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CHAPTER 1

The Theoretical Foundations of Evolutionary Psychology

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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, more than a century and a half after *The Origin of Species* was published, many of the psychological, social, and behavioral sciences continue to be grounded on assumptions that evolutionarily informed researchers know to be false; the rest have only in the past few decades set to work on the radical reformulations of their disciplines necessary to make them consistent with findings in the evolutionary sciences, information theory, computer science, physics, the neurosciences, molecular and cellular biology, genetics, behavioral ecology, hunter-gatherer studies, biological anthropology, primatology, and so on (Pinker, 1997, 2002; Tooby & Cosmides, 1992). Evolutionary psychology is the long-forestalled 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 and information theory on a full and equal basis, but that systematically works out all the revisions in existing belief and research practice that such a synthesis requires (Tooby & Cosmides, 1992).

The first long-term scientific goal toward which evolutionary psychologists are working is the mapping of our universal human nature. By mapping human nature, we mean the progressive construction and refinement of a set of empirically validated, high-resolution models of the evolved adaptations (genetic, developmental, anatomical, neural, information processing, etc.) that collectively constitute universal human

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We dedicate this chapter to the late Irven DeVore, professor emeritus, Department of Anthropology, Harvard University, dear mentor and friend.

nature. Because the focus in the behavioral and social sciences is on explaining mind, behavior, and social interactions, initially the emphasis has been placed on adaptations that are behavior-regulating, and which researchers may call a variety of names, such as evolved psychological (mental, cognitive) programs, neurocomputational programs, behavior-regulatory programs, adaptive specializations, "modules," information-processing mechanisms, and so on. However, because the architecture of the human species evolved as a set of functional interactions at all physical and temporal scales, it follows that genetic, cellular, developmental, anatomical, physiological, endocrinological, and life-historical processes are also considered as fully part of human nature, and, therefore, part of the systems of evolved interrelationships that evolutionary psychology needs to deal with. Because the evolved function of a regulatory mechanism is computational—to regulate behavior, development, and the body adaptively (over the short term and the long term) in response to informational inputs—such a model consists of a description of the functional circuit logic or information-processing architecture of the mechanism, in a way that eventually should incorporate its physical implementation (Cosmides & Tooby, 1987; Tooby & Cosmides, 1992). More completely, these models must sooner or later include descriptions of the regulatory logic of the developmental programs that, in interaction with environments, lead to the unfolding succession of designs that constitute the organism's changing phenotype across its life history (Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2003—see review in Del Giudice, Gangestad, & Kaplan, Chapter 2, this volume). As scientific knowledge grows in the longer term, these models will eventually come to incorporate descriptions of the neural and genetic implementations of these mechanisms.

The second long-term scientific goal toward which evolutionary psychologists and their allies are working is a comprehensive reconstruction of the social sciences (and many of the humanities) that an accurate, natural science-based model of human nature will both make possible and require. At present, the social sciences are a stew of mutually contradictory claims, with no theoretical unity or clear progressive direction. Major components of the social sciences are sufficiently incoherent to qualify—in Paul Dirac's phrase—as not even wrong. Genuine, detailed specifications of the circuit logics of the neuroregulatory programs that compose human nature are expected to become the theoretical centerpieces of a newly reconstituted set of social sciences. This is because each model of an evolved component of human nature (e.g., the human-language competence) makes predictions about (and explains) those sets of developmental, psychological, behavioral, and social phenomena that its circuits generate or regulate (e.g., the existence of and the patterns found in human language; Pinker, 1994; the existence of and patterns found in incest aversion and kin-directed altruism; Lieberman, Tooby, & Cosmides, 2007). 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 and developmental architecture (for an analysis of the SSSM, see Pinker, 2002; 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. These processes are thought to be analogous to the operation of a video camera— the content of the recording originates in the world, whereas the mechanism of recording adds no content of its own to the mix. As Thomas Aquinas put this seemingly self-evident view, "There is nothing in the mind that was not first in the senses." 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 from the processes in the social world (what we call the Durkheimian causal arrow). More importantly, social scientists have considered it to be unshakably well-established that content does not flow outward from evolved organization in individual minds to organize culture or the social world (Geertz, 1973; Sahlins, 1976). Now that this hypothesis is being empirically tested, however, it is regularly falsified (e.g., Buss, 1989; Lieberman, Tooby, & Cosmides, 2003, 2007; Peterson, Sznycer, Sell, Cosmides, & Tooby, 2013; Sell, Tooby, & Cosmides, 2009).

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 programs—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 dismantled. 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 programs that underlie sexual behavior, mate choice, attractiveness, intrasexual competition, intersexual conflict, and mateship maintenance, reviewed in many chapters in this volume (for notable earlier work, see Buss, 1994, 2000; Daly & Wilson, 1988; Symons, 1979). The patterned incidence of violence is partly explained by the evolved programs governing our species' psychology of aggression, parenting, and sexuality (Campbell, Daly & Wilson, 1988; Simpson & Campbell, Chapter 3, this volume); the foundations of trade can be located in evolved cognitive specializations for social exchange (Cosmides & Tooby, 1992; Tooby & Cosmides, Chapter 25, this *Handbook*, Volume 2); both incest avoidance and love for family members are rooted in evolved mechanisms for kin recognition (Lieberman, Tooby, & Cosmides, 2003, 2007). Similarly, the evolutionarily specialized mechanisms underlying human alliance psychology help to explain phenomena such as racism, coalitions, morality, social sanctions, and group dynamics (e.g., Delton, Cosmides, Guemo, Robertson, & Tooby, 2012; Kurzban, Tooby, & Cosmides, 2001;

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Pietraszewski, Cosmides, & Tooby, 2014; Tooby & Cosmides, 2010; Tooby, Cosmides & Price, 2006).

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 and developmental mechanisms; in the broad sense, it includes the project of reformulating and expanding the social sciences (and medical sciences, as somatic adaptations become incorporated into the synthesis) in the light of the progressive mapping of our species' evolved architecture. This *Handbook* contains reviews of the rich harvest of projects and discoveries that have already emerged out of this young paradigm. Even though the field is in its infancy, evolutionary psychologists have already identified a very large set of examples that touch almost every aspect of human life. In the light of such rapidly accumulating findings, many hallowed beliefs in anthropology, sociology, political science, social psychology, cognitive psychology, and (to a lesser extent) economics will have to be completely revised. However, we are only in the earliest phases of what is expected to be an ever-widening transformation of the human and nonhuman behavioral sciences, an enterprise so large that may take remainder of this century, and which is sure to include surprises as more and more strands of conceptual unification proceed.

It is important to emphasize that evolutionary psychology in the broad sense is not just about the design of the individual, nor is it just a revision of the present academic field of psychology. Instead, this reformulation encompasses and integrates the entire sweep of the human sciences. This is because our minds' programs evolved in ancestral social, demographic, and informational environments that gradually produced and refashioned various epidemeological and population- and group-level phenomena such as cultural traditions, languages, social groups, and demographic structures. These, in turn, acted as selection pressures that collectively engineered our constellation of evolved programs to operate functionally with respect to these supra-individual phenomena. That is, these programs evolved to functionally produce some of these phenomena (e.g., alliances; language); they also evolved to act functionally within environments that included these phenomena (e.g., fitness-promoting behavior guided by an alliance detector; communication made possible by language competence). Hence, the extended phenotypes (in Dawkins' 1982 sense) that these programs produce are not only individual traits (in the folk sense), but are designed to interact with each other to produce or exploit complex collective phenotypes (e.g., languages, cultural elements, traditions, exchange networks, social groups, agent-like coalitions, mobs, wars, small-scale hierarchies, some small-scale institutions). Moreover, on their way to producing the functional socially extended phenotypes they were designed ancestrally to produce, our evolved programs and their outputs also produce many modern and complex group and population-level phenomena as byproducts (e.g., global networks of exchange, fashions, supply and demand curves, aristocracies, social classes, complex hierarchies, complex institutions, religions, different languages, etc.).

All these are objects of study for social scientists, and because these are patterned by our evolved programs, evolutionary psychology provides the integrating framework for the social sciences. It is the specifics of our adaptations' decision-making architectures that strongly shape how individuals assemble themselves into larger social structures in the modern world, and that generate the cultural outputs that our minds dynamically build and reshape over time.

Because the Standard Social Science Model's claim for the source of essentially all human mental content is free-form culture downloaded into individual minds, it is vital to realize how different the evolutionary psychological explanation is of the origin of mental content, and the nature of culture. The evolutionary psychological claim is that—for our evolved computational problem-solvers to actually solve the adaptive problems faced by our ancestors (food acquisition, parenting, mate acquisition)—they had to be richly structured by selection in a content-specific way. That is, they are endowed by what philosophers would once have called innate ideas or *a priori* concepts (e.g., food, child, my child, male-female, ingroup-outgroup, mother, kin, cheater, free-rider, snake, spider, animacy, number, noun, object, aggressive formidability, friend, enemy, predator, leader, and perhaps thousands of others). These may be built in to evolved modes of interpretation, conceptual-motivational systems, or evolved intuitive ontologies, in what might be thought of as a Darwinian-Kantian-computational synthesis of how our evolved programs organize experience (Boyer & Barrett, Chapter 5, this volume; Cosmides & Tooby, 1994b; Tooby, Cosmides, & Barrett, 2003). This different approach explains and often predicts the (previously unappreciated) set of human universals (see, e.g., Brown, 1991) as reliably developing adaptations, their byproducts, and their interactive products. It predicts and explains principled cross-cultural variation; for example, adaptations have been designed by selection to take relevant local conditions as input to produce output that is calibrated to local circumstances (e.g., Gaulin & Schlegel, 1980; Schmitt, 2005; Sznycer et al., 2012). This approach can even explain highly particularistic cultural phenomena as unique patterns of activation of species-typical evolved mechanisms (e.g., Boyer, 2001).

