that most discussions in psychology and the social sciences are hopelessly confused. We pull the major questions apart and look at them one by one. Some of them are conceptual confusions, whereas others are genuine scientific questions whose resolution will depend on research, rather than on clear thinking alone.

Despite widespread belief to the contrary, evolutionary psychology is not another swing of the nature-nurture pendulum (Tooby & Cosmides, 1992). It shatters the traditional framework and the old categories entirely, rather than siding with any position within the old debate. Indeed, a defining characteristic of the field is the explicit rejection of the usual nature-nurture dichotomies—instinct versus reasoning, innate versus learned, biological versus cultural, nativist versus environmentalist, socially determined versus genetically determined, and so on—because they do not correspond to the actual distinctions that need to be made in the real world. Evolutionary psychologists do not see nature and nurture as in a zero-sum relationship. Nature and nurture exist in a positive sum relationship: More nature allows more nurture (Boyer, 2001; Tooby & Cosmides, 1992).

"Innate" Is Not the Opposite of "Learned" Everyone is a nativist, whether she knows it or not. Even the most extreme advocates of the role of the environment in shaping human behavior, from Skinner to the postmodernists, make nativist claims about the "innate" structure of the evolved neural machinery that learns or responds to the environment. The only difference is whether they make the na-

⁸It is not known how children learn facts in school—the notion that it is via some form of general-purpose learning is an assumption, not a finding for which there is evidence. Indeed, there is starting to be evidence that school learning piggybacks off domain-specific inference mechanisms (e.g., Hirschfeld & Gelman, 1994; Sperber, 1996).

ture of their claims about this machinery explicit or allow them to remain implicit, forcing the reader to deduce them from their arguments about why people act as they do.

Imagine that you are an engineer and your project is to create a brain that can learn. To be able to learn, this brain would have to have a certain kind of structure—after all, 3-pound cauliflowers do not learn, but 3-pound brains do. To get your brain to learn, you would have to arrange the neurons in particular ways. You would have to create circuits that cause learning to occur. In short, you would have to equip your brain with programs that *cause* it to learn. The same is true when natural selection is the engineer.

Even if a program that causes a particular kind of learning was itself learned, there had to be a prior program that caused that learning to occur, and so on. Logic forces us to conclude that there had to be, at some point in the causal chain, a program that caused learning but that was itself unlearned. These unlearned programs are a part of the brain by virtue of being part of its evolved architecture. They are programs that reliably develop across the ancestrally normal range of human environments.

Both environmentalists and nativists—Pavlov, Skinner, and Chomsky alike—must agree on this point. They may disagree strongly about the computational structure of the evolved programs that cause learning but not about whether evolved learning programs exist. For example, classical and operant conditioning are widely viewed as the simplest and most general forms of learning in humans and other animals. Yet, even operant conditioning presumes the existence of evolved mechanisms that change the probability of a behavior by a certain amount, as a function of its consequences (and according to very precise equations). It also presumes that a handful of consequences—food, water, pain—are “intrinsically” reinforcing (i.e., the fact that these consequences are capable of changing the probability of a subsequent behavior is a design feature of the brain). Classical conditioning presumes the existence of a great deal of evolved equipment. In addition to the programs that compute contingencies, the animal is filled with unconditioned—that is, *unlearned*—responses, such as salivating in response to meat. Salivating in response to meat is considered to be part of the dog’s evolved architecture, and what the evolved learning program does is calculate when an arbitrary stimulus, such as a bell, predicts the appearance of the meat (Gallistel & Gibbon, 2000). Thus, even in classical conditioning, the learned link between information and behavior—salivating to the sound of the bell—is caused by an evolved learning program, which takes as input both evolutionarily privileged stimulus-response pairs (meat and salivation) and information from the external environment (the contingency between the sound of the bell and the appearance of meat). The only substantive disagreement between a Skinner and a Chomsky is about the structures of the evolved programs that cause learning.

Consequently, any learned behavior is the joint product of “innate” equipment interacting with environmental inputs and, therefore, cannot be solely attributed to the action of the environment on the organism. Thus, *innate* cannot be the opposite of *learned*. It is just as mistaken to think of *evolved* as the opposite of *learned* because our evolved learning programs were organized by evolution to learn some things and not others.

To say a behavior is learned in no way undermines the claim that the behavior was organized by evolution. Behavior—if it was learned at all—was learned

32 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

through the agency of evolved mechanisms. If natural selection had built a different set of learning mechanisms into an organism, that organism would learn a different set of behaviors in response to the same environment. It is these evolved mechanisms that organize the relationship between the environmental input and behavioral output and thereby pattern the behavior. For this reason, *learning is not an alternative explanation to the claim that natural selection shaped the behavior*, although many researchers assume that it is. The same goes for culture. Given that cultural ideas are absorbed via learning and inference—which is caused by evolved programs of some kind—a behavior can be, at one and the same time, *cultural, learned, and evolved*. (For an excellent discussion of how evolved inference mechanisms produce and structure cultural transmission, see Boyer, 2001; Sperber, 1996.)

Moreover, there does not appear to be a single program that causes learning in all domains (consider kin detection, food aversions, snake phobias, and grammar acquisition). Evidence strongly supports the view that learning is caused by a multiplicity of programs (Gallistel, 2000; Tooby & Cosmides, 1992). Without specifying which program is the cause, little is explained, if anything, by invoking learning as an explanation for a behavior. Labeling something learning does not remove the requirement to spell out the evolved machinery involved; it only makes the weak claim that interaction with the environment participated in the process (which is always the case, anyway). In short, learning is a phenomenon that requires explanation, rather than constituting an explanation itself. A coherent explanation for how people learn about a given domain must include (1) a description of what the evolved learning program looks like; (2) why it came to have that structure, both developmentally and over evolutionary time; and (3) what information is available to the organism that is executing that evolved program.

Everyone is also an environmentalist, whether he or she knows it or not. Even the most die-hard nativist understands that organisms learn—or, even more broadly, that an organism's evolved mechanisms extract information from the environment and process it to regulate behavior. Hence the environment regulates behavior, and it is the presence of evolved mechanisms that makes this possible.

Thus, evolved programs—instincts—are not the opposite of learning. They are the engines through which learning takes place. We learn only through instincts—learning and reasoning instincts. There are instincts in songbirds for learning songs, instincts in geese for learning which individual is one's mother, instincts in desert ants for learning how to return home, and instincts in humans for learning a language. The greater the number of specialized learning programs we come equipped with, the more we can learn from experience.

Specialized or General Purpose? If the *innate versus learned* controversy is meaningless, there are genuine and illuminating questions to be answered: *What is the precise structure of these evolved learning and regulatory programs? Are there many or just a few? Which embody knowledge about enduring aspects of the world, and what knowledge do their procedures reflect? To what extent is a program—whether it governs learning or not—functionally specialized to produce the outcome that you have observed?*

What effect a given environmental factor will have on an organism depends critically on the details of the designs of its evolved cognitive programs. So the discovery of their structure is a pivotal question. Indeed, one of the few genuine

nature-nurture issues concerns the extent to which each evolved program is specialized for producing a given outcome (Cosmides & Tooby, 1987; Symons, 1987; Tooby & Cosmides, 1992). Most nature-nurture issues disappear when more understanding is gained about evolution, cognitive science, and developmental biology, but this one does not.

Thus, the important question for any particular behavior is not, "Is it learned," but, "What kind of evolved programs produced it?" More specifically, "What is the nature of the universal, species-typical evolved cognitive programs through which the organism learns this particular type of behavior, acquires this kind of knowledge, or produces this form of behavior?"

For any given outcome, there are three alternative possibilities: (1) It is the product of domain-general programs, (2) it is the product of cognitive programs that are specialized for producing that outcome, or (3) it is a by-product of specialized cognitive programs that evolved to solve a different problem.

The debate about language acquisition, which began in 1959 when Noam Chomsky reviewed B. F. Skinner's book, *Verbal Behavior*, brings this issue into sharp focus, because Chomsky and Skinner disagreed about precisely these issues (Chomsky, 1959; Skinner, 1957). Both sides in the ensuing controversy admit, as coherence demands, that the human mind contains innate learning programs. But the two camps differ in their answer to the question: Does a single set of general-purpose, cognitive programs cause children to learn everything, with language as one incidental example? Or is language learning caused, in part or in whole, by programs that are specialized for performing this task—that is, by what Chomsky called a *language acquisition device*?

Questions about functional specialization cannot be answered a priori by theory or logic alone. Each hypothesis about the computational architecture of a learning mechanism—general, or specialized—must be evaluated on the basis of its coherence; explanatory economy and power; retrodictive consistency with known phenomena; and its ability to make successful, novel predictions. The theoretical tools and empirical studies necessary will differ, depending on whether the proposal is about language learning, inferring mental states, acquiring gender roles, developing friendships, eliciting jealousy, or something else. For language, 45 years of research support the hypothesis that humans have evolved programs specialized for various aspects of language acquisition, although the debate remains heated (Pinker, 1994). With the emergence of evolutionary psychology and under the weight of discoveries in many areas of biology, the debate over adaptive specializations has now widened to include all human competences.

Present at Birth? Sometimes people think that to show that a program is part of our evolved architecture, researchers need to show that it is present from birth. Otherwise, the behavior is "learned" (by which they implicitly mean learned through general-purpose processes). But this assumes that all of the evolved programs that cause maturational development operate before birth and none after birth.

This assumption is clearly false. Teeth, breasts, and axillary hair are all standard parts of our evolved architecture, but they develop after birth, 10 or 15 years after in the case of breasts. Newborns lack teeth, but does this mean that infants and toddlers acquire their first set through learning? Does cultural pressure lead them to lose the first set in favor of the second?

34 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

Organs and design features can mature at any point of the life cycle, and this applies to the cognitive programs in our brains just as much as it does to the features of our bodies. Thus, the fact that a behavior emerges after birth tells us very little about how it was acquired or why it has a certain organization. Organs can be disassembled on schedule as well: Consider the placenta, umbilical cord, and fetal hemoglobin. Evolutionists expect—and observations confirm—that many mechanisms appear and disappear on a timetable based on when they would have been needed, under ancestral conditions, to solve the challenges of that life stage. Infants need the suckling reflex but not sexual desires; adolescents need sexual desires but not the suckling reflex.

Presence at birth is only a function of what is needed at birth, not an indicator of whether something is or is not part of our evolved architecture. Accordingly, much of what is present in adult minds may have been put there by evolution and activated through neural maturation, without depending on the accidents of personal experience. For example, infants who cannot crawl do not need a fear of heights, whereas infants who can crawl do. But experiments have demonstrated that a fear of heights is not learned by trial and error; rather, it is an evolved competence that is triggered when the baby starts to self-locomote, even if researchers contrive the situation such that the baby never experiences a fall (Campos, Bertenthal, & Kermoian, 1992).

Of course, the early presence of features is not completely irrelevant when evaluating alternative hypotheses about our evolved design. For example, the early emergence of a competence, before the social world could plausibly have acted, may falsify or undermine a particular social constructionist hypothesis. But the early *absence* of a competence does not by itself undermine the claim that it is part of our evolved design.

The Twin Fallacies of Genetic Determinism and Environmental Determinism Traditional researchers hold a series of beliefs that are widely accepted and that sound eminently reasonable but are based on a series of fallacies about how development works. The first belief is that some behaviors are genetically determined whereas others are environmentally determined. The second is that evolutionary psychology deals only with behavior that is genetically determined, not the much larger set of behaviors that are environmentally determined. These beliefs are wrong for many reasons (Tooby & Cosmides, 1990b, 1992; Tooby, Cosmides, & Barrett, 2003), of which we mention just two (see also Hagen, Chapter 5, this volume).

First, genes are regulatory elements that use environments to construct organisms. Thus, every single component of an organism is codetermined by the interaction of genes with environments. Moreover, some of those components are computational mechanisms, designed to produce behavior on the basis of information from the environment. Seen in this way, it is senseless to ask whether kin detection or language acquisition or snake phobias are caused by the genes or the environment: These phenomena are caused by evolved mechanisms that operate on information from the environment in particular ways, and these evolved mechanisms were themselves constructed by the interaction of genes with the environment.

Second, the view that evolutionary psychology deals only with “genetic” behaviors erroneously assumes that environmental causation is nonevolutionary. In order to understand this, it is useful to distinguish “the environment” (in the

sense of all properties of the universe) from a given species' developmentally relevant environment. By *developmentally relevant environment* we mean the set of properties of the world that affect the development of organisms of a given species.

Evolution acts *through* genes, but it acts on the *relationship* between the genes and the environment, choreographing their interaction to cause evolved design. Genes are the so-called units of selection, which are inherited, selected, or eliminated, so they are indeed something that evolves. But every time one gene is selected over another, one design for a developmental program is selected as well. (We all start as a single cell—brainless, limbless, gutless. Every cell and organ system subsequently develops from that cell, nonrandomly climbing toward specific organizational forms despite the onslaughts of entropy. For manifest organization to emerge, there must be naturally selected processes that cause this to happen: developmental programs.)

Developmental programs, by virtue of their design, make some parts of the world relevant to development and other parts irrelevant. Over evolutionary time, genetic variation in developmental programs (with selective retention of advantageous variants) explores the properties of the environment, discovering those that are useful sources of information in the task of regulating development and behavior; equally, selection renders those features of the environment that are unreliable or disruptive irrelevant to development. Step by step, as natural selection constructs the species' gene set (chosen from the available mutations), it selects in tandem which enduring properties of the world will be relevant to development. Thus, a species' *developmentally relevant environment*—that set of features of the world that a zygote and the subsequently developing organism depend on, interact with, or use as inputs—is just as much the creation of the evolutionary process as the genes are. Hence, natural selection can be said to store information necessary for development both in the environment and the genes.