Hence, our content-inflected mental adaptations reliably develop, as well as generate, some of the particular content of human culture, and form the raw materials out of which the rest is developmentally and socially elaborated in an immense and endlessly shifting play of combinatorics. This content is then present to be adopted or modified by evolved programs situated in other members of the population, or shaped by social interactions. This gives rise to epidemiological and historical population-level processes, located in particular ecological, economic, demographic, and intergroup social contexts or environments, which themselves impact their cross-individual and cross-generational dynamics. From this perspective, culture is the manufactured product of our evolved neurocomputational programs situated in individuals living in groups. To flag how different this theory of culture is from classical general learning transmission approaches, we gave our book *The Adapted Mind* (Barkow, Cosmides, & Tooby, 1992) the subtitle *Evolutionary Psychology and the Generation of Culture*. The recognition that the mind contains a large array of evolved programs leads to another departure from standard thought: Culture is not a unitary stuff, nor is culture in any way independent of evolved psychological processes. Instead, "culture" is located inside our evolved programs, and different kinds of culture are located inside different programs (and their combinations). Different types of information live inside distinct computational habitats as their native settings—that is, habitats built out of different evolved mental programs. The computational specifics of these different habitats give meaning to these data structures; they impose meaningful structure on content; they determine the rules by which potential changes to content can happen; they determine what inputs from which other programs provide the raw material that a given program operates on; they determine which contents in which internal habitats can become outputs. "Culture" and "learning" are not theoretical rivals to evolutionary psychology; they are instead phenomena to be explained by reference to and in terms of the design of the evolved neural programs that produce them (plus a description of the local inputs provided to these mechanisms).

So there is fear-of-snakes culture (living "inside" the snake-phobia system, that can be transmitted as intensities of fear-response passed to others), grammar culture (living "inside" the language competence), food-preference culture, group- identity culture, disgust culture, contempt culture, sharing culture, aggression culture, and so on. The set of cultural competences arose as a response to the opportunity afforded by the fact that other humans with their own calibrated programs are rich potential sources of information. Any time a program can cost effectively improve its performance by censusing programs situated in other brains, then selection will favor the evolution of inference systems to do so. All these distinct effects have been confusingly aggregated under the single name "culture," misleading people into thinking "culture" is a homogeneous stuff moving according to unitary principles free of the influence of our evolved psychology. Instead, brains are linked by many causally distinct pathways, built to perform distinct functions. Each brain is bristling with many independent "tubes" that propagate many distinct kinds of stuff to and from a diversity of brain mechanisms in others. This is why evolutionary psychology is not restricted to studying the static determinants of individual behavior taken in isolation from culture or social and historical setting. Instead, this is why evolutionary psychology in the broad sense integrates with and provides a nonoptional foundational framework for the social sciences (e.g., Boyer, 2001; Pinker, 2002; Sperber, 1996; Tooby, 2014; Tooby & Cosmides, 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 SSSM. 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 SSSM 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 or alleviated if the scientific community had not chosen to postpone or forgo a more accurate social and behavioral science.

THE INTELLECTUAL ORIGINS OF EVOLUTIONARY PSYCHOLOGY

Despite the marginalization of Darwinism within the behavioral and social sciences during the 20th 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 often 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 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, information, computational architecture, adaptation, organization, design, entropy, selection, replication, selection pressure, byproduct, 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 often inconsistent) disciplinary building blocks could be integrated into a single unified framework (for discussion, see Tooby & Cosmides, 1992). The building blocks from which evolutionary psychology was assembled include (a) the modern adaptationist revolution in theoretical evolutionary biology (Williams, 1966); (b) the rise of information theory and the computational sciences (Shannon, 1948; Weiner, 1948); (c) the emergence of serious attempts to reconstruct the ancestral conditions and ways of life of humans and prehumans and the selection pressures they imposed on our lineage (e.g., Cheney, Seyfarth, Smuts, & Wrangham, 1987; Isaac, 1989; Kaplan & Hill, 1985; Lee & DeVore, 1968, 1976); and (d) an adaptationist/computationalist resolution of the debate between environmentalists and nativists (e.g., Cosmides & Tooby, 1987; Pinker, 1997; 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 & Williams, 1957; Williams, 1966); 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. Oneface 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) has been called sociobiology, behavioral ecology, evolutionary ecology, or simply evolutionary biology. In addition to evolutionary genetics, a key foundation of the improvements in our understanding of replicator dynamics was the application of game theory (von Neumann & Morgenstern, 1944) to genetic and organismal interactions—a program that rapidly developed into evolutionary game theory (Maynard Smith, 1982). (We think this process will continue as evolutionary game theory morphs into what might be called *adaptationist game theory* (e.g., Delton, Krasnow, Cosmides, & Tooby, 2011; Krasnow, Delton, Cosmides & Tooby, 2015).[1] The other face of this revolution in biology is modern adaptationism (Williams, 1966)—a set of deductions that are still often misunderstood, even in biology (Alcock, 2001; Thornhill, 1997; Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2003). 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 (neurocomputational) 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. Whatever the sociology of

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[1] We think that, although there are many valuable results that have emerged from evolutionary game theory, other widely cited and influential results are not truly applicable to real species such as humans. The goal of adaptationist game theory is to replace a series of limitations in standard evolutionary game theory (such as highly biologically implausible conditions, radically impoverished strategy-types, etc., that were adopted to make the mathematics tractable or other reasons of preference or convenience) with modeling decisions chosen to make the results more biologically realistic. This is made possible by moving from primarily analytic approaches to agent-based population simulations; by endowing the simulated world with, for example, more plausible information ecologies; giving agents locations; by endowing agents with richer and more realistic strategies—specified psychologies—that include background capacities humans actually have, such as individual recognition; by allowing relevant decision-making variables to evolve—that is, not restricting strategy sets to a small number of discontinuous types such as defector and cooperator but, instead, for example, allowing the probability of cooperation allowed to evolve from 0 to 1. For example, it was widely thought that humans were irrationally generous, by cooperating in one-shot games, purportedly showing individual selection could not explain human game performance. By simply recognizing that interactions don't come pre-typologized for the agent as either one-shot or repeated, and that the organism must make this discrimination under uncertainty, simulations demonstrate that reciprocity under biologically plausible conditions spontaneously evolves to manifest the observed (and no-longer mysterious) generosity-bias (Delton, Krasnow, Cosmides, & Tooby, 2011; see also Krasnow, Delton, Cosmides, & Tooby, 2013).

academic tribes, scientifically psychology (along with the other social and behavioral sciences) is a subbranch of evolutionary biology and can no longer be defensibly divorced from it.

George Williams's 1966 volume, *Adaptation and Natural Selection: A critique of Some Current Evolutionary Thought*, was central to both the adaptationist and selectionist 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, byproducts of adaptations, or noise; and usefully distinguished the present usefulness of traits (if any) from their evolved functions (if any).[2] 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 nonvitalistically in physical processes (Weiner, 1948). With the rise of information theory (Shannon, 1948), the development of the first computers (von Neumann, 1945), and advances in cybernetics and neuroscience (Weiner, 1948), it became widely understood that mental events consisted of transformations of structured informational relationships embodied as aspects of organized physical systems in the brain. This spreading appreciation constituted the cognitive revolution. The world of the mental was no longer a mysterious, indefinable realm, but locatable in the physical world in terms of precisely describable, highly organized causal relations. Why do these informational relationships emerge in physical systems in organisms? The adaptive problem of regulating behavior in a fitness-promoting way could be seen as the selection pressure that led to the emergence of systems for natural computation—that is, as naturally engineered behavior control systems for organisms—adaptationist cybernetics.

Evolutionary psychology can, therefore, be seen as the inevitable intersection of the computationalism of the cognitive revolution with the adaptationism of Williams' 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

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[2] The arguments that not every trait is an adaptation, not all beneficial effects of a trait are its functions, that phenotypes are full of byproducts, 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' development of strict standards of evidence can be used to distinguish adaptations from nonadaptations, rendering the issue a matter of empirical research rather than post hoc rhetoric.

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 (if temporarily) 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 adaptationists/selectionist 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 (often under other names such as behavioral or evolutionary ecology.[3]

At Harvard, for example, under the sponsorship of Irven DeVore and E.O. Wilson, one of the most influential and dynamic of these communities gathered and matured. This research community fluoresced in Irven DeVore's living room, where Harvard's Simian Seminar was held from 1971 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 extended periods. Among many others, these included George Williams, Bill Hamilton, John Maynard Smith, Ernst Mayr, Edward O. Wilson, Richard Alexander, Richard Dawkins, Tim Clutton-Brock, Paul Harvey, Lionel Tiger, Robin Fox, Diane Fosse, Jane Goodall, Robert Hinde, Richard Leakey, Joseph Shepher, Richard Lee, Stephen Jay Gould, Martin Daly, and Margo Wilson, and the editor of this *Handbook*, David Buss. Among the students or proteges DeVore mentored in this environment were Bob Bailey, Peter Ellison, John Fleagle, Steve Gaulin, Henry Harpending, Paul Harvey, Sarah Blaffer Hrdy, Melvin Konner, Jeff Kurland, Jim Moore, Nadine Peacock, Peter Rodman, Robert Sapolsky, John Seger, Marjorie Shostak, Barbara Smuts, Karen Strier, Bob Trivers, Carol Worthman, Richard Wrangham, John Yellen, and ourselves (John Tooby and Leda Cosmides). Although 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, proteges, and colleagues. Deeply interested in human origins, DeVore pioneered three major research movements. He initiated and then championed the systematic study of primate social behavior under natural conditions (DeVore, 1962, 1965). Thisled him to want to incorporate human hunter-gatherers into the same careful scientific framework. With Lee and many other colleagues, in 1963 he inaugurated the systematic, empirical, quantitative investigation of living

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[3] Intellectuals 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.

hunter-gatherers with the Kalahari Research Project and the famous Man the Hunter meetings (Lee & DeVore, 1968, 1976). Then, together with Chagnon, Irons, and many anthropologists, he worked on applying the new selectionist biology to anthropological questions.

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. (Imagine the state of physics if one physicist studied the electron, another the mu meson, etc.) 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, health, and lives of the !Kung San people in Botswana's Kalahari desert, before hunting and gathering as a way of life disappeared 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. Medical researchers 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). Although 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—as evolutionary psychologists argue—are collections of mechanisms designed to solve the adaptive problems posed by the ancestral world, then hunter-gatherer studies and primatology become indispensable sources of knowledge about the adaptations that constitute modern human nature, and how our evolved psychology and soma organizes modern social, cultural, and economic processes. 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 SSSM arguments that learning had insulated human life from evolutionary patterning. On the one hand, 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, etc.). 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 (invited by his observations, because he was in fact largely a biologist), 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 (involving the future pursuit and realization of valued goals). 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 forward causal physical process—natural selection—that produces biological outcomes that had once been attributed to natural teleological processes (Darwin, 1859). The theory of natural selection explains how biological systems could have sets of properties (adaptations) that naturally emerged because of the functions they served. 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 and yet be directed toward goals (either apparently or actually) (Weiner, 1948). The teleological end that seems to exist in the future as the point toward which things tend is in reality a feedback-driven regulatory process—a regulatory process that need not but sometimes does include a representation of a goal state 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, because the human mind evolved in the midst of biological and mental phenomena that can be compactly and efficiently represented and predicted using intuitive teleology, our brains evolved teleological representations as one natural causal format: we are all implicitly drawn to explain things in teleological terms. Hence, the implicit or explicit substrate underlying many attempts to apply Darwinism to human behavior was a return to the intuition 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 individual 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 implicitly 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, children, or inclusive fitness). Indeed, the concept of "learning" within the SSSM itself tacitly invokes unbounded rationality, in that "learning" is often implicitly treated as the tendency of the general-purpose, equipotential mind to grow—by an unspecified and as yet 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, nonmodularist cognitive scientists, blank-slate learning theorists, and traditional economists (but not neuroeconomists or behavioral economists) 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, large numbers of men will pay to have nonreproductive sex with prostitutes they believe and hope are contracepting, but have to be paid to contribute to sperm banks that, with high probability, may lead to offspring. 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. Humans are not mesmerized by accounts of Hutterites or Tsimane—people who average roughly 10 children per family.

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 level of informational or computational adaptations. 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 reliably developing 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.

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 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 individual, social, and cultural life. To get a genuine purchase on human behavior and society, researchers need to know the architecture of each 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 "striving" to increase our reproduction.

Hence, one of several reasons that evolutionary psychology is distinct from the fitness-teleological branch of 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 that fitness plays in the present is in 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, regardless of whether this corresponds to current fitness maximization. Organisms are adaptation executers, not fitness pursuers. Mapping the computational architecture of the mechanisms will give a precise theory of behavior, whereas 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 (and developmental regulation) 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 inherently and fundamentally 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, primatology, and behavioral ecology were providing data about the adaptive problems our ancestors had to solve to survive and reproduce and the environments in which they did so.
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> *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 keylearning process governed by reward and punishment—was wrong.
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> *Advance 4:* Evolutionary biology was revolutionized by (a) being placed on a more rigorous, formal foundation of replicator dynamics (e.g., Hamilton, 1964; Maynard Smith, 1982; Williams, 1966), leading to the derivation of a diversity of powerful selectionist theories, and by the development of adaptationism, which includes the analytic tools to recognize and differentiate adaptations, from byproducts, and stochastically generated evolutionary noise (Williams, 1966). Enduring selection pressures (recurrent adaptive problems), operating over evolutionary time within sets of enduring environmental regularities, act to construct in species reliably developing solutions (adaptations) to their enduring adaptive problems. Evolutionary change involves the change in a population's gene frequencies, and those environmental characteristics that are transient and variable cannot, by their very nature, systematically push gene frequencies directionally upward for long enough to cumulatively produce complex functional species-typical design. Hence adaptationists necessarily emphasize the role that a species-particular history of enduring selection pressures and environmental regularities plays in explaining complex functional design (see the discussion of the *environment of evolutionary adaptedness* or *EEA* following). The composite of enduring selection pressures (the EEA) that pushed the alleles underlying adaptation upward to stably high frequencies are that specific part of the past that caused the adaptation and hence explains its existence and design.
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> 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. Standard cognitive neuroscience partially and erratically accepts 1 and 3, but omits 2 and 4. Aside from 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 painstakingly pieced together into an integrated framework that successfully addressed the difficulties that had plagued evolutionary and nonevolutionary approaches alike. The reason that the synthesis had not emerged earlier in the century was because the key concepts and theories (e.g., adaptationism, computationalism, etc.) were scattered across fields that were institutionally and intellectually distant from each other. Consequently, relatively few were in the lucky position of being professionally equipped to see all the necessary 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 (and immoral) from other vantage points. Nevertheless, those researchers working along these and similar lines were confident that by bringing all four advances together, the evolutionary sciences could be united with the computationalist 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*.[4] Its long-term goal is to eradicate disciplinary boundaries, and unify the evolutionary, genetic, neural, cognitive, psychological, behavioral, and social sciences, because the idea that these are different fields is a sociological vestige rooted in the isolated perspectives native to the independent disciplines when they were founded. Reality has no such boundaries, and the eventual theoretical unification of these fields should reflect the undivided nature of the reality we are studying.

EVOLUTIONARY PSYCHOLOGY

Like other 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 laboratory methods from experimental cognitive and social psychology, developmental psychology, experimental economics, cognitive neuroscience, and cross-cultural fieldwork.

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

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[4] We sometimes read that the term *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 various evolutionary psychologists have themselves 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, and some at the Center for Advanced Study in the Behavioral Sciences. Politics and the press did not enter these discussions, and of course 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 characterizing the adaptations comprising the psychological/developmental 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 in the same way that cognitive psychology was different from behaviorist psychology—necessitating a new name in each case.

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. Indeed, evolutionary psychology is unique among theoretical orientations in psychology in the degree to which it derives from independently established theories principled predictions about previously unknown aspects of the species-typical psychological architectures of humans and other species (see, e.g., Buss, 1999; Daly & Wilson, 1988; Gaulin, 1995; Symons, 1979).

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):

- 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 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?
- 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.
- 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 hundreds 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 new neurocomputational programs of any complexity.[5]

- 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 typically of 50 to 150 people, many of whom were close relatives. Yet, our cognitive programs were designed for that social world.
- 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 causal 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.

To survive and reproduce reliably as hunter-gatherers required the solution of large and diverse arrays 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.

This difference can be most clearly seen by using results from evolutionary game theory (Advance 4) and data about ancestral environments (Advance 2) to define adaptive problems and then carefully dissecting the computational requirements of any program capable of solving those problems. For example,

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[5] Simple, unidimensional traits, caused by quantitative genetic variation (e.g., taller, shorter), can be adjusted in less time; see Tooby and Cosmides, 1990b. Moreover, intense selection pressures, such as those caused by diseases (e.g. malaria) or new food sources (milk from domesticated animals) can propel some alleles rapidly upward in frequency on a timescale of centuries. For example, all mammals have the adaptations to digest milk in infancy and then lose it after weaning, but some human populations who get milk from livestock benefited from the tweaking of the lactose-digesting enzyme production system so that the preexisting ability to digest milk is maintained into adulthood. In contrast, despite being surrounded, for millions of years, by forests of sugar (cellulose) whose digestion would have prevented all starvation, no humans have evolved the appropriate enzymes to break down the beta acetal linkages that prevent the digestion of cellulose. Complex adaptations are difficult to evolve rapidly.

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).

- 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 tape recorder, 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 (a) are complexly specialized for solving an adaptive problem, (b) reliably develop in all normal human beings, (c) develop without any conscious effort and in the absence of formal instruction, (d) are applied without any awareness of their underlying logic, and (e) 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 an instinct (Pinker, 1994). In fact, we can think of these specialized circuits as *reasoning instincts, decision 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 neurocomputational 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.

Reasoning 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 we attribute them 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 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 exactingly 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 (for a map of the design of this system, see Lieberman, Tooby, & Cosmides, 2007). 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 (for evidence about the design of such a system, see Lieberman et al., 2007). 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 (in the general case) behavior that increased the frequency of the alleles underlying the behavior; typically, this means behavior that systematically promoted the net lifetime reproduction of the individual and/or (with appropriate trade-offs) 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 lifetime kin-weighted reproduction because reproduction 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 (or in an enduring subset of) 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 were regularly encountered by members of a population or species, and that recurred across sufficiently many generations such that natural selection has enough time to design 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 that fit together to form an integrated structure or device (e.g., a retina, a claw, an incest avoidance program) 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 byproducts 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 self- and kin reproduction in the ancestral past. Adaptive problems are the only kind of problem that natural selection can design machinery for solving. They are the source of and explanation of our evolved functional design.

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 hominin line is thought to have originated in African open woodlands, 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 4, 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 2 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 bees 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 did 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, 1996a; 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 et al., 1999; Todd, Hertwig, & Hoffrage, Chapter 37, this *Handbook*, Volume 2). These procedures are *ecologically rational,* providing good solutions when operating in the task environments for which they evolved (Cosmides & Tooby, 1996b; Delton, Krasnow, Cosmides, & Tooby, 2011; Tooby, Cosmides, & Barrett, 2005, 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 hominins 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) and others 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 with siblings. All these conditions (along with tens of thousands of others) are known, and all pose adaptive problems. By considering these selection pressures, a careful, well-informed, intelligent researcher 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 hominins were ground-living primates; omnivores,[6] 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, typically nomadic, kin-based bands often of 20 to 150; they would rarely 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, raiding, defense, and aggressive coalitions; and they made tools and engaged in extensive amounts of implicit and explicit exchange, food-sharing, cooperation, and deferred reciprocation. 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 use of evolutionary game theory (see Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2) and/or optimal foraging models. 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 predicted 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). Indeed, the "irrational" risk aversion posited in Kahneman and Tversky's (1979) prospect theory can be replaced by an evolutionarily revised prospect theory (Rode et al., 1999), in which individuals can be shown to be adaptively risk-seeking or adaptively risk averse depending on their need level and the probability distribution they faced.