The developmentally relevant environment can be viewed as a second system of inheritance comparable in some ways to genetic systems of inheritance. A zygote in an environment can be seen as inheriting a set of genetic determinants (including cellular machinery) and simultaneously a set of environmental determinants. The environmental determinants are transmitted or inherited in a peculiar fashion: They simply endure as physical arrangements in the world across generations over the range where the lineal series of zygotes appears. Some environmental determinants are perfectly replicated across generations (e.g., the three-dimensional nature of space, the properties of light, the properties of chemical compounds, the presence of other humans for a zygote that survives); others are replicated reliably but imperfectly (e.g., mother smiling in response to an infant's smile, the presence of fathers during childhood, a correlation between duration of childhood coresidence and genetic relatedness, cycles of drought and rain). Organismic designs successfully reproduce based on the degree to which their genetic and environmental inheritances are coordinated with each other. Change in either inheritance (either through genetic mutation or environmental change) disrupts the coordination, and the greater or more rapid the change, the greater is the disruption.

This view of development is not gene-centered or a form of "genetic determinism" if by that one means that genes by themselves determine everything, immune from environmental influence—or even that genes determine "more" than

36 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

the environment does. Although not gene-centered, however, this view is very much natural selection-centered, because it is natural selection that chooses some genes rather than others and, in so doing, orchestrates the interaction between the two inheritances so that high degrees of recurrent functional order can emerge and persist, such as eyes or maternal love.

Moreover, this view explains how reliable development both can and does ordinarily occur—that is, it explains why a robust, species-typical design emerges in almost all individuals (e.g., what can be seen in *Gray's Anatomy*; Gray, 1918). The species-typical features of the genome interact with the features of evolutionarily long-enduring, species-typical environments to produce the species-typical design observable in organisms. Failures of reliable development are attributable to genetic mutation, to environmental mutation (change), or both.

The closest that the world comes to the fallacious distinction between biologically or genetically determined traits versus environmentally or socially determined traits is in the following real distinction: Some neural programs were designed by natural selection to take in substantial amounts of environmental input (e.g., the language acquisition device) whereas others were designed to take in less information (e.g., the reflex that causes the eye to blink in response to a looming figure). But in all cases, there is an underlying neural program designed by natural selection and a set of environmental regularities necessary for that program's reliable development. Indeed, as we discuss later, there is not a zero-sum relationship between nature and nurture: More nature means more nurture.

Universal Architectural Design versus Genetic Differences How are we to reconcile the claim that there is a universal species-typical design—including a universal human nature—with the existence of individual differences, especially those caused by genetic differences between people?

At a certain level of abstraction, every species has a universal, species-typical evolved architecture. For example, we humans all have a heart, two lungs, a stomach, and so on. This is not to say there is no biochemical individuality, especially in quantitative features. Stomachs, for example, vary in size, shape, and amount of hydrochloric acid produced. Yet, all stomachs have the same basic *functional* design: They are attached at one end to an esophagus and at the other to the small intestine, they secrete the same chemicals necessary for digestion, they are made of the same cell types, and so on. Indeed, when humans are described from the point of view of their complex adaptations, differences tend to disappear, and a universal architecture emerges. This universality is not only theoretically predicted, but is empirically established (e.g., *Gray's Anatomy* describes this architecture in minute detail). This phenotypic universality is expected to be reflected at the genetic level through a largely universal and species-typical genetic architecture (“the” human genome) as well.

The logic is as follows (see Tooby, 1982; Tooby & Cosmides, 1990b, for a more complete explanation):

- Complex adaptations are intricate machines. Adaptations that consist of complexly structured functional elements require, in turn, complex specification at the genetic level. That is, they require coordinated gene expression, often involving hundreds or even thousands of genes to regulate their development.

- Like any other intricate machine, the parts of a complex adaptation must all be present and fit together precisely if the adaptation is to work properly. Parts of complex adaptations are functionally interdependent. All the genes necessary to build each component part and assemble it correctly must be reliably brought together in the same individual. Fitting together the parts specified by new genetic combinations is not a problem for organisms that reproduce by cloning but it is for sexual reproducers.
- Each new human originates sexually. A randomly selected complement of the mother's genes is recombined with a randomly selected half of the father's genes. During gamete and zygote formation, sexual reproduction automatically breaks apart existing sets of genes and randomly generates in the offspring new combinations at those loci that vary from individual to individual. This would not be a problem if the mother and father were genetically identical at all loci. But it is a problem to the extent that their genes differ at those loci underlying complex adaptations.
- Hence, the successful assembly of a complex adaptation in a new individual requires that all of the genes necessary for that adaptation be supplied by the two gametes, even though gametes are both randomly generated and consist of only half of each parent's DNA. Successful assembly would not be possible if only some individuals in the population had the complex adaptation (and the suite of genes that specified all of its necessary component parts). If in a given generation, different individuals had different complex adaptations, each of which was coded for by a different suite of genes, then during the formation of the gametes for the next generation the random sampling of subsets of the parental genes would break apart each suite. During zygote formation, these incomplete specifications of incompatible adaptations would be shuffled together. Consequently, the offspring generation would be a handicapped jumble of fragments of functionally incompatible adaptations. The simultaneous demand for functional compatibility of complex adaptations and sexual reproduction places strong constraints on the nature and distribution of functional variation.
- Specifically, the only way that each generation can be supplied with the genetic specification for complex adaptations is if the entire suite of genes necessary for coding for each complex adaptation is effectively universal and hence reliably supplied by each parent regardless of which genes are sampled. By analogy, if you attempted to build a new car engine by randomly sampling parts from two parent cars, you would fail if one parent were a Toyota and the other a Jaguar. To build a new engine whose component parts fit together, you would have to salvage parts from two parents that were of the same make and model.
- By the same token, sexually reproducing populations of organisms freely tolerate genetic variation to the extent that this variation does not impact the complex adaptive organization shared across individuals. In the car engine example, the color of the parts is functionally irrelevant to the operation of the car and thus can vary arbitrarily and superficially among cars of the same make and model. But the shapes of the parts are critical to functional performance and cannot vary if the offspring design is to function successfully.

38 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

- The constraint of functional universality applies only to adaptations whose genetic basis is complex—that is, whose genetic basis involves multiple independently segregating loci. This selection pressure starts when there are two independent loci and becomes combinatorially more powerful with each additional locus. However, if an adaptation can be coded for by a single gene in a way that is not impacted by genes at other loci, then sexual recombination does not disassemble it, and individuals may vary locally or regionally. Similarly, quantitative genetic variation (e.g., height, arm length, how easily an individual is angered) is not constrained by sexual reproduction and functional compatibility and thus may also vary locally or regionally. Quantitative genetic variation is genetic variation that shifts phenotypes dimensionally, but not outside the boundaries imposed by the demand for functional compatibility.
- Some evolved outcomes are the result of frequency-dependent selection. That is, the population stabilizes at intermediate frequencies with two or more alternative designs, such as male and female, because the relative reproductive advantage of being one over the other decreases with increasing frequency (Fisher, 1930). If the adaptation involves only a single locus, two or more alternative designs can persist indefinitely in the species.
- Finally, selection for genetic universality in complex adaptations does not rule out the possibility that some individuals express complex adaptations that others do not (as the two sexes and different life stages do). Such expression, however, must be based on a genetic architecture that is largely universal and simply activated by an environmental trigger or a simple genetic switch such as a single locus (e.g., the unrecombining regions of the Y chromosome). For example, women express a different set of complex reproductive organs than men, but not because men lack the genes necessary to code for ovaries and a uterus. If males and females were different because each lacked the complex genetic specification of the adaptations of the other sex, then when they produced offspring they would be non-reproductive individuals of intermediate sex. In other words, *functional* aspects of the architecture tend to be universal at the genetic level, even though their expression may be limited to a particular sex or age or be contingent on the presence of an eliciting cue in the environment or at a single locus.
- The living world sharply clusters into sets of organisms that share properties—species—because of the demand for functional compatibility among sexual reproducers. Indeed, it is striking the degree to which species are characterized by complex, shared, and instantly recognizable designs. Still, the degree to which functional variation can be tolerated in a species is a function of a number of variables, such as fecundity, migration rate, and population density. In species where successful parents have large numbers of offspring, reproductive rates are high, and migration rates are low between populations, populations may diverge in some complex adaptations because local mates are more likely to share functionally compatible genotypes even if there is variation elsewhere in the species. Compared with the great majority of other species, however, ancestral humans had very low fecundity, had an open breeding structure, and migrated across substantial distances. For these reasons, humans are both expected to be, and are ob-

served to be, characterized by a greater tendency toward species typicality than many other species.

Thus, humans are free to vary genetically in their superficial, nonfunctional traits but are constrained by natural selection to share a largely universal genetic design for their complex, evolved functional architecture. Even relatively simple cognitive programs must contain a large number of interdependent processing steps, limiting the nature of the variation that can exist without violating the program's functional integrity. The psychic unity of humankind—that is, a universal and uniform human nature—is necessarily imposed to the extent and along those dimensions that our psychologies are collections of complex adaptations. In short, selection, interacting with sexual recombination, tends to impose at the genetic level near uniformity in the functional design of our complex neurocomputational machinery.

Evolutionary Psychology and Behavior Genetics Ask Different Questions The preceding discussion provides a framework for thinking about universal design and genetic differences. Behavior geneticists, through twin studies and comparisons of kin raised together and apart, explore the extent to which *differences* between individuals are accounted for by *differences* in their genes. This difference is expressed as a heritability statistic— $h = Vg/Vg + Ve + Vge$ —which tells you the proportion of variance in a population of individuals that is caused by differences in their genes (compared to all causes: variance due to differences in environment, genes, and their interaction). In contrast, evolutionary psychologists primarily explore the design of the universal, evolved psychological and neural architecture that we all share by virtue of being human.

Evolutionary psychologists are usually less interested in human characteristics that vary due to genetic differences because they recognize that these differences are unlikely to be evolved adaptations central to human nature. Of the three kinds of characteristics that are found in the design of organisms—adaptations, by-products, and noise—traits caused by genetic variants are predominantly evolutionary noise, with little adaptive significance, while complex adaptations are likely to be universal in the species.

Why is uniformity associated with functionality and variability associated with lack of function? The first reason involves the constraints on organic design imposed by sexual recombination, as explained earlier. Second, alternative genes at the same locus (the same location in the human genome) are in a zero-sum competition for relative frequency in the species: The more common one allele is, the less common the others are. Natural selection tends to eliminate genetic differences whenever two alternative alleles (genes) differ in their ability to promote reproduction (except in the case of frequency-dependent selection). Usually, the better functioning gene increases in frequency, squeezing out the less functional gene variant, until it disappears from the species. When this happens, there is no longer genetic variability at that locus: Natural selection has produced genetic uniformity instead. The more important the function, the more natural selection tends to enforce genetic uniformity. Thus, our important functional machinery tends to be universal at the genetic level, and the heritability statistic associated with this machinery will be close to zero (because there is little variation between individuals caused by genes). In contrast, whenever a mutation fails to

40 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

make a functional difference, selection will not act on it, and such minor variants can build up at the locus until there is substantial genetic variability for the trait. Hence, its heritability statistic will be high (because most variation between individuals is caused by variation in genes). For this reason, genetic variability is commonly nonadaptive or maladaptive evolutionary noise: neutral variants, negative mutations on their way to being eliminated, and so on. Such variants may be, of course, of the greatest medical, personal, or practical significance, as, for example, in the search for possible genetic causes of schizophrenia, depression, and autism or the discovery that a formerly neutral variant causes differential drug metabolism. The point is, however, genetic variants causing medical vulnerabilities or personality differences are generally unlikely to be adaptations designed to cause those effects. If something is highly functional, selection usually acts to spread its genetic basis to the entire species.

There is, nonetheless, a great deal of genetic variability within species, which is in tension with the functional advantages of genetic uniformity. Aside from mutations and neutral variants, there is a third reason for this genetic diversity. Genetic variability, such as the ABO blood group system, is retained in the species because genetically based, biochemical individuality interferes with the transmission of infectious diseases from host to host (Tooby, 1982). Diseases that use or depend on a protein found in their present host are thwarted when the next individual they jump to has a different protein instead. Hence, natural selection sifts for genetic variants that supply approximately the same functional properties to the adaptations they participate in but that taste different from the point of view of disease organisms. Because we catch diseases from those we have contact with—such as our family, neighbors, and other locals—selection favors maximizing genetically based protein diversity locally, which requires pulling into every local population as many of the genetic variants found anywhere in the species as possible. Thus, this explains why individuals are so genetically different from one another, but different populations tend to be so surprisingly genetically similar.

This large collection of genetic differences introduces minor perturbations into our universal designs. The result is that each normal human expresses the universal human design, but, simultaneously, each human is slightly different from every other in personality, structure, temperament, and appearance. Macroscopically, these differences tend to be quantitative in nature—a little more of this, a little less of that—while the overall architecture remains the same.

One final category is the possibility of alternative, genetically based psychological designs that are maintained through frequency-dependent selection. The existence of male and female—two alternative designs—shows that such frequency-dependent equilibria are not only possible but also real for humans. Moreover, multiple behavioral strategies often emerge in theoretical models through frequency-dependent selection. Nevertheless, the constraints created by sexual reproduction place strong limitations on the emergence of such systems in real species (even the system of two sexes is based almost entirely on genetic uniformity). Indeed, as the case of the sexes shows, alternative phenotypic strategies can be based more easily on substantial genetic uniformity and alternative developmental pathways than on genetic differences encoding the alternative adaptations. At present in humans there are no well-established cases of frequency-dependent adaptive behavioral strategies based on alternative alleles, except for the two sexes.

The interaction of universal design with genetic variation has many implications for understanding personality variation; for discussion, see Tooby and Cosmides (1990b).

EVOLUTIONARY VERSUS TRADITIONAL APPROACHES TO PSYCHOLOGY:
HOW ARE THEY DIFFERENT?

If all psychologists are engineers working in reverse, and if the goal of all psychologists is to discover the design of the human mind, then how does evolutionary psychology differ from traditional approaches?

Traditional approaches to psychology are not guided by any specific theory of what the mind was designed to do. As animal species go, humans are startling in their capabilities—from making lemon chiffon pies to writing waka to sending probes to Titan, we are capable of solving many problems that no hunter-gatherer ever had to solve (and that no other animal does solve). It, therefore, seemed obvious to many that our minds are not designed to do anything in particular; rather, they are designed to reason and to learn, by virtue of mechanisms so general in function that they can be applied to any domain of human activity. Reasoning and learning require certain auxiliary processes: a memory to retain what is learned or inferred, perceptual systems to bring sense data to the learning and reasoning mechanisms, and attention to spotlight some aspects of perception for further analysis. But these auxiliary processes were also thought to be domain-general. Noting the disconnection between assumptions in psychology and biology, Galistel (2000, p. 1179) made the following observation about the study of learning:

Biological mechanisms are hierarchically nested adaptive specializations, each mechanism constituting a particular solution to a particular problem. . . . One cannot use a hemoglobin molecule as the first stage in light transduction and one cannot use a rhodopsin molecule as an oxygen carrier, any more than one can see with an ear or hear with an eye. Adaptive specialization of mechanism is so ubiquitous and so obvious in biology, at every level of analysis, and for every kind of function, that no one thinks it necessary to call attention to it as a general principle about biological mechanisms. In this light, it is odd but true that most past and contemporary theorizing about learning does not assume that learning mechanisms are adaptively specialized for the solution of particular kinds of problems. Most theorizing assumes that there is a general-purpose learning process in the brain, a process adapted only to solving the problem of learning. There is no attempt to formalize what the problem of learning is and thereby determine whether it can in fact be conceived as a single or uniform problem. From a biological perspective, this assumption is equivalent to assuming that there is a general-purpose sensory organ, which solves the problem of sensing.

The same passage could have been written about reasoning, memory, or attention. The reigning assumption has been that the function of the mind is general—to acquire information that is (roughly) true—which requires programs general enough to handle content drawn from any and all domains. Thus, the study of reasoning has concentrated on procedures that are content-free. Examples include logical procedures (which are designed to produce true conclusions from true premises, no matter what the subject matter of the premises is); mathematical

42 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

procedures, such as Bayes's theorem or multiple regression (which operate over quantities of anything); and heuristics of judgment that use very general principles such as similarity (the representativeness heuristic), frequency (the availability heuristic), or what came first (anchoring and adjustment; e.g., Kahneman, Slovic, & Tversky, 1982; Rips, 1994; but see Cosmides & Tooby, 1996; Gigerenzer, Todd, & the ABC Group, 1999). Memory has been conceived as a single system—after all, it had to be able to store and retrieve information from all domains of human life. When multiple memory systems are proposed, they are usually individuated by information modality or source (a storage system for perceptual representations? motor skills? general knowledge?) rather than by information content (Schacter & Tulving, 1994; but see Caramazza & Shelton, 1998; Klein, 2005; Klein, Cosmides, Tooby, & Chance, 2002; Sherry & Schacter, 1987). Attention has primarily been seen as a content-free mechanism that selects some information in an array for further processing. If true—if attention contains no domain-specialized selection procedures—it should be safe to study it using artificial stimuli that are easy to modify and manipulate in a controlled fashion (Posner, 1978; Triesman, 2005; but see Braun, 2003; Li, Van Rullen, Koch, & Perona, 2002; New, Cosmides, & Tooby, under review).

The traditional view of the mind is radically at variance with the view that emerges from evolutionary psychology. Evolutionary psychologists expect a mind packed with domain-specific, content-rich programs specialized for solving ancestral problems. For example, evolutionary psychologists would view *attention* not as a single mechanism, but as an umbrella term for a whole *suite* of mechanisms, each designed to select different information from a scene for different processing purposes. Some of these may be relatively domain-general and deployed via volitional systems to any task-relevant element in a scene—these are the attentional mechanisms that have been studied most, using artificial stimuli. The mistake is not to think these exist, but to think they are *all* that exist (Braun, 2003). For example, research with change detection and attentional blink paradigms is uncovering attentional systems that are highly domain-specific and deployed in the absence of any specific task demand. One system preferentially attends to human faces (Ro, Russell, & Lavie, 2001). A similar system snaps attention to the location at which a pair of eyes is gazing (Friesen & Kingstone, 2003). Yet another monitors animals for changes in their state and location: Changes to animals are detected more quickly and reliably than changes to buildings, plants, tools—even vehicles (New, Cosmides, & Tooby, under review). Better change detection for animals than vehicles is significant because it shows a monitoring system tuned to ancestral rather than modern priorities. Our ability to quickly detect changes in the state and location of cars on the highway has life or death consequences and is a highly trained ability in twenty-first century America, where the studies were done. Yet, we are better at detecting changes in the states and locations of animals—an ability that had foraging or sometimes predatory consequences for our hunter-gatherer ancestors but is merely a distraction in modern cities and suburbs.

The point is not just that attention will be composed of many different domain-specific mechanisms, but that each domain-specialized attentional mechanism will be part of a vertically integrated system linking the attended objects to domain-specialized inferential, learning, and memory systems. True, animals needed to be closely monitored because they presented either dangers

(e.g., predators) or opportunities for hunting (prey). But once detected, other specialized processing is needed. Barrett has shown that a predator-prey inference system develops early, regardless of relevant experiences: 3- and 4-year-old children have a sophisticated understanding of predator-prey interactions, whether they grow up in urban Berlin or in a Shuar village in the jaguar- and crocodile-infested Amazon, eating animals that their fathers hunted and killed (Barrett, Chapter 7, this volume; Barrett, Tooby, & Cosmides, in press-a). Steen and Owens (2001) have shown that chase play in toddlers and preschoolers has features of special design as a system for practicing and perfecting escape from predators (see also Marks, 1987).

Learning about animals is specialized as well. Mandler and McDonough (1998) have shown that babies distinguish animals from vehicles by 7 months of age and make different inferences about the two by 11 to 14 months. A detailed knowledge of animal behavior is necessary for successful hunting (Blurton Jones & Konner, 1976; Walker, Hill, Kaplan, & McMillan, 2002), and preschoolers as well as adults are equipped with systems specialized for making inductive inferences about the properties of animals (Keil, 1994; Markman, 1989; Springer, 1992; and discussion thereof in Barrett, Cosmides, & Tooby, in press; Boyer, 2001; Boyer & Barrett, Chapter 3, this volume). Atran and colleagues (Atran, 1998; López, Atran, Coley, Medin, & Smith, 1997) provide cross-cultural evidence for a system specialized for sorting living kinds into hierarchically organized, mutually exclusive taxonomic categories that organize inductive inferences: The closer two species are in this taxonomic structure, the more likely someone is to assume that a trait of one is present in the other. Barrett, Cosmides, & Tooby (in press) have found a second parallel inductive system that uses predatory role to guide inferences. This system assumes that two species are more likely to share a trait if they are both predators than if one is a predator and the other an herbivore. This system categorizes animals as predators or not on the basis of minimal dietary information scattered amid other facts about the species' natural history. That is, the category *predator* is triggered by the information "eats animals" and guides inductive learning; the effect on trait induction is strong—twice the size of the taxonomic effect (Barrett, Chapter 7, this volume; Barrett et al., in press-a). Animal-specialized memory systems appear to exist as well. For example, Caramazza provides neuropsychological evidence that information about animals is stored in a category-specific memory system, functionally and neurally separate from that which stores information about artifacts (Caramazza, 2000; Caramazza & Shelton, 1998). From a traditional psychological perspective, content effects concerning animals are no more significant than hypothetical effects about door knobs, floorings, or words that rhyme with Quetzlcoatl. From an evolutionary perspective, however, animals were a selective agent of great magnitude and duration, and it would be a surprise if our brains were not strongly shaped by their hundreds of millions of years of interaction with other species.

We are emphasizing the content-specialized nature of processing about animals to illustrate an important point. The benefit of an attentional system specialized for monitoring animals is enhanced if its output is fed into inferential systems that infer their mental states and use this information to predict their likely behavior. The inferences and predictions generated by the mental state system are more useful if they are reliably fed into decision rules that determine whether escape is necessary. The monitoring system should also feed learning mechanisms

44 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

that incidentally acquire information about the animal's properties; these, in turn, should feed memory systems designed to encode, store, and retrieve information about the animals monitored, according to ecologically relevant categories such as *predator*, *taxonomically related*, and so on. Animal-specialized attentional, inferential, behavioral, learning, and memory systems should be *functionally integrated with one another*, forming a distinct, category-based *system*. The same should be true for other content domains. Distinct, content-based information processing systems will exist to the extent that the computational requirements for adaptive problem solving for one content area are functionally incompatible with those for another (Sherry & Shacter, 1987; Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2005).

Seen from this perspective, the ordinary categories of psychology dissolve. To have a textbook chapter on *attention* and a separate one on *memory* and then *learning* and *reasoning* does not necessarily divide the mind in the most appropriate way. Evolutionary psychologists suspect that there may be a domain-specialized system for dealing with animals, with its own associated attentional, inferential, behavioral, learning, and memory circuitry that are designed to work together as an integrated system.

The organization of these specialized systems are expected to look nothing like Fodor's (1983, 2000) "pipelines" (for discussion, see Barrett, in press-b; Boyer & Barrett, Chapter 3, this volume). Some components of the system for making inferences about animals will also be activated for plants and other living things as well (e.g., taxonomic organization, Atran, 1990, or inferences that parts have functions, Keil, 1994). Other components of the animal system will be activated only in response to animals—or, more precisely, to things manifesting those psychophysical properties the system uses to detect animals, such as contingent reactivity or self-propelled motion, whether the manifesting entity is a meerkat, a robot, or a cartoon. Because many components of the animal system will be functionally specialized for solving animal-specific adaptive problems, they will be composed of representations and procedures that have little in common with those in a system for making inferences about plants, artifacts, or cooperation between people (Boyer & Barrett, Chapter 3, this volume). Nor will the boundaries between category-based systems be clean. People may be attended by the animal monitoring system but also by the system for monitoring social gestures; people may be processed as animals for inferences about growth and bodily functions, but not for inferences about social behavior. The organization of specializations will be complex and heterarchical, but with a functional logic that arose because of its excellence at solving ancestral problems of survival and reproduction.

The old categories of psychological research have not led to robust models of the human mind because they do not carve nature at the joints. Content specialization is the rule, not the exception. The easiest way to make a domain-general model of learning, reasoning, attention, or memory collapse is to introduce stimuli drawn from different adaptive domains (e.g., Anderson & Phelps, 2001; Boyer & Barrett, Chapter 3, this volume; Braun, 2003; Cosmides & Tooby, Chapter 20, this volume; Gallistel, 2000). A more reasoned research strategy is to start developing some formal (or even informal) analyses of specific adaptive problems and let these guide research. If there are general systems or principles to be found, they will eventually emerge as we gain a clear understanding of how each content-specialized system functions (for an example, see Leslie, German, & Polizzi, 2005).

Biology is not split into evolutionary biology and nonevolutionary biology: All of biology is organized by evolutionary principles. At some point, all psychology will be evolutionary psychology, simply because it will make no sense to wall off the study of humans from the rest of the natural world. When that happens, textbooks in psychology will no longer be organized according to folk psychological categories, such as *attention*, *memory*, *reasoning*, and *learning*. Their chapter headings will be more like those found in textbooks in evolutionary biology and behavioral ecology, which are organized according to adaptive problems animals must solve to survive and reproduce: foraging (hunting, gathering), kinship, predator defense, resource competition, cooperation, aggression, parental care, dominance and status, inbreeding avoidance, courtship, mateship maintenance, trade-offs between mating effort and parenting effort, mating system, sexual conflict, paternity uncertainty and sexual jealousy, signaling and communication, navigation, habitat selection, and so on (e.g., see Buss, 1999). Future psychology textbooks will surely contain some additional chapters that capture zoologically unusual aspects of human behavior, such as language acquisition, coalition formation, deep engagement friendships, counterfactual reasoning, metarepresentation, and autobiographical memory. But theories of the computational mechanisms that make these unusual abilities possible will include how they interact with and are supported by a wide variety of adaptive specializations (e.g., Boyer, 2001; Cosmides & Tooby, 2000a; Klein, German, Cosmides, & Gabriel, 2004; Leslie, German, & Polizzi, 2005; Sperber, 1994; Sperber & Wilson, 1995; Tooby & Cosmides, 1996).

COGNITION AND MOTIVATION

In principle, modern cognitive scientists should understand that any mechanism that processes information must have a computational description. This should include psychological mechanisms that are responsible for motivation. For example, mechanisms that cause fear, romantic love, sexual jealousy, sexual attraction, the perception of beauty, or disgust should all be describable in computational or cognitive terms, which specify the relevant inputs, representations, the procedures that act on them, and regulatory outputs. Yet, most cognitive scientists would not even recognize these topics as within their domain of study.

One reason why cognitive psychologists arbitrarily limit their scope is the folk psychological distinction made between knowledge acquisition on the one hand and motivation, emotion, and preferences on the other. Those who make this distinction view cognition as the study of knowledge acquisition and leave motivation, emotion, and action to other research communities (e.g., Fodor, 2000)—a practice that presumes that knowledge and motivation are not inseparably coevolved aspects of the same unified systems of representation and action.