Knowledge of ancestral life, ancestral conditions, and ancestral adaptive problems are like treasure maps that can supercharge the discovery of previously unknown

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[6] Fossil 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, and for hunting to be a dispropoportionately male activity not only in humans but in chimpanzees and baboons.

psychological and developmental mechanisms. Although behavioral scientists can be certain about a huge inventory of facts about the ancestral world that has 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 likely 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 and must rely on the random walk of blind empiricism. There are certainly many features of the ancestral world about which we are completely ignorant: These features simply do not form the basis for experiments. Traditional research programs involve proceeding either with blind empiricism, on the basis of no theory of function, or to proceed guided by necessarily false theories of function. It is difficult to see any valid argument for doing either, because (a) random empirical tests are unlikely to efficiently guide researchers to the correct experimental procedures that are capable of detecting and mapping of complex neural or developmental programs, and (b) invalid nonevolutionary theories are even less likely to be productive. (The physics of entropy together with replicator dynamics tell us that the only origin of complex functional design in undomesticated species is natural selection; hence, all correct theories of function will be and must be evolutionary.)

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 brain/mind 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 the human brain/mind: 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 neurocomputational and developmental 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, which 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 byproduct, or noise.

Many Properties of Organisms Are Not Adaptations The cross-generationally recurrent design of an organism can be partitioned into (a) adaptations, which are present because they were selected for, (b) byproducts 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 (c) 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 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 byproducts 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). Indeed, entropy is pervasive, and so the designs of organisms are the product of mutation-selection balance. All organisms contain many negative genetic mutations, on the way to being selected out, and the environments of development change, generating environmental "mutations"—changes—that induced developmental perturbations. Moreover, organisms may only have been exposed to an adaptive problem recently. So evolutionarily informed researchers do not expect optimality, and are not confounded when nonoptimality is found. They only expect that designs are to be found in regions of design-space that are vastly better than random from a functional perspective, and that by modeling or considering "optimality" or good design, these rare regions can be identified.

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 conceive 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.[7]

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.[8] To see the organization that exists in a complex

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[7] In 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.

[8] Imagine 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 byproducts of the functional ones (Hagen, Chapter 4, this volume).

system, researchers need to be able to distinguish its functional components from the byproducts 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 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 and allows a mouth access to it; and it has a heat-dissipating handle that allows it to be lifted without burning the lifter. 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—the container need not be watertight, 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 why it was constructed in the way that it was. 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, a device for executing bathers, or a means for toasting slices of bread (for discussion, see Dawkins, 1996).

In the same way, design evidence is the criterion 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.

Researchers can identify an aspect of an organism's physical, developmental, or psychological structure—its phenotype—as an adaptation by showing that (a) it has many design features that are improbably well suited to solving an ancestral adaptive problem, (b) these phenotypic properties are unlikely to have arisen by chance alone, and (c) they are not better explained as the byproduct 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 byproduct, 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 (i.e., its *information ecology*). 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 experimentally, using methods from cognitive, social, and developmental psychology, cognitive neuroscience/neuropsychology, experimental economics, cross-cultural studies—whichever methods are most appropriate for illuminating programs with the hypothesized properties.

If the predicted properties 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 (usually adaptations are predicted to be species-typical). However, a universal program may often produce different expressions triggered by different environmental or social conditions, or show 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, Tooby, & Cosmides, 2003, 2007). Avoiding the deleterious effects of inbreeding was an important adaptive problem faced by our hominin 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 a ancestral hunter-gatherers. 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 co-residence 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 estimate (that we call a kinship index) for each individual in the person's social world. The kinship index serves as an 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. Independently, the kinship index in one individual's mind about a particular other individual should regulate altruism: The higher the kinship index, the more an individual should be motivated to sacrifice for the relative. 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 co-residence—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., Leiberman, Tooby, & Cosmides, 2003, 2007). 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.

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 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, Tooby, & Cosmides, 2003, 2007). 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.[9]

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 (For an excellent, early treatment of these issues, see Tinbergen, 1963).

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.

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[9] It 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 such as being fed linguistic representations (e.g., Hirschfeld & Gelman, 1994).

Evolutionary psychologists do not see nature and nurture as existing in an explanatory zero-sum relationship. Nonevolutionary researchers have typically assumed that there is a spectrum in the nature-nurture debate, that it runs from the nativist extreme (most things are "genetically determined") to the environmentalist extreme (most things are "environmentally determined"), and that the true position (the subject of the debate) lies somewhere along this spectrum. But all properties of the organism equally develop through 100% gene-environment interaction. The key point at which the adaptationist approach pivots to a new framework for understanding development lies in the following recognition: As will be explained in greater depth, a species' history of selection acted over evolutionary time to organize and tune the interaction between genes and environment to produce the reliable development of that species' adaptations—adaptations whose program logic, in turn, specifies how environmental inputs are operated on to become behavioral outputs. (Whereas selection acts antientropically to functionally tune gene-environment interactions, random genetic and environmental changes—mutations—act to entropically disrupt reliable development.)

Innate Is Not the Opposite of Learned Everyone is a nativist, regardless of whether she knows it. 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 nature 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 developmental 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 particular 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 innate 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 innate 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 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 is true for culture. Given that cultural ideas are absorbed via learning, inference, and interaction payoffs—which themselves are caused by evolved programs of some kind in interaction with the environment—a behavior can be, at one and the same time, *cultural, learned,* and *evolved.* (For excellent discussions 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, alliance detection, 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 (and knowing its functional architecture), nothing whatsoever is explained by invoking learning as an explanation for a behavior. Labeling something as 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 all anatomical and behavioral phenotypes). In short, learning (like culture) is a phenomenon that itself requires explanation, rather than being any kind of explanation itself. A coherent explanation for how humans and nonhumans learn about a given domain must include (a) a description of what the evolved learning program looks like (that is, its circuit logic, code, or program architecture); (b) what selection pressures and other evolutionary effects led it to acquire its present structure over evolutionary time; (c) what set of gene-environment interactions lead it to develop its structure at any given point in the organism's life history, (d) what information was and is available to the organism that is executing that evolved program.

Everyone is also an environmentalist, regardless of whether she knows it. 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. Indeed, the entire function of a brain is to allow the organism's responses to be sensitively contingent to the information provided by the environment.

Thus, evolved programs—instincts—are not the opposite of learning. They are the engines or programs 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 or who our genetic relatives are. The greater the number of specialized learning (or cognitive) programs we come equipped with, the more we can learn from experience. Evolved programs do not constrain a "flexibility" that organisms otherwise would have; each additional program endows the organism with competences it would not otherwise have. To take just one example, the evolved language competence vastly multiplies the behavioral repertoire of humans. Humans can respond with intricate contingency to the world because of these endowments. This is why nature and nurture do not exist in a zero sum relationship, but in a positive sum relationship. More nature (evolved systems of regulation and computation) allows more nurture (exquisitely sensitive responsiveness to the world) (Boyer, 2001; Tooby & Cosmides, 1992).

Specialized or General Purpose? If the *innate versus learned* controversy is meaningless, there is a genuine and illuminating question 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—regardless of whether it governs learning—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 neurocomputational 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 architecture of the 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 (functional) 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 a more inclusive set of which the outcome in question is one instance), or (3) it is a byproduct 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: 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, 55 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 about large numbers of diverse, specialized adaptive problems 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 the evolved programs that cause maturational development operate before birth and none after birth.

This assumption is clearly false. Teeth and milk-delivering breasts are uncontroversially standard parts of our evolved architecture, but they develop after birth, 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?

Organs and design features can mature at any point of the life cycle, and this applies to the adaptations 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 the evidence appears to bear them out, that many mechanisms will appear and disappear on a condition-specific or life-history linked timetable based on when they would have been needed, under ancestral conditions, to solve the challenges of that life stage. Infants need the sucking reflex but not sexual desires; adolescents need sexual desires but not the suckling reflex. For an example of a condition-specific adaptation, consider pregnancy sickness. It does not manifest itself according to a developmental schedule, but is triggered by a condition: Women during the first trimester of pregnancy (that is, during fetal organogenesis) need a different set of thresholds inhibiting the ingestion of substances that could cause birth defects than do nonpregnant women, so their disgust thresholds are adaptively adjusted by the condition of pregnancy (Profet, 1992).

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 in any way undermine the claim that it is part of our evolved design. We all start out as a single-celled zygote, so everything develops.

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. Unfortunately, they 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 et al., 2003), of which we mention just two (see also Hagen, Chapter 4, this volume).

First, genes are regulatory elements that use environments to construct organisms. Thus, as discussed, every single component of an organism is co-determined 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 (a nonexistent class) erroneously assumes that environmental causation is nonevolutionary. In order to understand why environmental causation is every bit as "evolved" as the genes, 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 subset of properties of the world that evolution has made relevant to the development of the adaptations of a given species.

Evolution acts by selecting some genes over others, but in so doing 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 on 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. Selection tailors developmental programs to engage in organized interactions with facets of the developmentally relevant environment to successfully produce highly ordered, functional phenotypes. Selection also acts to render 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. Because for humans the amount of information stored in the environment is much vaster than the quantity of genetic information, one can think of the zygote, its genome, and its parentally supplied cellular and uterine environment as analogous to a computer's basic input/output system (BIOS)—self-extracting kernels that bootstrap the single cell toward its highly organized, realized set of adaptations (as expressed at a given point in life history). We manifest species-typical (or population-tuned) evolved designs not because genes are the only things that influence phenotypes, but because selection orchestrates the interplay of gene-environment interactions through genes.

Hence, 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 in which the lineal series of zygotes appears. They must regularly recur often enough that they select for developmental programs that interact with them to cause reliable development every generation of the functional species-typical design. From the point of view of any given subcomponent of the organism, other parts of the organism are, of course, stable features of the environment, and so high levels of functional interrelationship and developmental interdependence accumulate among a body's parts. In addition, some aspects of the environment outside the organism are also enduring features of the ancestral world that interacted reliably with the organism's design, and so subcomponents of the organism typically manifest highly functional interrelationships with them (e.g., wings and air; eyes and light; digestive enzymes and available diet), as well as developmentally interdependent relationships with them (e.g., lung size and altitude during development). 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 existence of two sexes, the presence of caretakers for infants that survive); 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 co-residence and genetic relatedness). In spite of omnipresent, order-destroying entropy, organismic designs successfully develop the functional species-typical design (and its locally tuned expressions) based on the degree to which their genetic and environmental inheritances were functionally coordinated with each other by selection adjusting them over evolutionary time so that they interactively produced an adaptive phenotype. Gene–organism–environment webs have been experimentally tested generation after generation; those interactions that led to maladaptive development were discarded by selection. This evolutionarily orchestrated coordination of genome and environment is how organisms are able to overcome entropic processes that would otherwise preclude the existence of life (Tooby, Cosmides & Barrett, 2003). Change in either of the two inheritances (either through genetic mutation or change in the developmentally relevant environment) disrupts the coordination, and the greater or more rapid the change, the greater is the disruption in the always imperfect actual phenotype.