THE WEAKNESS OF CONTENT-FREE ARCHITECTURES

To some it may seem as if an evolutionary perspective supports the case that our cognitive architecture consists primarily of powerful, general-purpose problem solvers, inference engines that embody the content-free normative theories of mathematics and logic. After all, wouldn't an organism be better equipped and better adapted if it could solve a more general class of problems over a narrower

46 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

class? And won't mathematical and logical inference engines produce knowledge that is true, thereby providing a sound basis for choosing the most adaptive course of action?

To be a plausible model of how the mind works, any hypothetical domain-general cognitive architecture would have had to reliably generate solutions to all of the problems that were necessary for survival and reproduction in the Pleistocene. For humans and most other species, this is a remarkably diverse, highly structured, and very complex set of problems. If it can be shown that there are essential adaptive problems that humans must have been able to solve to have propagated and that domain-general mechanisms cannot solve them, the view of the mind as consisting solely or primarily of domain-general programs fails. There appear to be a very large number of such problems—at minimum, any kind of information processing problem that involves motivation and many others as well. This leads to the inference that the human cognitive architecture contains many information processing mechanisms that are domain-specific, content-dependent, and specialized for solving particular adaptive problems (Cosmides, 1985; Cosmides & Tooby, 1987, 1994a, 1994b; Tooby & Cosmides, 1990a, 1992; Tooby, Cosmides, & Barrett, 2005).

Content-Free Is Content-Poor Some inferences are usefully applied to some domains but not to others. For example, when predicting the behavior of people, it is useful to assume they have *beliefs* and *desires*: invisible mental states that can be inferred but never observed. When predicting the behavior of rocks rolling down a hill, computing their beliefs and desires is useless. Accordingly, the human cognitive architecture has evolved two separate inference systems for these two domains: a mind-reading system for inferring the mental states of people (which can be selectively impaired in autism; Baron-Cohen, 1995; Leslie & Thaiss, 1992) and an object mechanics system for understanding the interactions of inanimate objects (Leslie, 1994; Spelke, 1990). Each inference system is designed to be activated by cues particular to its domain of applicability (e.g., human behavior for the mind-reading system, inanimate motion for the object mechanics system). Because their domain of applicability is restricted, specialized inferences appropriate for one domain can be made without producing absurd inferences for another. This property allows domain-specific systems to include rich, contentful inferential rules. For example, in content-free logics, "If P, then Q" does not imply, "If Q, then P" because it would lead to absurd inferences ("If you saw a horse, then you saw an animal" does not imply, "If you saw an animal, then you saw a horse"). But a "logic" restricted to situations of social exchange, operating over a more content-restricted set of representations (*benefits*, *entitlement*, *obligation*, and so on), can usefully specify, "If you take the benefit, then you are obligated to satisfy the requirement" implies, "If you satisfy the requirement, then you are entitled to take the benefit"—an inference that is invalid for any content-free logic (see Cosmides & Tooby, Chapter 20, this volume). Because they can have content-restricted, specialized inference rules, domain-specific systems can arrive at correct conclusions that more general rules are necessarily barred from making. As a result, small inputs of information can generate many inductions or deductions.

Notice, however, that these powerful, content-rich inference systems are unavailable to a truly domain-general system. To maintain its domain generality, a system must be equipped with rules that generate valid inferences across all domains—people, rocks, plants, tools, nonhuman animals, and so on. It cannot take

advantage of any inference rules that are useful for one domain but misleading if applied to another. It can have no mind-reading system, no object mechanics system, no predator-prey inference system, or no specializations for tool use (e.g., Defeyter & German, 2003; German & Barrett, in press). The only kinds of inference rules that are left are content-free ones, such as those found in logic and mathematics. Domain-general systems are crippled by this constraint.

Combinatorial Explosion Combinatorial explosion paralyzes even moderately domain-general systems when encountering real-world complexity. Imagine trying to induce what caused your nausea in the absence of any privileged hypotheses. Your entire life preceded the nausea, and a truly open-minded system would have to consider every action, thought, sight, smell, taste, sound, and combination thereof as a potential cause. In deciding how to respond, every possible action would have to be considered. There would be nothing to privilege the hypothesis that the cause was a recently consumed food and nothing to privilege vomiting or future avoidance of that food as behavioral responses.

As the generality of a system is increased by adding new dimensions to a problem space or new branch points to a decision tree, the computational load increases with catastrophic rapidity. A content-free, specialization-free architecture contains no rules of relevance, procedural knowledge, or privileged hypotheses and thus could not solve any biological problem of routine complexity in the amount of time an organism has to solve it (for further discussion, see, e.g., Carruthers, in press; Gallistel, Brown, Carey, Gelman, & Keil, 1991; Gigerenzer & Selten, 2002; Keil, 1989; Markman, 1989; Tooby & Cosmides, 1992).

Acknowledging the necessity of a few “constraints” on learning will not solve this problem. As Gallistel (2000, p. 1180) notes:

Early work focusing on the role of adaptive specialization in learning tended to formulate the problem in terms of the constraints . . . or boundaries . . . that biological considerations placed on *the* learning process. . . . [The contrasting argument] is that there is no such thing as *the* learning process; rather there are many different learning processes. While it is true that the structure of these processes constrain the outcome of learning in interesting ways, the more important point is that it is the problem-specific structure of these processes that makes learning possible.

Problem-specific learning specializations are necessary because the problem of combinatorial explosion cannot be overcome by placing a few constraints on a single, general learning process. Instead of asking, “How much specialization does a general-purpose system require?” psychologists should be asking, “How many degrees of freedom can a system *tolerate*—even a specialized, highly targeted one—and still compute decisions in useful, real-world time.” Combinatorics guarantee that real systems can tolerate only a limited number. Without domain-specialized learning mechanisms, we would learn nothing at all.

Clueless Environments Animals subsist on information. The single most limiting resource to reproduction is not food or safety or access to mates, but what makes them each possible: the information required for making adaptive behavioral choices. Many important features of the world cannot be perceived directly, however. Content-free architectures are limited to knowing what can be validly

derived by general processes from perceptual information and sharply limit the range of problems they can solve. When the environment is clueless, the mechanism will be, too.

Domain-specific mechanisms are not limited in this way. When perceptual evidence is lacking or difficult to obtain, they can fill in the blanks by using cues (perceivable states or events) to infer the status of important, nonperceivable sets of conditions, provided there was a predictable probabilistic relationship between the cues and the unobservables over evolutionary time. For example, it is difficult or impossible to tell from experience that sex with siblings has a higher chance of producing defective offspring—many conceptions are lost in utero, and whatever problems exist in children born of such matings could have been caused by any number of prior events. In contrast, a domain-specialized system can trigger disgust at the prospect of sex with a sibling, drastically reducing the probability of inbreeding. This will work, without individuals having to obtain any knowledge, conscious or otherwise, about the pitfalls of inbreeding. Incestuous sex will simply seem disgusting and wrong (Haidt, 2001; Lieberman et al., 2003). Similarly, ancestral hominids had no method by which they could directly see another person's genes to tell whether they are blood siblings or not. But a mind equipped with a domain-specific kin detection system can estimate kinship on the basis of cues, such as coresidence during childhood, that were correlated with genetic relatedness ancestrally. The person need not be aware of the cues used by this system, the computational process employed, or even the concept *genetic relative*.

What counts as adaptive behavior differs markedly from domain to domain. An architecture equipped only with content-free mechanisms must succeed at survival and reproduction by applying the same procedures to every adaptive problem. But there is no domain-general criterion of success or failure that correlates with fitness (for argument, see Cosmides & Tooby, 1987). For example, what counts as a "good" mate has little in common with a "good" lunch or a "good" brother. Designing a computational program to choose foods based on their kindness or to choose friends based on their flavor and the aggregate calories to be gained from consuming their flesh suggests the kind of functional incompatibility issues that naturally sort human activities into incommensurate motivational domains. Because what counts as the wrong thing to do differs from one class of problems to the next, there must be as many domain-specific subsystems as there are domains in which the definitions of successful behavioral outcomes are incommensurate.

A *motivational domain* is a set of represented inputs, contents, objects, outcomes, or actions that a functionally specialized set of evaluative procedures was designed by evolution to act over (e.g., representations of foods, contaminants, animate dangers, people to emulate, potential retaliations to provocations). For a given species, there is an irreducible number of these motivational domains; within each motivational domain, there is an irreducible set of domain-specific criteria or value-assigning procedures operating. For the food domain in humans, for example, criteria and value-assigning operations include salt, sweet, bitter, sour, savory, fat affordances, putrefying smell avoidance, previous history with the aversion acquisition system, temporal tracking of health consequences by the immune system, stage of pregnancy, boundaries on entities and properties considered by the system, perhaps maggot-ridden food avoidance, and scores of other factors. When the required assignments of value within a domain (e.g., food) can-

not all be derived from a common neurocomputational procedure, the number of motivational elements must necessarily be multiplied to account for the data.

Thus, by evolved design, different content domains should activate different evolved criteria of value, including different trade-offs between alternative criteria. Cases of motivational incommensurability are numerous and easily identified via careful analyses of adaptive problems. Distinct and incommensurable evolved motivational principles exist for food, sexual attraction, mate acquisition, parenting, kinship, incest avoidance, coalitions, disease avoidance, friendship, predators, provocations, snakes, spiders, habitats, safety, competitors, being observed, behavior when sick, certain categories of moral transgression, and scores of other entities, conditions, acts, and relationships.

There has been little progress over the past century toward constructing an inventory of motivational domains. Without any proof or even an informal argument, psychologists have presumed that most values are derived from the environment, by computing contingencies between environmental conditions and a tiny set of reinforcers (food, water, sex, pain; Herrnstein, 1977). As a field, we have been shrugging off the issue of evolved motivations through the shell game of implying that any given motivation is secondarily acquired, without obliging ourselves to specify computationally how and from what. Yet, there are strong reasons to doubt that a system of this kind would track fitness at all (Cosmides & Tooby, 1987; Tooby, Cosmides, & Barrett, 2005).

Value and behavior cannot be induced from the environment alone. No environmental stimulus intrinsically mandates any response or any value hierarchy of responses. In the tangled bank of coevolved organisms that Darwin memorably contemplated at the end of the *Origin of Species*, naturally selected differences in the brains of different species cause them to treat the same objects in a rich and conflicting diversity of ways. The infant that is the object of caring attention by one organism is the object of predatory ambition by another, an ectoparasitic home to a third, and a barrier requiring effortful trajectory change to a fourth. It is the brains of these organisms that introduce behavior-regulatory valuation into the causal stream and natural selection that introduced into brains the neural subsystems that accomplish valuation. The same stimulus set cannot, by itself, explain differences in the preferences and actions they provoke, nor indeed, the preferences themselves.

Value is not in the world even for members of the same species. Members of the same species view the same objects differently. The very same object is one person's husband and another's father—an object of sexual preference in one case and sexual aversion in the other. Moreover, because each evolved organism is by design the center of its own unique valuer-centered web of valuations, evolved value by its nature cannot have an objective character (Cosmides & Tooby, 1981; Hamilton, 1964). Because of the structure of natural selection, social organisms are regularly in social conflict, so that the objective states of the world that are preferred by some are aversive or neutral to others (e.g., that this individual and not that should get the contested food, mating opportunity, territory, parental effort, status, grooming, and so on). This structure gives value for organisms an intrinsically indexical quality. Indeed, fitness "interests"—the causal feedback conditions of gene frequency that value computation evolved to track—cannot be properly assigned to such a high-level entity as a person but are indexical to sets of genes inside the genome defined in terms of their tendency to replicate under

the same conditions (Cosmides & Tooby, 1981). Whatever else might be attainable by sense data and content-free operations, value or its regulatory equivalents must be added by our evolved architecture.

Values and Knowledge We can now address why knowledge acquisition cannot be computationally divorced from motivation, valuation, and preferences.

To behave adaptively, some actions, entities, or states of affairs must be valued more than others, with a motivational system organized to pursue higher over lower valued options. The computations whereby value is assigned typically involve many of the same elements of conceptual structure that are the traditional objects of cognitive science (representations of persons, foods, objects, animals, actions, events). Thus, the evolution of motivational elements will mandate the evolution of an irreducible set of conceptual elements as well. Why? A valuation is not meaningful or causally efficacious for regulating behavior unless it includes some specification of *what is valued*. That is, the specification of what the value applies to generally involves conceptual structure.

For example, for natural selection to cause safe distances from snakes to be preferred to closeness to snakes, it must build the recognition of snakelike entities into our neurocomputational architecture. This system of recognition and tagging operations is, for certain purposes, equivalent to having a snake *concept*, albeit a skeletally specified one. Evidence supports the view that humans and related species do indeed have a valuation system specialized to respond to snakes (e.g., Marks, 1987; Mineka & Cook, 1993; Mineka, Davidson, Cook, & Keir, 1984; Yerkes & Yerkes, 1936). This one consideration alone forces us to add a fourth "innate idea" to Kant's space, time, and causality. Yerkes and Yerkes's finding of evolved snake fear in chimps counts as empirically based philosophical progress and as straightforward progress in the cognitive science of knowledge—derived (*pace* Fodor) from evolutionarily motivated theories of function.

This argument not only establishes the necessity of evolved motivational elements but also resurrects the argument for the necessity of "innate ideas," that is, evolved conceptual procedures within the cognitive architecture that embody knowledge about the world and are triggered by stimuli with certain features (however abstractly described). It is the specificity of the coupling to the particular valuation procedure that individuates the concept with respect to the set of motivational functions (e.g., *beloved* [your children], *suspicious* [snakes]).

Consider, for example, the series of interacting conceptual components necessary to build a snake avoidance system. The system needs a psychophysical front-end: One of its subcomponents assigns the evolved, internal tag *snake* through visual and biomechanical motion cues to a perceptual representation of some entity in the world. It has a second subcomponent that maps in a parameter, *distance*, between the *snake* and the valued entity (e.g., *self* or *child*). The distance-representing component is used by many systems. However, it also must have a component that assigns and updates different specific valuation intensities for different distances, so that farther away is better than closer for snakes (but not for food or other motivational domains). A particular bad event (e.g., an imagined snake bite) need not be specifically represented as a negative goal state in the snake avoidance system, with distance acquiring its significance through backward induction and means-ends analysis. The distance-fear relationship could fill the representation of space with a motivational manifold that itself motivates

avoidance (closeness is increasingly unpleasant). But such action-inviting affordances are not the same, computationally, as a represented goal state.

The metric of valuation against distance (and its update rules) is proprietary to snakes, but the output value parameter it produces must be accessible to other systems (so that distance from snakes can be ranked against other goods, like getting closer to extract your child from the python's coils). Snake, distance, person, and the *distance* (person, snake) valuation metric all necessarily operate together for this simple system to work. Snakes, the entity to be protected, and distance cannot be assigned to one computational process, with valuation assigned to another. Even in this simple example, conceptual and valuation functions indivisibly interpenetrate each other, with the representations necessarily coexisting within the same structure.

Learning, another clearly cognitive topic, is implicated in snake aversion as well, but the learning process is domain-specific. It appears that the snake avoidance system recalibrates based on individual experience, possibly slowly habituating in the absence of negative experiences or observations and increasing sharply if snake contact leads to injury. It also narrowly accepts inputs from the social world—a conspecific expressing fear toward a snake (but not toward other stimuli such as rabbits or flowers)—and uses this information to recalibrate the individual's snake valuation (Mineka & Cook, 1993; Mineka et al., 1984). Presumably, recalibration from observing conspecifics evolved because the system operates more functionally by upregulating or downregulating fear as a function of the local distribution of fear intensities in others, which index to some degree the local rate at which venomous snakes are encountered.

The key point is that even this apparently simple, one-function motivational system involves a series of evolved content-specific conceptual elements, including snakes, distance, conspecifics, that fear-faces have specific referents in the world, that snakes are one of the privileged referents of a fear-face, and the output of fear itself. Not all of these elements are unique to the snake system (although several are), but their pattern of distribution among motivational systems is heterarchical and itself not something that could be derived by content-independent operations acting on experience.

As this form of analysis is applied to the other tasks humans perform, we think it will be impossible to escape the general conclusion that cognitive science intrinsically involves motivation and that the science of motivation intrinsically involves cognition. The brain evolved as a control system, designed to generate action. From this perspective, there is not just a cognitive science of areas such as language, intuitive physics, and number, but also a cognitive science of parenting, eating, kinship, friendship, alliance, groups, mating, status, fighting, tools, minds, foraging, natural history, and scores of other ancient realms of human action. Separating knowledge acquisition from motivation has placed the study of motivation in cognitive eclipse and diverted cognitive scientists from studying conceptual structure, motivation, and action as a single integrated system (which they seem likely to be). It ignores the many causal pathways whereby our evolved architecture should have been designed to manufacture, store, communicate, and act on the basis of representations that would not qualify as a rational architecture's efficient attempt at constructing true beliefs (Gigerenzer & Murray, 1987; Haselton & Buss, 2000; Tooby & Cosmides, in press). Evolved systems for motivational computation use conceptual structure in targeted ways, so motivational

computation and knowledge computation cannot be isolated from each other into separate systems. (For a more complete discussion, see Tooby, Cosmides, & Barrett, 2005.)

EMOTIONS AS A SOLUTION TO THE PROBLEM OF MECHANISM COORDINATION

The preceding discussion leads us to view the mind as a crowded network of evolved, domain-specific programs. Each is functionally specialized for solving a different adaptive problem that arose during hominid evolutionary history, such as face recognition, foraging, mate choice, heart rate regulation, sleep management, or predator vigilance, and each is activated by a different set of cues from the environment. But the existence of all these microprograms itself creates an adaptive problem: Programs that are individually designed to solve specific adaptive problems could, if simultaneously activated, deliver outputs that conflict with one another, interfering with or nullifying one another's functional products. For example, sleep and flight from a predator require mutually inconsistent actions, computations, and physiological states. It is difficult to sleep when your heart and mind are racing with fear, and this is no accident: Disastrous consequences would ensue if proprioceptive cues were activating sleep programs at the same time that the sight of a stalking lion was activating ones designed for predator evasion. To avoid such consequences, the mind must be equipped with superordinate programs that override some programs when others are activated (e.g., a program that deactivates sleep programs when predator evasion subroutines are activated). Furthermore, many adaptive problems are best solved by the simultaneous activation of many different *components* of the cognitive architecture, such that each component assumes one of several alternative states (e.g., predator avoidance may require simultaneous shifts in both heart rate and auditory acuity). Again, a superordinate program is needed that coordinates these components, snapping each into the right configuration at the right time.

We have proposed that emotions are such programs (Cosmides & Tooby, 2000b; Tooby, 1985; Tooby & Cosmides, 1990a). To behave functionally according to evolutionary standards, the mind's many subprograms need to be orchestrated so that their joint product at any given time is functionally coordinated, rather than cacophonous and self-defeating. This coordination is accomplished by a set of superordinate programs: the emotions. On this view, emotions are adaptations that have arisen in response to the adaptive problem of mechanism orchestration. This view implies that the exploration of the statistical structure of ancestral situations and their relationship to the mind's battery of functionally specialized programs is central to mapping the emotions because the most useful (or least harmful) deployment of programs at any given time will depend critically on the exact nature of the confronting situation.

How did emotions arise and assume their distinctive structures? Fighting, falling in love, escaping predators, confronting sexual infidelity, experiencing a failure-driven loss in status, responding to the death of a family member, and so on each involved conditions, contingencies, situations, or event types that recurred innumerable times in hominid evolutionary history. Repeated encounters with each kind of situation selected for adaptations that guided information processing, behavior, and the body adaptively through the clusters of conditions, de-

mands, and contingencies that characterized that particular class of situation. These functions could be accomplished by engineering superordinate programs, each of which jointly mobilizes a subset of the psychological architecture's other programs in a particular configuration. Each configuration would be selected to deploy computational and physiological mechanisms in a way that, when averaged over individuals and generations, would have led to the most fitness-promoting subsequent lifetime outcome given that ancestral situation type.

This coordinated adjustment and entrainment of mechanisms is a mode of operation for the entire psychological architecture and serves as the basis for a precise computational and functional definition of each emotion state. Each emotion entrains various other adaptive programs—deactivating some, activating others, and adjusting the modifiable parameters of still others—so that the whole system operates in a particularly harmonious and efficacious way when the individual is confronting certain kinds of triggering conditions or situations. The conditions or situations relevant to the emotions are those that (1) recurred ancestrally, (2) could not be negotiated successfully unless there was a superordinate level of program coordination (i.e., circumstances in which the independent operation of programs caused no conflicts would not have selected for an emotion program and would lead to emotionally neutral states of mind), (3) had a rich and reliable repeated structure, (4) had recognizable cues signaling their presence,⁹ and (5) an error would have resulted in large fitness costs. When a condition or situation of an evolutionarily recognizable kind is detected, a signal is sent out from the emotion program that activates the specific constellation of subprograms appropriate to solving the type of adaptive problems that were regularly embedded in that situation and deactivates programs whose operation might interfere with solving those types of adaptive problems. Programs directed to remain active may be cued to enter subroutines that are specific to that emotion mode and were tailored by natural selection to solve the problems inherent in the triggering situation with special efficiency.

According to this theoretical framework, an emotion is a superordinate program whose function is to direct the activities and interactions of many subprograms, including those governing perception, attention, inference, learning, memory, goal choice, motivational priorities, categorization and conceptual frameworks, physiological reactions (e.g., heart rate, endocrine function, immune function, gamete release), reflexes, behavioral decision rules, motor systems, communication processes, energy level and effort allocation, affective coloration of events and stimuli, and the recalibration of probability estimates, situation assessments, values, and regulatory variables (e.g., self-esteem, estimations of relative formidability, relative value of alternative goal states, efficacy discount rate). An emotion is not reducible to any one category of effects, such as effects on physiology, behavioral inclinations, cognitive appraisals, or feeling states, because it involves evolved instructions for all of them together, as well as other mechanisms distributed throughout the human mental and physical architecture.

All cognitive programs—including superordinate programs of this kind—are sometimes mistaken for homunculi, that is, entities endowed with free will. A homunculus scans the environment and freely chooses successful actions in a

⁹If there is no repeated structure or no cues to signal the presence of a repeated structure, selection cannot build an adaptation to address the situation.

54 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

way that is not systematic enough to be implemented by a program. It is the task of cognitive psychologists to replace theories that implicitly posit such an impossible entity with theories that can be implemented as fixed programs with open parameters. Emotion programs, for example, have a front-end that is designed to detect evolutionarily reliable cues that a situation exists (whether these cues reliably signal the presence of that situation in the modern world); when triggered, they entrain a specific set of subprograms: those that natural selection chose as most useful for solving the problems that situation posed in ancestral environments. Just as a computer can have a hierarchy of programs, some of which control the activation of others, the human mind can as well. Far from being internal free agents, these programs have an unchanging structure regardless of the needs of the individual or his or her circumstances because they were designed to create states that worked well in ancestral situations, regardless of their consequences in the present.

FEAR (AN EXAMPLE)

The ancestrally recurrent situation is being alone at night and a situation-detector circuit perceives cues that indicate the possible presence of a human or animal predator. The emotion mode is a fear of being stalked. (In this conceptualization of emotion, there might be several distinct emotion modes that are lumped together under the folk category *fear* but that are computationally and empirically distinguishable by the different constellation of programs each entrains.) When the situation detector signals that the individual has entered the situation “possible stalking and ambush,” the following kinds of mental programs are entrained or modified:

- There are shifts in perception and attention. You may suddenly hear with far greater clarity sounds that bear on the hypothesis that you are being stalked but that ordinarily you would not perceive or attend to, such as creaks or rustling. Are the creaks footsteps? Is the rustling caused by something moving stealthily through the bushes? Signal detection thresholds shift: Less evidence is required before you respond as if there were a threat, and more true positives will be perceived at the cost of a higher rate of false alarms.
- Goals and motivational weightings change. Safety becomes a far higher priority. Other goals and the computational systems that subservise them are deactivated. You are no longer hungry; you cease to think about how to charm a potential mate; practicing a new skill no longer seems rewarding. Your planning focus narrows to the present; worries about yesterday and tomorrow temporarily vanish. Hunger, thirst, and pain are suppressed.
- Information gathering programs are redirected. Where is my baby? Where are others who can protect me? Is there somewhere I can go where I can see and hear what is going on better?
- Conceptual frames shift, with the automatic imposition of categories such as *dangerous* or *safe*. Walking a familiar and usually comfortable route may now be mentally tagged as dangerous. Odd places that you normally would not occupy—a hallway closet, the branches of a tree—suddenly may become salient as instances of the category *safe* or *hiding place*.

- Memory processes are directed to new retrieval tasks. Where was that tree I climbed before? Did my adversary and his friend look at me furtively the last time I saw them?
- Communication processes change. Depending on the circumstances, decision rules might cause you to emit an alarm cry or be paralyzed and unable to speak. Your face may automatically assume a species-typical fear expression.
- Specialized inference systems are activated. Information about a lion's trajectory or eye direction might be fed into systems for inferring whether the lion saw you. If the inference is yes, a program automatically infers that the lion knows where you are; if no, the lion does not know where you are (the "seeing-is-knowing" circuit identified by Baron-Cohen, 1995, and inactive in people with autism). This variable may automatically govern whether you freeze in terror or bolt (Barrett, Chapter 7, this volume). Are there cues in the lion's behavior that indicate whether it has eaten recently and thus is unlikely to be predatory in the near future? (Savanna ungulates, such as zebras and wildebeests, commonly make this kind of judgment; Marks, 1987.)
- Specialized learning systems are activated, as the large literature on fear conditioning indicates (e.g., LeDoux, 1995; Mineka & Cook, 1993; Pitman & Orr, 1995). If the threat is real and the ambush occurs, the victim may experience an amygdala-mediated recalibration (as in posttraumatic stress disorder) that can last for the remainder of his or her life (Pitman & Orr, 1995).
- Physiology changes. Gastric mucosa turn white as blood leaves the digestive tract (another concomitant of motivational priorities changing from feeding to safety); adrenalin spikes; heart rate may go up or down (depending on whether the situation calls for flight or immobility), blood rushes to the periphery, and so on (Cannon, 1929; Tomaka, Blascovich, Kibler, & Ernst, 1997); instructions to the musculature (face and elsewhere) are sent (Ekman, 1982). Indeed, the nature of the physiological response can depend in detailed ways on the nature of the threat and the best response option (Marks, 1987).
- Behavioral decision rules are activated. Depending on the nature of the potential threat, different courses of action will be potentiated: hiding, flight, self-defense, or even tonic immobility (the latter is a common response to actual attacks, both in other animals and in humans).¹⁰ Some of these responses may be experienced as automatic or involuntary.