This view of development is not gene centered or a form of "genetic determinism" if that is interpreted to mean that genes by themselves determine everything, immune from environmental influence—or even that genes determine "more" than 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, kin-directed altruism, language, 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 to 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 and express themselves less contingently (e.g., the typical form of the anger facial display of emotion; Sell, Cosmides & Tooby, 2014). But in all cases, there is an underlying regulatory or 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 (more evolved content specificity) allows more nurture (richer stores of ontogenetically elaborated data and locally contingent behavior). For example, the highly organized language acquisition device allows marvelously rich and variable verbal expression (Pinker, 1994).

From this perspective, successful development has to accomplish two tasks (Tooby & Cosmides, 2001). The first is the reliable construction of the set of (largely species-typical) adaptations required at each point in the organism's life history (given its sex). The second is to bring each adaptation into a state of readiness to perform its evolved functions, given the organism's situation. Accordingly, adaptations can be conceptualized as operating in two different modes (Cosmides & Tooby, 2000a; Tooby & Cosmides, 2001). The first is its functional mode, when it is performing its evolved function (e.g., the incest avoidance system, calling up aversion at the prospect of sex with a close relative). This is the aspect of the adaptation we normally think about. The second is its organizational mode. This mode of operation is designed to construct the adaptation, and in so doing, to furnish it with the information, neuroendocrinological pathways, correct weightings in decision variables, procedures, and representations it needs to behave adaptively when called upon to do so. In general, the goal of the organizational mode of an adaptation is to cause it to develop a better organization for carrying out its function so that, when it is called on to operate, it discharges its function well (e.g., the kin detection front-end of the incest-avoidance system, processing cues in its local environment into a kinship map of who the individual's genetic relatives are).

Although a natural first step for researchers is mapping adaptations operating in their functional mode, it may be that solving the problem of correct assembly and calibration of an adaptation is a much harder problem for the organism (given entropy) than merely running the device, once it has been assembled. So, for example, babbling, word learning, local syntax acquisition, the intrinsically entertaining nature of verbal play, and so on, all seem to be the language system operating in its organizational mode, so that when the individual needs to speak or understand, the underlying adaptations are ready to perform their function. Rough and tumble play are adaptations for fighting and defense operating in their organizational mode (Symons, 1978). The organizational mode of an adaptation or set of adaptations will generate different organizations (such as bodies of knowledge, habits, neuroendocrinological calibration, fear-sensitivity, etc.) in the minds of each individual, given the individual's unique experience or ontogenetic trajectory. This is the most basic way that the evolved adaptations that compose our species-typical design lead to large sets of functionally intelligible individual differences, without this outcome being in any tension with an adaptationists perspective on human psychology and behavior (Cosmides & Tooby, 2000a; Tooby & Cosmides, 2001).

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 among 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, and Tooby & Cosmides, 1990b, for a more complete explanation, and a discussion of how to relate individual differences to universal design):

1. 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.
2. 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 them 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.
3. Each new human originates sexually. A randomly selected half 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.
4. Hence, the successful assembly of a complex adaptation in a new individual requires that all 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 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.
5. 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.
6. 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.

7. The constraint of functional universality applies to only 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 quantitatively, but not outside the boundaries imposed by the demand for functional compatibility.
8. 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.
9. 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, with, for example, the placenta, fetal hemoglobin, teeth, the reproductively mature uterus, testes). 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 nonreproductive 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 typically limited to a particular sex or age or be contingent on the presence of an eliciting condition (e.g., pregnancy adaptations) or at a single nonrecombining stretch of DNA (e.g., biological sex in humans).
10. 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 (like different car models). 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 in which 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 observed 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 adaptive 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 latent or potential functional design of our complex neurocomputational machinery, and very high levels of expressed architecture uniformity at a given sex and age.

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* among individuals are accounted for by *difference*s 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 arbitrary 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, byproducts, and noise—traits caused by genetic variants are predominantly (but not exclusively) evolutionary noise, with little adaptive significance, while complex adaptations are likely to be universal in the species.

Why is uniformity generally associated with functionality and variability typically 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 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, and its heritability statistic will be high (because most variation between individuals in the trait will be caused by variation in genes). For this reason, genetic variability tends to be predominantly nonadaptive or maladaptive evolutionary noise: neutral or nearly 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. Fundamentally, selection acts to decrease entropy in phenotypic design, while mutation acts to increase it. Because of entropy, genomes are never close to flawless, but are instead a balance between mutation and selection.

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, health, anatomy, and appearance. These differences tend to be quantitative in nature—a little more of this, a little less of that—whereas the overall functional architecture remains the same.

Another 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 real for humans. Moreover, multiple behavioral strategies often emerge in theoretical models through frequency-dependent selection (e.g., cooperators and free-riders). 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. It remains unclear the extent to which humans exhibit allele-based frequency-dependent behavioral strategies, and so far there are no well-established cases aside from the two sexes. For most challenges, strategy selection might most advantageously take place when the challenge is faced, so the strategy matches the challenge; this may be why genetic commitments to strategies seem rare and would be generally disadvantageous. However, the longer the period it will take to develop a good phenotype for a future adaptive problem (as is arguably the case in mammals for developing a male or female phenotypic design), the more it might pay to make an early commitment, undertaken in greater ignorance of what future conditions will be like. Commitment by genetic switch (e.g., XY sex determination) is the extreme case, where strategy commitment occurs randomly at conception.The question of why there should be systems of heritable dimensional personality variation will be addressed in the section on epigenetics and parametric coordinative adaptations.

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

If all psychologists are engineers working in reverse, 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-gatherers 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 must be 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, Gallistel (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 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, 1996a; Gigerenzer et al., 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). If true, principles derived from experiments involving artificial stimuli should easily generalize to natural scenes and stimuli—but they do not (Braun, 2003; Li, Van Rullen, Koch, & Perona, 2002; New, Cosmides, & Tooby, 2007).

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, 2007). 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. By applying adaptationist approaches, it is easy to predict and discover new principles of visual attention, such as the evolved animacy bias, which would never have been discovered by a metatheory that the brain consists primarily of general-purpose processes (New, Cosmides, & Tooby, 2007).

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 9, this volume; Barrett, Tooby, & Cosmides, in press). 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 Boyer, 2001; Boyer & Barrett, Chapter 5, this volume; Barrett, Cosmides & Tooby, in press). 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, which 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, and 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 amidst 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 9, this volume; Barrett, Cosmides, & Tooby, in press). 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 that hypothetical effects about door knobs, floorings, or words that rhyme with Quetzalcoatl. 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 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 et al., 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 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, 2005, 2015; Boyer & Barrett, Chapter 5, 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 5, 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; for inferences about growth and bodily functions, people may be processed as animals but perhaps 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 5, this volume; Braun, 2003; Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2; 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 et al., 2005; Sperber, 1994; Sperber & Wilson, 1995; Tooby & Cosmides, 1996).

COMPUTATIONAL ADAPTATIONIST APPROACHES TO MOTIVATION AND EMOTION

In principle, all modern behavioral 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, gratitude, sexual aversion to close relatives, romantic love, guilt, anger, sexual jealousy, sexual attraction, the perception of beauty, or disgust should all be describable in computational terms, which specify the relevant inputs, representations, the procedures that act on them, and regulatory outputs. Yet, until recently, most cognitive scientists, for example, would not even recognize these topics as within their domain of study.

One reason for why even cognitive psychologists arbitrarily limit their scope is the folk psychological distinction made between knowledge acquisition on the one hand and motivation, emotion, feeling, 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—a practice that presumes that knowledge and motivation are separable rather than coevolved aspects of the same unified systems of representation and action (see Fodor, 2000, for an example).

THE WEAKNESS OF CONTENT-FREE ARCHITECTURES

To some, it may seem as if an evolutionary perspective supports the case that our species-typical psychological 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 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? The difficulty with this intuition is that the more general the problem-solving strategy is, the weaker and more nonfunctional it is. What makes something a more general problem-solving strategy is that it can be applied across a broader class of problems; to do this, it must be stripped of strategies that yield correct answers on some subsets of problems and incorrect answers on others. Domain-specific or content-sensitive architectures are not limited in this way; if they can appropriately apply a program that evolved to solve a specific subset of problems (e.g., kin detection), and others on other problem types (optimal foraging; language acquisition), then it can solve a broader array of problems than the one using content-independent general strategies. So our brains should use the principle of preemptive specificity—use the program specialized for the the content, if there is one, and if there is not, fall back to strategies that work on more inclusive problem types.

To be a plausible model of how the mind works, any hypothetical domain-general neurocomputational architecture would have had to reliably generate solutions to all of the problems that were necessary for survival and reproduction ancestrally. 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, 1985; Tooby & Cosmides, 1990a, 1992; Tooby et al., 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 psychological 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 (e.g., 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 25, this *Handbook*, Volume 2). 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 general system must be equipped only 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, 2005). 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 singly and in combination. 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, 2006; 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 small number. Without domain-specialized learning mechanisms, we would learn nothing at all. Because the set of problems our ancestors had to solve was not a random sample of the set of all logically possible information relationships, the highly clustered relationships in real adaptive problems would have selected, in many (perhaps all) cases, for networks of efficient specialization, along with whatever strategies worked over broader sets of problems.

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 this drastically limits 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 unobservable states 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, 2007). Similarly, ancestral hominins had no method by which they could directly see another person's genes to tell whether they are genetic siblings or not. But a mind equipped with a domain-specific kin detection system can estimate kinship on the basis of cues, such as maternal perinatal association, or co-residence 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 of *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 or a "good" person to assault or a "good" place to set up camp. 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 are an irreducible number of these motivational domains; within each motivational domain, there are an irreducible set of domain-specific criteria or value-assigning procedures operating. For the domain of *food* 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 of specific foods by the immune system,[10] stage of pregnancy (because of the vulnerability of fetal organogenesis to chemical disruption), 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) cannot 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.