From the point of view of avoiding danger, these computational changes are crucial: They are what allowed the adaptive problem to be solved with high probability, on average over evolutionary time. In any single case they may fail because

¹⁰Marks (1987, pp. 68–69) vividly conveys how many aspects of behavior and physiology may be entrained by certain kinds of fear: "During extreme fear humans may be 'scared stiff' or 'frozen with fear.' A paralyzed conscious state with abrupt onset and termination is reported by survivors of attacks by wild animals, by shell-shocked soldiers, and by more than 50% of rape victims (Suarez & Gallup, 1979). Similarities between tonic immobility and rape-induced paralysis were listed by Suarez and Gallup (features noted by rape victims are in parentheses): (1) profound motor inhibition (inability to move); (2) Parkinsonian-like tremors (body-shaking); (3) silence (inability to call out or scream); (4) no loss of consciousness testified by retention of conditioned reactions acquired during the immobility (recall of details of the attack); (5) apparent analgesia (numbness and insensitivity to pain); (6) reduced core temperature (sensation of feeling cold); (7) abrupt onset and termination (sudden onset and remission of paralysis); (8) aggressive reactions at termination (attack of the rapist after recovery); (9) frequent inhibition of attack by a predator . . ."

they are only the evolutionarily computed best bet, based on ancestrally summed outcomes; they are not a sure bet, based on an unattainable perfect knowledge of the present.

Whether individuals report consciously experiencing fear is a separate question from whether their mechanisms assumed the characteristic configuration that, according to this theoretical approach, defines the fear emotion state. Individuals often behave as if they are in the grip of an emotion, while denying they are feeling that emotion. It is perfectly possible that individuals sometimes remain unaware of their emotion states, which is one reason subjective experience should not be considered the *sine qua non* of emotion. At present, both the function of conscious awareness and the principles that regulate conscious access to emotion states and other mental programs are complex and unresolved questions. Mapping the design features of emotion programs can proceed independently of their resolution, at least for the present. This computational approach also allows testing for the presence of emotion programs cross-culturally. The design features of an emotion mode should be present and ascertainable experimentally, whether the language has a word for an emotion state or not (Lutz, 1988).

THE FUNCTIONAL STRUCTURE OF AN EMOTION PROGRAM EVOLVED TO MATCH THE EVOLUTIONARILY SUMMED STRUCTURE OF ITS TARGET SITUATION

According to this framework, the sets of human emotion programs assumed their evolved designs through interacting with the statistically defined structure of human environments of evolutionary adaptedness. Each emotion program was constructed by a selective regime imposed by a particular evolutionarily recurrent situation—a cluster of repeated probabilistic relationships among events, conditions, actions, and choice consequences that endured over a sufficient stretch of evolutionary time to have had selective consequences on the design of the mind and were probabilistically associated with cues detectable by humans.

For example, the condition of having a mate plus the condition of your mate copulating with someone else constitutes a situation of sexual infidelity—a situation that has recurred over evolutionary time, even though it has not happened to every individual. Associated with this situation were cues reliable enough to allow the evolution of a “situation detector” (e.g., observing a sexual act, flirtation, or even the repeated simultaneous absence of the suspected lovers are cues that could trigger the categorization of a situation as one of infidelity). Even more importantly, there were many necessarily or probabilistically associated elements that tended to be present in the situation of infidelity as encountered among our hunter-gatherer ancestors. Additional elements include: (1) a sexual rival with a capacity for social action and violence, as well as allies of the rival; (2) a discrete probability that an individual’s mate has conceived with the sexual rival; (3) changes in the net lifetime reproductive returns of investing further in the mating relationship; (4) a probable decrease in the degree to which the unfaithful mate’s mechanisms value the victim of infidelity (the presence of an alternative mate lowers replacement costs); (5) a cue that the victim of the infidelity will likely have been deceived about a range of past events, leading the victim to confront the likelihood that his or her memory is permeated with false information; and (6) the victim’s status and reputation for being effective at defending his or her interests in

general would be likely to plummet, inviting challenges in other arenas. These are just a few of the many factors that constitute a list of elements associated in a probabilistic cluster; they constitute the evolutionary recurrent structure of a *situation* of sexual infidelity. The emotion of sexual jealousy evolved in response to these properties of the world—this situation—and there should be evidence of this in its computational design (Buss, 2000; Daly, Wilson, & Weghorst, 1982).

Emotion programs have evolved to take such elements into account, whether they can be perceived or not. Thus, not only do cues of a situation trigger an emotion mode, but also embedded in that emotion mode is a way of seeing the world and feeling about the world related to the ancestral cluster of associated elements. Depending on the intensity of the jealousy evoked, less and less evidence will be required for an individual to believe that these conditions apply to his or her situation. Individuals with morbid jealousy, for example, may hallucinate counterfactual but evolutionarily thematic contents.

To the extent that situations exhibit a structure repeated over evolutionary time, their statistical properties will be used as the basis for natural selection to build an emotion program whose detailed design features are tailored for that situation. This tailoring is accomplished by selection, acting over evolutionary time, differentially incorporating program components that dovetail with individual items on the list of properties probabilistically associated with the situation.

For example, if in ancestral situations of sexual infidelity, there was a substantially higher probability of a violent encounter than in its absence, the sexual jealousy program will have been shaped by the distillation of those encounters, and the jealousy subroutines will have been adjusted to prepare for violence in proportion to the raised probability in the ancestral world. (Natural selection acts too slowly to have updated the mind to post-hunter-gatherer conditions.) Each of these subelements and the adaptive circuits they require can be added to form a general theory of sexual jealousy.

The emotion of sexual jealousy constitutes an organized mode of operation specifically designed to deploy the programs governing each psychological mechanism so that each is poised to deal with the exposed infidelity. Physiological processes are prepared for things such as violence, sperm competition, and the withdrawal of investment; the goal of deterring, injuring, or murdering the rival emerges; the goal of punishing, deterring, or deserting the mate appears; the desire to make yourself more competitively attractive to alternative mates emerges; memory is activated to reanalyze the past; confident assessments of the past are transformed into doubts; the general estimate of the reliability and trustworthiness of the opposite sex (or indeed everyone) may decline; associated shame programs may be triggered to search for situations in which the individual can publicly demonstrate acts of violence or punishment that work to counteract an imagined or real social perception of weakness; and so on.

It is the relationship between the summed details of the ancestral condition and the detailed structure of the resulting emotion program that makes this approach so useful for emotion researchers. Each functionally distinct emotion state—fear of predators, guilt, sexual jealousy, rage, grief, and so on—corresponds to an integrated mode of operation that functions as a solution designed to take advantage of the particular structure of the recurrent situation or triggering condition to which that emotion corresponds. This approach can be used to create theories of each individual emotion, through three steps: (1) reconstructing the clusters of properties

58 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

of ancestral situations, (2) constructing engineering analyses about how each of the known or suspected psychological mechanisms in the human mental architecture should be designed to deal with each ancestral condition or cluster of conditions and integrating these into a model of the emotion program, and (3) constructing or conducting experiments and other investigations to test and revise the models of emotion programs.

Evolutionarily recurrent situations can be arrayed along a spectrum in terms of how rich or skeletal is the set of probabilistically associated elements that defines the situation. A richly structured situation, such as sexual infidelity or predator ambush, will support a richly substructured emotion program in response to the many ancestrally correlated features. Many detailed adjustments will be made to many psychological mechanisms as instructions for the mode of operation. In contrast, some recurrent situations have less structure (i.e., they share fewer properties in common), so the emotion mode makes fewer highly specialized adjustments, imposes fewer specialized and compelling interpretations and behavioral inclinations, and so on. For example, surges of happiness or joy are an emotion program that evolved to respond to the recurrent situation of encountering unexpected positive events. The class of events captured by "unexpectedly positive" is extremely broad and general and has only a few additional properties in common. Emotion programs at the most general and skeletal end of this spectrum correspond to what some call "mood" (happiness, sadness, excitement, anxiety, playfulness, homesickness, and so on).

RECALIBRATIONAL EMOTIONS, EVOLVED REGULATORY VARIABLES, AND
IMAGINED EXPERIENCE

Information about outcomes is not equally spread throughout all points in time and all situations. Some situations are information dense, full of ancestrally stable cues that reliably predicted the fitness consequences of certain decisions or revealed important variables (e.g., discovering who your father really is or how good a friend someone has been to you) and could, therefore, be used to alter weightings in decision rules.

Indeed, we expect that the architecture of the human mind is full of evolved variables whose function is to store summary magnitudes that are useful for regulating behavior and computation. These are not explicit concepts, representations, or goal states, but rather registers or indices that acquire their meaning by the evolved behavior-controlling and computation-controlling procedures that access them. Such regulatory variables may include measures of how valuable to the individual a mate is, a child is, your own life is, and so on; how stable or variable the food productivity of the habitat is; the distribution of condition-independent mortality in the habitat; your expected future life span or period of efficacy; how good a friend someone has been to you; the extent of your social support; your aggressive formidability; your sexual attractiveness; your status or self-esteem; the status of the coalition you belong to; present energy stores; present health; the degree to which subsistence requires collective action, and so on.

Most evolutionarily recurrent situations that select for emotion programs involve the discovery of information that allows the recomputation of one or more of these variables. Recalibration (which, when consciously accessible, appears to produce rich and distinct feeling states) is, therefore, a major functional compo-

ment of most emotion programs. Jealousy, for example, involves several sets of recalibrations (e.g., decrease in estimate of own mate value, decrease in trust). *Recalibrational emotion programs* are emotion programs such as guilt, grief, depression, shame, and gratitude, whose primary function is to carry out such recomputations (Tooby & Cosmides, 1990a), rather than to orchestrate any short-run behavioral response. These are emotion programs that have appeared puzzling from a functional perspective because the feelings they engender interfere with short-term utilitarian action that an active organism might be expected to engage in.

Consider guilt. Hamilton's (1964) rule defines the selection pressures that acted to build the circuits governing how organisms are motivated to allocate benefits between self and kin. This rule says nothing, however, about the procedures by which a mechanism could estimate the value of, for example, a particular piece of food to yourself and your kin. The fitness payoffs of such acts of assistance vary with circumstances. Consequently, each decision about where to allocate assistance depends on inferences about the relative weights of these variables. These nonconscious computations are subject to error. Imagine a mechanism that evolved to allocate food according to Hamilton's rule, situated, for example, in a hunter-gatherer woman. The mechanism in the woman has been using the best information available to her to weight the relative values of the meat to herself and her sister, perhaps reassuring her that it is safe to be away from her sister for a short time. The sudden discovery that her sister, since she was last contacted, has been starving and has become sick functions as an information-dense situation allowing the recalibration of the algorithms that weighted the relative values of the meat to self and sister. The sister's sickness functions as a cue that the previous allocation weighting was in error and that the variables need to be reweighted—including all of the weightings embedded in habitual action sequences. Guilt functions as an emotion mode specialized for recalibration of regulatory variables that control trade-offs in welfare between self and others (Tooby & Cosmides, 1990a).

One significant subcomponent of these recomputational bouts is imagined experience, including both factual and counterfactual elements, to potentiate branching decision points and the variables that govern them (Cosmides & Tooby, 2000a, 2000b; Tooby & Cosmides, 2001). Previous courses of action are brought to mind ("I could have helped then; why didn't I think to?"), with the effect of resetting choice points in decision rules. The negative valence of depression may be explained similarly: Former actions that seemed pleasurable in the past, but which ultimately turned out to lead to bad outcomes, are reexperienced in imagination with a new affective coloration, so that in the future entirely different weightings are called up during choices.

RECALIBRATIONAL RELEASING ENGINES

The environment of evolutionary adaptedness was full of event relationships (e.g., mother is dead) and psychophysical regularities (e.g., blood indicates injury) that cued reliable information about the functional meanings and properties of things, events, persons, and regulatory variables to the psychological architecture. For example, certain body proportions and motions indicated immaturity and need, activating emotion programs for nurturing in

response to “cuteness” releasers (see Eibl-Eibesfeldt, 1970). Others indicated sexual attractiveness (Buss, 1994; Symons, 1979). To be moved with gratitude, to be glad to be home, to see someone desperately pleading, to hold your newborn baby in your arms for the first time, to see a family member leave on a long trip, to encounter someone desperate with hunger, to hear your baby cry with distress, to be warm while it is storming outside—these all *mean* something to us. How does this happen?

In addition to the situation-detecting algorithms associated with major emotion programs such as fear, anger, or jealousy, humans have a far larger set of evolved specializations that we call *recalibrational releasing engines* that involve situation-detecting algorithms and whose function is to trigger appropriate recalibrations, including affective recalibrations, when certain evolutionarily recognizable situations are encountered. By coordinating the mental contents of individuals in the same situation (because both intuitively know that, e.g., the loss of your mother is, as a default, experienced as a sad and painful event), these programs also facilitate communication and culture learning, both of which depend on a shared frame of reference. Although these pervasive microprograms construct a great deal of our world, investigations are only beginning into adaptations of this nature.

The Role of Imagery and Emotion in Planning Imagery is the representation of perceptual information in a format that resembles actual perceptual input. In the evolution of animal nervous systems, simpler designs preceded more complex designs. The evolutionary designs of all modern species, including humans, use distinctive constellations of perceptual inputs as signals of states of affairs (for the rabbit, the outline of a hawk silhouette means a hawk is swooping in). Consequently, the key to unlocking and activating many complex evolved decision and evaluation programs was chained to the present—to being in an environment displaying specific perceptually detectable cues and cue constellations (sweetness, predators, running sores, emotion expressions).

A large inventory of wisdom is stored in such programs, but this information, initially, could be used only by organisms in the environment displaying the activating cues—a profound limitation. An important design advance was achieved when psychological architectures evolved in which these programs could be accessed by feeding a decoupled fictional or counterfactual set of perceptual images, or event relations, so that the response of these programs could be unleashed, experienced, and analyzed as part of planning and other motivational and recalibrational functions (Cosmides & Tooby, 2000a, 2000b; Tooby & Cosmides, 1990a, 2001). For example, the earlier design would go into a fear emotion mode and flee the predator when encountered. The new design could imagine that a planned course of action would, as a side effect, bring it into confrontation with a predator, experience (in appropriately attenuated and decoupled form) the fear program, and recognize that prospective, potential course of action as one to be avoided.