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[10] Humans and omnivorous nonhumans have a surprising ability to pick efficacious herbs to medicate themselves with, to avoid foods with slow as well as fast acting toxins, to match nutritionally complementary foods, to identify effective nutrient releasing or detoxifying food processing practices, and to differentially select foods with nutrients they are deficient in even with no obvious odor clues. To explain these facts, we hypothesize that there is a set of adaptations that (a) exploits the immune system's ability to recognize alien proteins to construct recognition profiles of the digestive products of ingested substances; (b) maps these recognition profiles to the sensory properties of foods ingested in temporal proximity to the immune system's exposure to the protein breakdown products; (c) identifies various components of health (which specific detoxification pathways are overloaded, essential nutrient profile, immune categorization of health, other short-term and long-term health consequences); (d) performs the matrix algebra of backward inducing the temporal profiles of the health consequences of dietary substances onto the immune database of recognized foods (plausibly using the Gallistelian time-series analysis component of conditioning); and (e) maps the computational outputs of these analyses back to sensory food recognition templates, along with valences that reweight how desirable or undesirable the food is to the organism.

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, motor skill acquisition, 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 et al., 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 co-evolved 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 wife and another's mother—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 trinity of space, time, and causality. Yerkes's finding of evolved snake fear in chimpanzees 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 evolved cue recognition systems that evolved to be specifically responsive to stimuli with certain cues (however abstractly described in the nervous system). It is the specificity of the coupling to the particular valuation procedure (closer is negative) that individuates the concept with respect to the set of motivational functions (e.g., *beloved* [your children], *wary* [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. (It is also worth pointing out that degrees of snake fear are, therefore, "cultural"—weights in snake fear calibrate each other in interacting primate communities.)

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 these elements are unique to the snake system (e.g., snake-recognition is; distance-to-self, fear-faces, fear-output are not), but their pattern of distribution among motivational systems is heterarchical and itself not something that could be derived by content-independent operations acting on unmediated 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 (Weiner, 1948), designed to generate action. From this perspective, there is not just a cognitive science of knowledge 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, threat, collective action, 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 integrated systems (which they will inevitably turn out 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, 1990a, 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, but instead evolves together. (For a more complete discussion, see Tooby et al., 2005.) Indeed, many evolved concepts arguably exist so we can have functional motivations about them (e.g., food, free rider, mother, child, predator, snake, unclean, sexually attractive).

EMOTIONS AS A SOLUTION TO THE SHORT-TERM 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 hominin 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 (e.g., digest food versus devote maximum blood resources to the cardiopulmonary system and muscles executing escape). They may also make conflicting demands on common computational resources. The existence of attention itself, where some things are selected to be processed with higher priority than others, demonstrates this. 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 neurocomputational 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 given the array of challenges prioritized by likely fitness consequences.

We have proposed that emotions are such programs (Tooby, 1985; Tooby & Cosmides, 1990a, 2008). 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 to produce a best-bet set of responses, rather than clashing in a cacophonous and self-defeating fashion. This coordination is accomplished by a set of superordinate programs, namely 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 (a) the statistical structure of ancestral situations (the EEA) and (b) 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 immediate situation being confronted.

How did emotions arise and assume their distinctive structures? Fighting, falling in love, responding to mistreatment by another, escaping predators, seeing a potential sexual or mate-recruitment opportunity, 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 hominin 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, demands, 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 class of ancestral situation type. So those designs that responded to large felid predators by approaching to better appreciate their beauty were selected out; those designs that motivated avoidance but did not accelerate heart rate and breathing were also selected out compared to designs that increased the maximum possible speed of retreat by accelerating heart rate and breathing (and suspend digestion, long-run somatic repair, attention to competing non-time-fused goals, and so on). Step by step, design variants that more thoroughly coordinate effective response sets become incorporated into the species design.

When we use the term *emotions*, we are linking these evolved programs to evolutionarily recurrent situations (whether challenges or opportunities) that have a short-term or moderately extended duration. These situations may terminate (e.g., with a rescuer killing the predator), gradually lose their structure (with the predator wandering away from your arboreal refuge, so that the predator risk returns to baseline levels), or be replaced by other situations that trigger new emotions (your child makes a misstep and is struggling not to fall out of the tree). Moreover, there is not only an abstract structure of a recurrent situation (to which we have evolved an organized response), but there will be recurrent dimensions of variation in the abstract structure of the recurrent situation, which are used to calibrate the response. That is, not only will there be predator-threat, but predator-threat varied in terms of speed, surprise, number, distance to safety, number of allies, and so on (Cosmides & Tooby, 2000b). Hence individual ontogenetically encountered situations will be responded to in terms of the long-term abstract structure of a situation, as parameterized by psychological variables that serve to meaningfully individuate the immediate situation in a way in which the architecture can recognize and to which it can deploy appropriately.

Moreover, the world does not dichotomously chop itself into short-term situations and long-term conditions. For convenience, we term programs that coordinate responses to short-term conditions *emotions*; we term coordinated responses to conditions of intermediate duration that recalibrate a constellation of decision-variables *calibrational adaptations* or (if related to traditionally recognized emotions) *moods*; and we term coordinated responses to enduring conditions *parametric coordinative adaptations*. As discussed later, the major dimensions of personality variation (including perhaps what researchers sometimes call temperaments) may be constructed by various parametric coordinative adaptations.

The coordinated adjustment and entrainment of mechanisms (emotions) functions as a mode of operation for the entire neurophysiological 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 (a) recurred ancestrally, (b) 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), (c) had a rich and reliable repeated structure, (d) had recognizable cues or situation-representations signaling their presence,[11] and (e) an error would have resulted in larger fitness costs than the remedy. When a condition or situation of an evolutionarily recognizable kind is detected, a signal is sent out from the emotion program that (a) activates the specific constellation of subprograms appropriate to solving the type of adaptive problems that were regularly embedded in that situation, and (b) 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, motor planning, 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 ("arousal"), behavioral inclinations, situation interpretations ("appraisals"), facial expressions, or consciously accessible 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.

For example, some emotion researchers consider that definitional to a basic emotion is an identifiable emotional expression, causing them to focus on a set of six or seven (happiness, sadness, anger, fear, surprise, disgust, and perhaps contempt). However, an evolutionary computational approach makes it plausible that emotions are far more numerous, but for only seven of these (identified so far) did it pay to broadcast the individual's emotional state to others (Tooby & Cosmides, 2008). We would add confusion to this list (since it is recognizable on the face), and because we think it is a mode of operation.[12] All psychological programs—including superordinate programs

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[11] If 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.

[12] An evolutionary recurrent situation can be extremely abstract, provided that there is a deployment of the architecture that improves performance given the detection of this abstract situation. To give a flavor of just how strangely abstract a "situation" can be, consider the hypothesis that confusion as a mental state might not be a failure of processing, as it is usually thought of, but rather itself an adaptation. Indeed, it seems likely that humans even have adaptations for confusion—that is, that confusion as a detected situation selected for a mode of operation (confusion) that improves resolution of the problem posed by confusion (the situation). What is the recurrent situation that confusion (the mode of operation) is a response to? Confusion may be defined as having insufficient information to decide on a single coherent representation of the organism's circumstances relevant to selecting a best response; this can involve feedback to behavior being highly inconsistent with expectation; being exposed to conflicting cues that imply mutually inconsistent conditions, or a situation requiring contradictory responses. Evolved best responses to the situation of confusion may be such computational adjustments as a suspension of ongoing action; a broadening of attentional focus beyond ongoing goal-pursuit; increasing the search for disambiguating cues; rapid shifts between different interpretations of data to see which has the best fit; increasing uncertainty weightings on decision-relevant variables; and dropping down the ladder of interpetations and responses to more conservative computational or behavioral strategies that yield positive returns over broader sets of conditions.

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 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 a computationally impossible entity with theories that can be implemented as information processing architectures with open parameters. Emotion programs, for example, have a front end that was designed to detect evolutionarily reliable cues that a situation exists (regardless of whether these cues still 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 execute their evolved code regardless of the needs and circumstances of the modern individual; they were designed to create states (fury) and implement actions that worked effectively in ancestral situations (e.g., murder a weaker rival), regardless of their consequences in the present (e.g., prison).

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 subserve them are deactivated. You are no longer hungry; you cease to think about how to charm a potential mate; or 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 9, 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; Öhman & Mineka, 2001; 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 and the immune system adjusts. 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).[13] Some of these responses may be experienced as automatic or involuntary.

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[13] Marks (1987) 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 & 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 . . ." (pp. 68–69).

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 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 (pace 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 payoffs. These would have had to have (a) endured over a sufficiently long stretch of evolutionary time (and proportion of the species range) to have had selective consequences on the design of the mind; and (b) be probabilistically associated with cues detectable by humans. To the extent that situations exhibit such a structure, their statistical properties are expected to have been used by selection to build an emotion program whose detailed design features are favored given that recurrent situation. That is, the architecture of the emotion program should manifest an advantageous complementarity with the structure of the recurrent situation, so that their interaction produces a better outcome (given ancestral conditions) than would have been produced without the program.

Emotion programs have evolved to take features of the recurrent statistical and causal structure into account, whether they could have been perceived ontogenetically or not. 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. Thus, embedded in an emotion mode is a way of interpreting the world in terms of parameters made meaningful by the recurrent structure, assuming causal connections (even unobservable ones) that were typically present, and being motivated to take action related to the ancestral cluster of probabilistically associated elements. So, for example, if ancestrally a new group moving into one's locale statistically foreshadowed eventual zero-sum conflict, competition, and potential expulsion from their existing resource base by the new group at some nontrivial rate, then humans should be designed to be more liable to experience intergroup fear, hostility, and rivalry. Similarly, if anger is an emotion program that evolved to orchestrate negotiative behaviors in conflicts of interest, and being perceived as stronger increases one's bargaining power (Sell, Tooby, & Cosmides, 2009), then evolution should have incorporated elements into the facial display of anger that enhanced the appearance of strength (as it appears to have done: Sell et al., 2014).