Re-creating cues through imagery in a decoupled, offline mode triggers the same emotion programs (minus their behavioral manifestations) and allows the planning function to evaluate imagined situations by using the same circuits

that evaluate real situations.¹¹ This process would allow alternative courses of action to be evaluated in a way similar to the way in which experienced situations are evaluated. In other words, image-based representations may serve to unlock, for the purposes of planning, the same evolved mechanisms that are triggered by an actual encounter with a situation displaying the imagined perceptual and situational cues. For example, imagining the death of your child can call up the emotion state you would experience had this happened, activating previously dormant algorithms and making new information available to many different mechanisms. As many have recognized, this simulation process can help in making decisions about future plans. Even though you have never experienced the death of a child, for example, an imagined death may activate an image-based representation of extremely negative proprioceptive cues that “tell” the planning function that this is a situation to be avoided. Paradoxically, grief provoked by death may be a by-product of mechanisms designed to take imagined situations as input. It may be intense so that, if triggered by imagination in advance, it is properly deterrent. Alternatively (or additionally), grief may be intense in order to recalibrate weightings in the decision rules that governed choices prior to the death. If your child died because you made an incorrect choice (and given the absence of a controlled study with alternative realities, a bad outcome always raises the probability that you made an incorrect choice), experiencing grief will recalibrate you for subsequent choices. Death may involve guilt, grief, and depression because of the problem of recalibration of weights on courses of action. A person may be haunted by guilt, meaning that courses of action retrospectively judged to be erroneous may be replayed in imagination over and over again, until the reweighting is accomplished. (From this perspective, the fact that counterfactual reasoning in children is triggered only by negative outcomes, German, 1999, may be a design feature of a recalibrational emotion.) Similarly, joyful experiences may be savored, that is, replayed with attention to all of the details of the experience so that every step of the course of action can be colored with positive weightings as it is rehearsed, again, until the simulated experience of these pseudo-“learning trials” has sufficiently reweighted the decision rules.

CONCLUSIONS

Now that we have sketched an evolutionary perspective on cognition, motivation, and emotion and the role that imagery and decoupled cognition play in human mental life, we briefly return to an earlier question. We began our discussion of traditional versus evolutionary approaches to psychology by noting that humans are able to solve a wide array of problems that were no part of their evolutionary

¹¹ Recently, there has been a set of misguided experiments that place people under cognitive load to show that certain putatively evolved emotion programs, such as sexual jealousy, perform differently under load (DeSteno, Bartlett, Braverman, & Salovey, 2002). The idea is that evolved mechanisms must be “automatic” and, therefore, should operate uniformly regardless of cognitive load. But this last inference is incorrect. If a situation, such as sexual infidelity, must be represented vividly to activate the jealousy program, then placing someone under cognitive load will interfere with activation.

62 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

history and that this observation lent appeal to the view that the mind is a general-purpose machine. But this is to confuse the range of problems solved with the architecture that solves it. One could get breadth not only by having a general-purpose architecture (an unspecified, hypothetical, and arguably incoherent entity), but alternatively by bundling an increasing number of specializations together, each capable of solving an additional class of problems. Moreover, it leaves open the possibility of evolved architectures that include numerous specializations, plus additional components designed to exploit the specializations as a flexibly deployable array of tools to attack novel problems.

What determines whether a program can solve a problem is its causal structure, which sometimes matches an evolutionarily novel problem well enough to provide a solution. Moreover, the set of conditions that activates a domain-specific program—its actual domain of application—is necessarily larger than its proper domain of application (i.e., the set of conditions for which it evolved; Sperber, 1994). Domain-specific programs are activated by cues that were correlated ancestrally with the presence of the adaptive problem they were designed to solve. But correlation is never perfect. Contingent reactivity and self-propelled motion may reliably indicate that an object is an animal, for example, but these cues can also be present when the individual sees a child interact with a self-propelled toy, a car moving on the freeway, cartoons, or even a wind-blown branch. After all, signal detection problems are ubiquitous and will apply to situation detectors and psychophysical activating cues as well as to other problems. As humans entered the cognitive niche (Tooby & DeVore, 1985), selection may have favored the emergence of the ability to reroute inputs and outputs among cognitive specializations to allow for greater improvisation.

Last, it would be wrong to exclude the machinery of *higher cognition* from an evolutionary analysis. The evolved architecture of the mind includes specialized mechanisms that permit offline, decoupled cognition, in which metarepresentations, imagery, and a scope syntax interact with the outputs of domain-specific mechanisms to allow the counterfactual and suppositional thinking (Cosmides & Tooby, 2000a; Leslie, 1987; Sperber, 1994). Decoupled cognition may have evolved to help calibrate or recalibrate mechanisms through synthesized experience, support planning, infer other people's mental contents, or imagine solutions to social, tool use, or other ancestral problems. But it seems likely that, whether as by-products or not, decoupled cognition also permits the kind of thinking that underlies scientific discovery, religious ideas, and other uniquely human preoccupations (Boyer, 2001; Cosmides & Tooby, 2000a, 2001; Sperber, 1994; Tooby & Cosmides, 2001).

In sum, the century-long scientific program that assumed that the human psychological architecture consisted predominantly of general purpose, content-independent, equipotential mechanisms has failed to explain much of human behavior. Indeed, it has failed even to develop a set of persuasive models about what the computational architecture of putatively general purpose learning, rationality, or intelligence would look like, and cannot account for any significant kind of human activity. In contrast, evolutionary theory when joined with a computational approach to the mind leads to the conclusion that the human psychological architecture is very likely to include a large array of adaptive specializations. Evolutionary psychologists, and others, have found detailed empirical confirmation of a large series of narrow, deductive predictions derived from models of evolutionarily specialized computational adaptations.

Accordingly, we think that, over the next three or four decades, as a large-scale collaborative goal by the scientific community, it may be possible to turn human nature from a vague idea into a set of precise, high-resolution models of our evolved computational architecture—models that can be cashed out genetically, at the cellular level, developmentally, physiologically, and neurally. It will be a fundamental advance for our species to have a true, natural science of humanity.

REFERENCES

- Alcock, J. (2001). *The triumph of sociobiology*. Oxford: Oxford University Press.
- Anderson, A., & Phelps, E. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, *411*, 305–309.
- Atran, S. (1990). *Cognitive foundations of natural history*. Cambridge: Cambridge University Press.
- Atran, S. (1998). Folk biology and the anthropology of science: Cognitive universals and cultural particulars. *Behavioral and Brain Sciences*, *21*, 547–611.
- Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind*. Cambridge, MA: MIT Press.
- Barrett, H. C. (1999). *From predator-prey adaptations to a general theory of understanding behavior*. Doctoral Dissertation, Department of Anthropology, University of California, Santa Barbara.
- Barrett, H. C. (in press-a). Adaptations to predators and prey. In D. M. Buss (Ed.), *Evolutionary psychology handbook*. New York: Wiley.
- Barrett, H. C. (in press-b). Enzymatic computation and cognitive modularity. *Mind and Language*.
- Barrett, H. C., Cosmides, L., & Tooby, J. (in press). *By descent or by design? Evidence for two modes of biological reasoning*.
- Barrett, H. C., Tooby, J., & Cosmides, L. (in press). *Children's understanding of predator-prey interactions: Cultural dissociations as tests of the impact of experience on evolved inference systems*.
- Blurton Jones, N., & Konner, M. (1976). !Kung knowledge of animal behavior (or The proper study of mankind is animals). In R. Lee & I. Devore (Eds.), *Kalahari hunter-gatherers: Studies of the !Kung San and their neighbors* (pp. 325–348). Cambridge, MA: Harvard.
- Boole, G. (1848). The calculus of logic. *Cambridge and Dublin Mathematical Journal*, *III*, 183–198.
- Boyer, P. (2001). *Religion explained: The evolutionary roots of religious thought*. New York: Basic Books.
- Boyer, P., & Barrett, H. C. (in press). Domain-specificity and intuitive ontology. In D. M. Buss (Ed.), *Evolutionary psychology handbook*. New York: Wiley.
- Brase, G., Cosmides, L., & Tooby, J. (1998). Individuation, counting, and statistical inference: The role of frequency and whole object representations in judgment under uncertainty. *Journal of Experimental Psychology: General*, *127*, 1–19.
- Braun, J. (2003). Natural scenes upset the visual appercept. *Trends in Cognitive Sciences*, *7*(1), 7–9. (January).
- Buss, D. M. (1994). *The evolution of desire*. New York: Basic Books.
- Buss, D. M. (1999). *Evolutionary psychology: The new science of the mind*. Boston: Allyn & Bacon.
- Buss, D. M. (2000). *The dangerous passion*. London: Bloomsbury Publishing.
- Campos, J., Bertenthal, B., & Kermoian, R. (1992). Early experience and emotional development: The emergence of wariness of heights. *Psychological Science*, *3*, 61–64.
- Cannon, W. (1929). *Bodily changes in pain, hunger, fear and rage*. Researches into the function of emotional excitement. New York: Harper & Row.
- Caramazza, A. (2000). The organization of conceptual knowledge in the brain. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed., pp. 1037–1046). Cambridge, MA: MIT Press.
- Caramazza, A., & Shelton, J. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience*, *10*, 1–34.
- Carruthers, P. (in press). The case for massively modular models of mind. In R. Stainton (Ed.), *Contemporary debates in cognitive science*. Oxford, England: Blackwell.
- Cheney, D., Seyfarth, R., Smuts, R., & Wrangham, R. (Eds.). (1987). *Primate societies*. Chicago: University of Chicago Press.
- Chomsky, N. (1959). A review of B. F. Skinner's verbal behavior. *Language*, *35*(1), 26–58.
- Chomsky, N. (1965). *Aspects of a theory of syntax*. Cambridge, MA: MIT Press.
- Cosmides, L. (1985). *Deduction or Darwinian Algorithms? An explanation of the "elusive" content effect on the Wason selection task*. Doctoral dissertation, Harvard University. (UMI No. #86-02206).

64 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

- Cosmides, L., & Tooby, J. (1981). Cytoplasmic inheritance and intragenomic conflict. *Journal of Theoretical Biology*, *89*, 83–129.
- Cosmides, L., & Tooby, J. (1987). From evolution to behavior: Evolutionary psychology as the missing link. In J. Dupre (Ed.), *The latest on the best: Essays on evolution and optimality*. Cambridge, MA: MIT Press.
- Cosmides, L., & Tooby, J. (1994a). Beyond intuition and instinct blindness: The case for an evolutionarily rigorous cognitive science. *Cognition*, *50*, 41–77.
- Cosmides, L., & Tooby, J. (1994b). Origins of domain-specificity: The evolution of functional organization. In L. Hirschfeld & S. Gelman (Eds.), *Mapping the mind: Domain-specificity in cognition and culture*. New York: Cambridge University Press.
- Cosmides, L., & Tooby, J. (1996). Are humans good intuitive statisticians after all?: Rethinking some conclusions of the literature on judgment under uncertainty. *Cognition*, *58*, 1–73.
- Cosmides, L., & Tooby, J. (2000a). Consider the source: The evolution of adaptations for decoupling and metarepresentation. In D. Sperber (Ed.), *Metarepresentations: A multidisciplinary perspective* (pp. 53–115). New York: Oxford University Press.
- Cosmides, L., & Tooby, J. (2000b). Evolutionary psychology and the emotions. In M. Lewis & J. M. Haviland-Jones (Eds.), *Handbook of emotions* (2nd ed., pp. 91–115). New York: Guilford Press.
- Cosmides, L., & Tooby, J. (2001). Unraveling the enigma of human intelligence: Evolutionary psychology and the multimodular mind. In R. J. Sternberg & J. C. Kaufman (Eds.), *The evolution of intelligence* (pp. 145–198). Hillsdale, NJ: Erlbaum.
- Cosmides, L., & Tooby, J. (in press). Neurocognitive adaptations designed for social exchange. In D. M. Buss (Ed.), *Evolutionary psychology handbook*. New York: Wiley.
- Daly, M., & Wilson, M. (1988). *Homicide*. New York: Aldine.
- Daly, M., Wilson, M., & Weghorst, S. J. (1982). Male sexual jealousy. *Ethology and Sociobiology*, *3*, 11–27.
- Darwin, C. (1859). *On the origin of species*. London: John Murray.
- Dawkins, R. (1986). *The blind watchmaker*. New York: Norton.
- Defeyter, M. A., & German, T. (2003). Acquiring an understanding of design: Evidence from children's insight problem solving. *Cognition*, *89*, 133–155.
- DeSteno, D., Bartlett, M., Braverman, J., & Salovey, P. (2002). Sex differences in jealousy: Evolutionary mechanism or artifact of measurement. *Journal of Personality and Social Psychology*, *83*(5), 1103–1116.
- Dennett, D. (1987). *The intentional stance*. Cambridge, MA: MIT Press/Bradford.
- DeVore, I. (1965) *Primate behavior: Field studies of monkeys and apes*. New York: Holt, Rinehart & Winston.
- Eaton, S. B., Shostak, M., & Konner, M. (1988). *The Paleolithic prescription: A program of diet, exercise and a design for living*. New York: Harper & Row.
- Eibl-Eibesfeldt, I. (1970). *Ethology: The biology of behavior*. New York: Holt, Reinhart & Winston.
- Ekman, P. (Ed.). (1982). *Emotion in the human face*. (2nd ed.). Cambridge, England: Cambridge University Press.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Fodor, J. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.
- Fodor, J. (2000). *The mind doesn't work that way*. Cambridge, MA: MIT Press.
- Frege, G. (1879). *Begriffsschrift ('concept notation'), eine der arithmetischen nachgebildete Formelsprache des reinen denkens*. Halle A. S.
- Friesen, C., & Kingstone, A. (2003). Abrupt onsets and gaze direction cues trigger independent reflexive attentional effects. *Cognition*, *87*, B1–B10.
- Gallistel, C. R. (2000). The replacement of general-purpose learning models with adaptively specialized learning modules. In M. S. Gazzaniga (Eds.), *The new cognitive neurosciences* (pp. 1179–1191). Cambridge, MA: MIT Press.
- Gallistel, C. R., & Gibbon, J. (2000). Time, rate and conditioning. *Psychological Review*, *107*, 289–344.
- Gallistel, C. R., Brown, A., Carey, S., Gelman, R., & Keil, F. (1991). Lessons from animal learning for the study of cognitive development. In S. Carey & R. Gelman (Eds.), *The epigenesis of mind*. Hillsdale, NJ: Erlbaum.
- Geertz, C. (1973). *The interpretation of cultures*. New York: Basic Books.
- German, T. P. (1999). Children's causal reasoning: Counterfactual thinking occurs for "negative" outcomes only. *Developmental Science*, *2*, 442–447.
- German, T. P., & Barrett, H. C. (in press). Functional fixedness in a technologically sparse culture. *Psychological Science*.

- Gigerenzer, G. (1991). How to make cognitive illusions disappear: Beyond heuristics and biases. *European Review of Social Psychology*, 2, 83–115.
- Gigerenzer, G., & Murray, D. (1987). *Cognition as intuitive statistics*. Hillsdale, NJ: Erlbaum.
- Gigerenzer, G., & Selten, R. (Eds.). (2002). *Bounded rationality: The adaptive toolbox*. Cambridge, MA: MIT Press.
- Gigerenzer, G., Todd, P., & the ABC Research Group. (1999). *Simple heuristics that make us smart*. New York: Oxford.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 205, 581–598.
- Gray, H. (1918). *Gray's anatomy* (20th ed.). W. Lewis (Ed.), Philadelphia: Lea & Febiger.
- Haidt, J. (2001). The emotional dog and its rational tail: A social intuitionist approach to moral judgment. *Psychological Review*, 108(4), 814–834.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, 7, 1–52.
- Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, 78, 81–91.
- Herrnstein, R. J. (1977). The evolution of behaviorism. *American Psychologist*, 32, 593–603.
- Hirschfeld, L. A., & Gelman, S. A. (Eds.). (1994). *Mapping the mind: Domain specificity in cognition and culture*. Cambridge, England: Cambridge University Press.
- Kahneman, D., Slovic, P., & Tversky, A. (Eds.). (1982). *Judgment under uncertainty: Heuristics and biases*. Cambridge, England: Cambridge University Press.
- Kaplan, H., & Hill, K. (1985). Food sharing among Ache Foragers: Tests of explanatory hypotheses. *Current Anthropology*, 26(2), 223–246.
- Keil, F. (1989). *Concepts, kinds, and cognitive development*. Cambridge, MA: MIT Press.
- Keil, F. C. (1994). The birth and nurturance of concepts by domains: The origins of concepts of living things. In L. A. Hirschfeld & S. A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture*. Cambridge, England: Cambridge University Press.
- Klein, S. (2005). The cognitive neuroscience of knowing one's self. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences, III* (pp. 1077–1089). Cambridge, MA: MIT Press.
- Klein, S., Cosmides, L., Tooby, J., & Chance, S. (2002). Decisions and the evolution of memory: Multiple systems, multiple functions. *Psychological Review*, 109, 306–329.
- Klein, S., German, T., Cosmides, L., & Gabriel, R. (2004). A theory of autobiographical memory: Necessary components and disorders resulting from their loss. *Social Cognition*, 22(5), 460–490.
- Kurzban, R., Tooby, J., & Cosmides, L. (2001). Can race be erased? Coalitional computation and social categorization. *Proceedings of the National Academy of Sciences*, 98(26), 15387–15392.
- LeDoux, J. (1995). In search of an emotional system in the brain: Leaping from fear to emotion to consciousness. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1049–1061). Cambridge, MA: MIT Press.
- Lee, R., & DeVore, I. (Eds.). (1968). *Man the hunter*. Chicago: Aldine.
- Lee, R., & DeVore, I. (Eds.). (1976). *Kalahari hunter-gatherers: Studies of the !Kung San and their neighbors*. Cambridge, MA: Harvard.
- Lenneberg, E. (1967). *Biological foundations of language*. New York: John Wiley & Sons.
- Leslie, A. (1987). Pretense and representation: The origins of "theory of mind." *Psychological Review*, 94, 412–426.
- Leslie, A. M. (1994). ToMM, ToBy, and agency: Core architecture and domain specificity. In L. A. Hirschfeld & S. A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture* (pp. 119–148). Cambridge, England: Cambridge University Press.
- Leslie, A. M., & Thaiss, L. (1992). Domain specificity in conceptual development: Neuropsychological evidence from autism. *Cognition*, 43, 225–251.
- Leslie, A. M., German, T. P., & Polizzi, P. (2005). Belief-desire reasoning as a process of selection. *Cognitive Psychology*, 50, 45–85.
- Li, F. F., Van Rullen, R., Koch, C., & Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. *Proceedings of the National Academy of Science, USA*, 99, 9596–9601.
- Lieberman, D., Tooby, J., & Cosmides, L. (2003). Does morality have a biological basis? An empirical test of the factors governing moral sentiments relating to incest. *Proceedings of the Royal Society London (Biological Sciences)*, 270(1517), 819–826.
- Lieberman, D., Tooby, J., & Cosmides, L. (in press-a). The evolution of human incest avoidance mechanisms: An evolutionary psychological approach. In A. Wolf & J. P. Takala (Eds.),

66 FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

- Evolution and the moral emotions: Appreciating Edward Westermarck*. Stanford, CA: Stanford University Press.
- Lieberman, D., Tooby, J., & Cosmides, L. (in press-b). The architecture of the human kin detection system.
- Lieberman, D., Tooby, J., & Cosmides, L. (in press-c). Kin detection and altruism in Dominica.
- López, A., Atran, S., Coley, J., Medin, D., & Smith, E. (1997). The tree of life: Universals of folkbiological taxonomies and inductions. *Cognitive Psychology*, 32, 251–295.
- Lutz, C. A. (1988). *Unnatural emotions: Everyday sentiments on a Micronesian Atoll and their challenge to western theory*. Chicago: University of Chicago Press.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge, England: Cambridge University Press.
- Mandler, J., & McDonough, L. (1998). Studies in inductive inference in infancy. *Cognitive Psychology*, 37(1), 60–96.
- Markman, E. (1989). *Categorization and naming in children*. Cambridge, MA: MIT Press.
- Marks, I. (1987). *Fears, phobias, and rituals*. New York: Oxford.
- Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. *Journal of Experimental Psychology: General*, 122, 23–38.
- Mineka, S., Davidson, M., Cook, M., & Keir, R. (1984). Observational conditioning of snake fear in rhesus monkeys. *Journal of Abnormal Psychology*, 93, 355–372.
- New, J., Cosmides, L., & Tooby, J. (under review). Category-specific attention to animals and people: Ancestral priorities or ontogenetic expertise?
- Pinker, S. (1994). *The language instinct*. New York: Morrow.
- Pinker, S., & Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences* 13(4): 707–784.
- Pinker, S. (2002). *The blank slate*. New York: Viking Press.
- Pitman, R., & Orr, S. (1995). Psychophysiology of emotional and memory networks in posttraumatic stress disorder. In J. McGaugh, N. Weinberger, & G. Lynch (Eds.), *Brain and memory: Modulation and mediation of neuroplasticity* (pp. 75–83). New York: Oxford.
- Posner, M. (1978). *Chronometric explorations of mind*. New York: Oxford.
- Rips, L. (1994). *The psychology of proof*. Cambridge, MA: MIT Press.
- Ro, T., Russell, C., & Lavie, N. (2001). Changing faces: A detection advantage in the flicker paradigm. *Psychological Science*, 12, 94–99.
- Rode, C., Cosmides, L., Hell, W., & Tooby, J. (1999). When and why do people avoid unknown probabilities in decisions under uncertainty? Testing some predictions from optimal foraging theory. *Cognition*, 72, 269–304.
- Sahlins, M. (1976). *The use and abuse of biology: An anthropological critique of sociobiology*. Ann Arbor: University of Michigan Press.
- Schacter, D., & Tulving, E. (Eds.). (1994). *Memory systems 1994*. Cambridge, MA: MIT Press.
- Shepard, R. N. (1984). Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychological Review*, 91, 417–447.
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27, 379–423 & 623–656.
- Shepard, R. N. (1987). Evolution of a mesh between principles of the mind and regularities of the world. In J. Dupre (Ed.), *The latest on the best: Essays on evolution and optimality* (pp. 251–275). Cambridge, MA: MIT Press.
- Sherry, D., & Schacter, D. (1987). The evolution of multiple memory systems. *Psychological Review*, 94, 439–454.
- Shostak, M. (1981). *Nisa: The life and words of a !Kung woman*. Cambridge, MA: Harvard.
- Skinner, B. F. (1957). *Verbal behavior*. New York: Appleton-Century-Crofts.
- Spelke, E. S. (1990). Principles of object perception. *Cognitive Science*, 14, 29–56.
- Sperber, D. (1994). The modularity of thought and the epidemiology of representations. In L. A. Hirschfeld & S. A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture*. Cambridge, England: Cambridge University Press.
- Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Oxford: Blackwell.
- Sperber, D., & Wilson, D. (1995). *Relevance: Communication and cognition* (2nd ed.). Oxford, England: Blackwell.
- Springer, K. (1992). Children's awareness of the implications of biological kinship. *Child Development*, 63, 950–959.

- Steen, F., & Owens, S. (2001). Evolution's pedagogy: An adaptationist model of pretense and entertainment. *Journal of Cognition and Culture*, 1(4), 289–321.
- Suarez, S. D., & Gallup, G. G. (1979). Tonic immobility as a response to rage in humans: A theoretical note. *Psychological Record*, 29, 315–320.
- Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.
- Symons, D. (1987). If we're all Darwinians, what's the fuss about. In C. B. Crawford, M. F. Smith, & D. L. Krebs (Eds.), *Sociobiology and psychology* (pp. 121–146). Hillsdale, NJ: Erlbaum.
- Symons, D. (1989). A critique of Darwinian anthropology. *Ethology and Sociobiology*, 10, 131–144.
- Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 137–159). New York: Oxford University Press.
- Tomaka, J., Blascovich, J., Kibler, J., & Ernst, J. (1997). Cognitive and physiological antecedents of threat and challenge appraisal. *Journal of Personality and Social Psychology*, 73, 63–72.
- Tooby J. (1982). Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology*, 97, 557–576.
- Tooby, J. (1985). The emergence of evolutionary psychology. In D. Pines (Ed.), *Emerging syntheses in science* (pp. 124–137). Santa Fe, NM: The Santa Fe Institute.
- Tooby, J., & Cosmides, L. (1990a). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375–424.
- Tooby, J., & Cosmides, L. (1990b). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*, 58, 17–67.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.
- Tooby, J., & Cosmides, L. (1996). Friendship and the banker's paradox: Other pathways to the evolution of adaptations for altruism. *Proceedings of the British Academy*, 88, 119–143.
- Tooby, J., & Cosmides, L. (2001). Does beauty build adapted minds? Toward an evolutionary theory of aesthetics, fiction and the arts. *SubStance*, 94/95(1), 6–27.
- Tooby, J., & Cosmides, L. (in press). Ecological rationality in a multimodular mind. In *Evolutionary psychology: Foundational papers*. Cambridge, MA: MIT Press.
- Tooby, J., Cosmides, L., & Barrett, H. C. (2003). The second law of thermodynamics is the first law of psychology: Evolutionary developmental psychology and the theory of tandem, coordinated inheritances. *Psychological Bulletin*, 129(6), 858–865.
- Tooby, J., Cosmides, L., & Barrett, H. C. (2005). Resolving the debate on innate ideas: Learnability constraints and the evolved interpenetration of motivational and conceptual functions. In P. Carruthers, S. Laurence, & S. Stich (Eds.), *The innate mind: Structure and content*. New York: Oxford University Press.
- Tooby J., & DeVore, I. (1987). The reconstruction of hominid behavioral evolution through strategic modeling. In W. Kinzey (Ed.), *Primate models of hominid behavior* (pp. 183–237). New York: SUNY Press.
- Triesman, A. (2005). Psychological issues in selective attention. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences, III* (pp. 529–544). Cambridge, MA: MIT Press.
- Vining, D. R. (1986). Social versus reproductive success: The central theoretical problem of human sociobiology. *Behavioral and Brain Sciences*, 9, 167–216.
- Walker, R., Hill, K., Kaplan, H., & McMillan, G. (2002). Age dependency of hunting ability among the Ache of eastern Paraguay. *Journal of Human Evolution*, 42, 639–657.
- Wang, X. T. (2002). Risk as reproductive variance. *Evolution and Human Behavior*, 23, 35–57.
- Weiner, N. (1948). *Cybernetics or control and communication in the animal and the machine*. Cambridge, MA: MIT Press.
- Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton, NJ: Princeton University Press.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Belknap Press.
- Wynn, K. (1998). Psychological foundations of number: Numerical competence in human infants. *Trends in Cognitive Sciences*, 2, 296–303.
- Yerkes, R. M., & Yerkes, A. W. (1936). Nature and conditions of avoidance (fear) response in chimpanzee. *Journal of Comparative Psychology*, 21, 53–66.