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: (a) a sexual rival with a capacity for social action and violence, as well as allies of the rival; (b) a discrete probability that an individual's mate has conceived with the sexual rival; (c) changes in the net lifetime reproductive returns of investing further in the mating relationship; (d) 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); (e) 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 (7) 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).

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 (e.g., with heart rate increase) in proportion to the raised probability in the ancestral world. (Natural selection acts too slowly to have significantly 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 (e.g., Buss, 2000).

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, gratitude, guilt, sexual jealousy, anger, 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: (a) reconstructing the clusters of properties of ancestral situations, (b) 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 (c) 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, selecting for differential responses (e.g., adjusting the reserve price for taking action down or up, so that joy makes people more energetic, whereas sadness deters action). 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).

Motivational Systems, Internal Regulatory Variables, and Recalibrational Emotions

Although traditional theories of motivation have tended to be general-purpose or very simple (e.g., motivation as goal seeking; motivation driven by a general-purpose operant conditioning system shaped by histories of reinforcement, linked to a small number of drives or reinforcers, such as food, water, sex, etc.). But evolutionary research has identified a large and expanding number of adaptive problems for which there exist no corresponding motivational theories in traditional psychology (e.g., kin-directed altruism, incest avoidance, exchange partner management, power-based negotiation, habitat selection, prevention of partner infidelity, contagion avoidance, child care, status-seeking, affiliation by association value, punitive deterrence of free-riding, advancement of one's coalition's interests with respect to competing coalitions, and so on). These do not involve freely chosen goals, nor do they appear to be well-captured by any extant drive-reduction theory. These adaptive problems are each so different from each other that they require distinct adaptive specializations to solve them (how much sexual aversion should you feel toward this half-sibling—incest avoidance; how much cost should you incur to struggle for a resource against this adversary—anger; how much should you recalibrate your disposition to help someone who helped you more than you expected to consolidate a higher level of mutual cooperation—gratitude; how determined should you be to punish a free rider—punitiveness; how much effort should you devote to your group, given the likely costs—loyalty).

Motivational adaptive problems are, abstractly, information processing problems involving evaluating expected fitness payoffs to alternative courses of action, given information available to the organism about its situation, in order to make decisions that are best bet responses. Ancestrally recurrent situations that required choices (e.g., have sex with this person given cues that he might be your brother?; punish or ignore free-riding?) can be organized into distinct sets or clusters with statistically recurrent features, cues, invisible concomitants, outcomes, and payoff distributions. This in turn led to selection for distinct motivational subsystems tailored to the special properties of each motivational problem-type (incest-avoidance; child care; sacrifice for the coalition; mateship maintenance; exploitation of opportunities for gain through aggression; satisfaction of curiousity). To operate, each of these will generally be associated with proprietary interpretive systems with reliably developing conceptual primitives such as *free-rider* (Delton, Cosmides, Guerno, Robertson, & Tooby, 2012), so that motivations such as punitive sentiment can be directed toward their functional targets (e.g., the transgressing person; see also Price, Cosmides, & Tooby, 2002). Conveniently, evolutionary biologists have developed a number of models of adaptive problems—that is, how selection acts in specific domains (such as kin selection, inbreeding depression, sexual selection, the asymmetric war of attrition); these models can be used to develop models of the computational architectures that specific motivational subsystems should have in order to be able to solve their respective adaptive problems.

In order to construct a theoretical framework capable of incorporating this new range of cases, we need to introduce a new class of computational elements that have no present counterpart in the cognitive sciences, traditional approaches to motivation, or folk psychology. That is, they are not thoughts, or feelings, or desires as ordinarily conceptualized. For sake of simplicity, we call these computational elements *internal regulatory variables* (Tooby & Cosmides, 2008; Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). They are needed to register properties of persons, acts, and situations that are needed to compute, implicitly or explicitly, the value and probability of an outcome of a particular kind, given a course of action; to segregate elements in the world into classes that can then be assigned motivationally relevant meanings (e.g., my child, a sexual opportunity, or a potential friend); or to store decision-making thresholds that partition the set of possible actions in the immediate situation that are fitness-promoting from those that are fitness-reducing (e.g., a welfare trade-off threshold). They not only encode necessary precursors (e.g. co-residence as one input into relatedness computation) necessary to specialized next-step input computations (e.g., update kinship index estimating how genetically related this person is); but they also can encode values themselves (a high kinship index can then lead to a computation that this specific relative is *valuable* to *this* degree); this in turn can be used to provide values (as parameters) to decision-making circuits (e.g., place a high weight on this person's welfare when making choices that affect the welfare of self versus other—welfare trade-off magnitudes).

According to this view, internal regulatory variables evolved to track those narrow, targeted properties of the body, the social environment, and the physical environment whose computation provided inputs needed by evolved decision-making programs in order to generate motivations relevant to choice and action. At their simplest, internal regulatory variables have discrete parameter values (e.g., target person represented as being male or female) or continuous magnitudes (target person is represented as having a kinship index ranging between 0 and some evolutionarily set possible upper bound). Final outputs of different motivational systems about the value of various outcomes need also to be expressed in a common neural currency, so that trade-offs and opportunity costs are incorporated into choice behavior for mutually exclusive choices. That is, ultimately, you choose to deliver the gazelle haunch to your band or to your sick brother in the neighboring village.

Therefore, we expect that the architecture of the human mind is full of evolved variables, existing embedded in evolved circuits, whose function is to store proprietary parameters that are useful for regulating valuation, choice behavior, and prospective computational preparation for future choice-forcing situations. Internal regulatory variables are not explicit concepts, representations, or goal states, but rather registers or indices that acquire their meaning by their location in the architecture—for example from the situational cues that feed into them (e.g., co-residence, perinatal association), and the evolved behavior-controlling and computation-controlling procedures that they in turn feed into (e.g., an estimated kinship index between self and individual *i*, in turn leading to aversion at the prospect of sex with *i*, a family member). 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; how long you have co-resided with an individual; your expected future life span or period of efficacy; how good a friend someone has been to you; the extent of your social support; how durable your social partnerships are expected to be; your association value to others; your own and others ability to inflict costs—aggressive formidabilities; your sexual attractiveness; your status or self-esteem; the status of the coalition you belong to; present energy stores; present health; how advantageous conception would be given your somatic condition and circumstances; the degree to which subsistence requires collective action, and so on.

Most evolutionarily recurrent situations and choice contexts that select for motivational subsystems and associated emotion programs involve the ongoing discovery of information that allows and requires the recomputation of one or more of these variables. Recalibration is, therefore, a major functional component of most emotion programs. *Recalibrational programs* are components of emotion programs such as guilt, gratitude, grief, depression, compassion and shame whose primary function is to carry out such recomputations of internal regulatory variables (Cosmides & Tooby, 2013; Tooby & Cosmides, 1990a, 2008; Tooby et al., 2008), rather than to orchestrate any specific short-run behavioral response. Jealousy, for example, involves several sets of recalibrations (e.g., decrease in estimate of own mate value, decrease in trust in mate, decrease in paternity confidence, increase in the benefit of eliminating the rival).

But information relevant to internal regulatory variables is not equally spread throughout all points in time and throughout all situations. Some situations are information dense, full of informative, ancestrally stable cues that reliably allowed more accurate calibrations of what these variables should be set at (e.g., discovering your child is dead; that your love is returned; your husband has not been faithful; who your father really is; or that someone you know sacrificed a great deal on your behalf). A well-designed architecture would exploit these information-dense situations to update the parameters in the system. This is particularly true since these variables would logically exist in mutually interrelated networks. Among other things, these networks need to exist to internally solve what microeconomists would call pricing problems—computational problems that exist when there a large variety of factors of production with different costs (e.g., different possible mutually constraining courses of action), different possible products (outcomes with different and mutually interacting payoffs), and so on. Externally caused changes in these factors require extensive and spreading recomputation through the motivational system. That is, new information relevant to opportunities, factors of production, pay-offs, and uncertainties will necessarily have to ramify through the system that governs the thousands of decisions a person makes each day. Accidentally spilling your dinner in the dirt may require just a quick pang of annoyance or disappointment to update; at the other extreme, discovering that your husband is dead will require major changes in tens of thousands of decision-variables, trade-offs, and habit-elements distributed throughout the architecture that have been calibrated in the past to assume his presence (Who are you going to turn to when you are in trouble? Who do you share food with? How vigilent do you have to be at night? Who will help care for the children? How much food do you need to forage tomorrow?). For reasons that are theoretically unclear, our brains are organized so that these recalibrational processes often appear to require conscious attention to allow the appropriate reweightings of the associated variables, and are associated with rich and distinct affective feeling states that constitute a major dimension of human experience). These emotions have often appeared puzzling from a functional perspective because the feelings they engender interfere with short-term utilitarian action that an active organism might otherwise be expected to engage in. For example, people voluntarily or involuntarily take time out from obviously productive activities like foraging, eating or sleeping in order to spend time feeling grief, depression, guilt, the onset of romantic love, etc.). The suggestion here is that customary actions and stored dispositions that were productive under one set of circumstances may no longer pay off when the landscape suddenly changes, and people feel less motivated to act. Indeed, people in grief or depression or infatuation show high levels of brain activity; they want to be left alone, without outside demands on their attention. The brain needs to revise large networks of regulatory and decision variables. The cognitive sciences have devoted far more attention to cold cognition—perception, categorization, language processing, object recognition—than to hot cognition. But we suspect that far more of the brain may be organized to computationally implement feeling, valuing, motivation, and emotion—hot cognition. Knowing what is in the world ("objective" knowledge) is generally a far easier computational problem than knowing what to do, and how much to value different courses of action ("subjective" valuation that was fitness-enhacing).

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-Ebesfeldt, 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 provide inputs into internal regulatory variables, and trigger appropriate recalibrations, including affective recalibrations, when certain evolutionarily recognizable situations are encountered. Although these pervasive microprograms construct a great deal of our world, investigations are only beginning into adaptations of this nature.

Welfare Trade-Off Functions and Recalibrational Emotions

Humans, like members of other social species, face a continuous flow of choices that force them either to sacrifice another's welfare to increase their own (selfish choices), or to sacrifice their own welfare to increase the welfare of one or more others (altruistic choices). Evolutionary biologists have identified a number of selection pressures for which (under specified conditions) selection can favor trading off the immediate welfare of the actor in favor of specific others. These include, among others, kin selection (Hamilton, 1964; for evidence of adaptations in humans, see Lieberman, et al, 2007), reciprocation or exchange (Trivers, 1971; for adaptations in humans, see Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2; Krasnow, Cosmides, Pedersen, & Tooby, 2012), the asymmetric war of attrition (Hammerstein & Parker, 1982; for adaptations in humans, see Sell et al., 2009), and externality management and partner choice (Tooby & Cosmides, 1996; see also Noë & Hammerstein, 1994).

For the human mind to solve the adaptive problem of motivating the actor to make the fitness-promoting set of trade-offs between her own welfare and the welfare of another under a given set of conditions, it must have adaptations designed to compute regulatory variables that correspond to the relevant decision parameters (genetic relatedness to this person—kinship index; did the person reciprocate previously?; how much does the other person need this benefit? the formidability index of this person—how much can this person injure me? the association value of this person, etc.) We and our colleagues think these are organized through a human-universal motivational subsystem in the mind which calculates, for each familiar individual, a welfare trade-off function that sets thresholds (welfare trade-off thresholds) partitioning sacrifices the individual is motivated to make on behalf of that familiar other from sacrifices the individual is unwilling to make (Tooby & Cosmides, 2008; Tooby et al., 2008). These thresholds should correspond, to the extent the system is well-engineered and operating under ancestral-like conditions, to sacrifices that were fitness-promoting, and sacrifices that were fitness-reducing. This system also has to make estimates of how valuable the act or resource is not only to the self, but also to the other party.

Each evolutionary theory of social interaction contains within it variables that help specify how fitness-promoting a given welfare trade-off threshold from *i* to *j* would be (the kinship index, how reliable an exchange partner is, how much they value you, the magnitude of benefits they can confer or withhold, etc.). This welfare trade-off threshold (WTT) should be a quasi-stable variable—that is, it should be stable until the system receives new information. When new information about these variables is received, then the welfare trade-off threshold should be recalibrated to the magnitude that is fitness-promoting under the new conditions.

When motivational problems are analyzed in terms of the internal regulatory variables that would be needed to solve them, a pleasing finding is that many hypothesized regulatory variables must be shared by a number of distinct motivational systems with different adaptive functions. For example, both of the independent adaptive problems of how altruistic one should be toward relative *i* and how sexually aversive one should find relative *i* require the same regulatory variable: the kinship index between self and *I* (Lieberman, et al 2007). One regulatory variable—the welfare trade-off threshold—keeps reappearing in a broad variety of independent adaptive motivational problems. For example, it is relevant to kin-directed altruism; to exchange and reciprocation; to mateships and parenting; to aggression-based negotiation; to benefit-based negotiation; to integrating externalities into social relationships; to the management of social valuation, and so on.

Indeed, welfare trade-off thresholds and their recalibration appear to be deeply embedded in the designs of a series of emotion programs: gratitude, anger, guilt, compassion, shame, and contempt, to take leading examples. *Anger* appears to be triggered when another person places too little weight on one's own welfare (their expressed WTT toward the self is too low), given the mind's implicit estimation of what welfare trade-off threshold it can plausibly enforce, given the person's ability to confer or withhold benefits, or inflict or withhold harms (Sell et al., 2009). That is, its function is to bargain for a better WTT of the other to the self (or, if their WTT was correct, but they did not understand how much you valued the service or resource, to reeducate them). In cooperative relationships, the incentivization provided by the angry individual to the other party is a threatened reduction in the angry individual's WTT towards the other: The other will no longer be able to expect the same delivery of benefits through sacrifices unless their own welfare trade-off threshold towards the angry individual is increased to acceptable levels. Guilt functions to recalibrate your own welfare trade-off function towards a specific other when you get new information indicating either that your previous welfare weighting on the other (as expressed behaviorally) was too low, or that your estimation of the value a service or good to the other person was too low—you did not know they cared that much (Tooby & Cosmides, 1990a, 2008). Shame is the recalibrational emotion designed to deal with the threat or actuality of negative information about you reaching others' minds, so that they would devalue you—that is, the adaptive threat is others recalibrating their welfare trade-off threshold toward you downwards in response to new information about you (Sznycer et al., 2012).

Gratitude, correspondingly, is the recalibrational emotion program that is activated in order to (1) increase the welfare trade-off threshold in the self toward another person (2) upon discovery of new information that the association value of the other person to the self is greater than previously estimated. For example, gratitude is triggered when another person trades off their welfare for yours at a much higher level than you had expected: They were unexpectedly kind to you, in a way not justified by your previous treatment of them. Good cooperative relationships are rare, and the higher the mutual welfare trade-off thresholds toward each other can become, (other things being equal) the more efficiently your joint welfare can be promoted. In order to stabilize this potential high level of mutual assistance, it is important to show the act was noticed, attributed to the correct person, appreciated, and led to an increase in the weight you place on your benefactor's welfare. So the emotion program creates communicative intent, and upregulates your welfare trade-off threshold toward the other. This leads to a model of cooperation that is stabilized by the threat of the other's welfare trade-off threshold being downregulated (through the anger program) if your WTT towards the other is too low; and your WTT toward the other being upregulated (through the gratitude program) if their trade-off threshold toward you is higher than yours presently justifies (Lim et al., forthcoming). A second kind of gratitude is not based on exchange, but on association value and externalities (Tooby & Cosmides, 1996). Gratitude is triggered by high valuation toward the other party. The individual may benefit by sacrificing for the welfare of a highly valued person, and the feeling of valuation toward the person is also often called gratitude (i.e., you are grateful your child lives; we are thankful for our blessings). Third, partner choice may be based on the magnititude of positive externalities given off by the potential partner.

RECURRENT DIMENSIONS OF ENVIRONMENTAL AND ORGANISMIC VARIATION SELECT FOR PARAMETRIC COORDINATIVE ADAPTATIONS

When discussing the relationship between behavior genetics and human universal design earlier, we postponed addressing one question: Why should some kinds of individual differences in organisms be organized into a small number of dimensions of variation? Over evolutionary time, many aspects of the world (including environments, organisms, and organism-environment interactions) shift within a evolutionarily recurrent covariant structure. That is, not only are there stable regularities in the world (e.g., gravity, the properties of light, the proportion of oxygen in the atmosphere), and stable regularities in the dimensions along which conditions and phenotypes vary, but there are also higher order covariant relationships in conditions and in phenotypes. For example, regional temperature may shift, but if the temperature increases then humidity increases in a coupled fashion. Moreover, aspects of the environment and internal species organization may systematically co-vary as well. For example, the environment may sometimes select for an increase in species size, and at other times a decrease in species size. For a functionally scaled organism to be maintained if (for example) head size increases, larger vertebrae are required, as are greater neck and torso muscles as well. If all the size dimensions of the organism were under independent genetic control, then for the species to grow (or shrink), selection would have to independently occur in all functionally interrelated traits throughout the organism, slowing down the rate at which the lineage can respond. A mutation in one of these may not even be advantageous without others. The ability of the lineage to shift in size in response to selection would be considerably impeded. Alternating selection for larger and smaller size ought to therefore also select to for welding together formerly independent growth in various traits into a far smaller number of developmental growth fields. This would be favored because then the organism's traits maintain functional allometric interrelationships while undergoing directional selection. That is, mutations will be favored that developmentally link formerly independent traits whose payoffs vary in response to a particular recurrently varying environmental dimension. Thus, genetic correlation among traits is not, as is often thought, a given, but is itself an evolved outcome. Given such genetic and developmental adaptations, expressed phenotypes should track recurrently variable environments with far less lag time, and remain somewhat closer to fitness optima. The covariant structure of conditions, and the covariant structure of the developmental system should evolve to complement each other over evolutionary time.

In the case of allometry, the number of (for example) growth fields ought to be reduced to the number of phenotypic dimensions that benefit by being tuned by selection independently. Quantitative genetic variation that moves designs along these dimensions is expected to have accumulated because adding numerous loci to the determination of a quantitative trait slows loss of variants, maintaining the ability of the lineage to respond more rapidly to reversals in directional selection. This reduces the risk of being stuck at fixation at a ceiling or floor when directional selection reverses again. (Surprisingly, Gould and Lewontin (1979) considered observed allometric relationships to be "constraints" on development and hence constraints on adaptive design itself, rather than adaptations themselves. Not only does simple mechanics support the functional nature of many of these scaling relationships, but selection must be actively maintaining these allometric relationships, because there are always outliers in populations and species that deviate from these relationships that selection could act on; and related species deviate from each other as well.)

Of course, a better design would be to have developmental adaptations that facultatively regulate trait expression so that the expressed phenotype matches the demands of the specific environment the organism matures in (rather than, if the the phenotype was determined by inherited genetic differences, a random sample out of a cross-generationally lagging quantitative genetic distribution). Indeed, many individual differences appear to be due to the operation of calibrational adaptations (muscle increase due to increased exercise; the development of calluses in response to abrasion; increased storage of fat in response to a history of calorie flow variance). Regardless of whether the phenotype is facultatively calibrated or just determined by alleles, the dimensions of variation would be the product of selection. For developmental adaptations for matching local demands, both the dimensions of variation and the regulation of the individual outcome would be an expression of the adaptative system. That is, adaptations would take environmental or organismic condition as input, and produce a facultatively calibrated phenotypic outcome. In contrast, for systems of individual differences caused directly by quantitative genetic variation, the system would be the product of selection, but the particular outcome for an individual would be a random but beneficially biased outcome. A third (and likely) possibility is that given there is genetic noise throughout the system, there should be phenotypic differences (like differences in strength) which species-typical adaptations would respond functionally to—what we have called reactive heritability (Tooby & Cosmides, 1990b)—see discussion of anger, strength, and heritable factors leading to differences in strength below. More generally, if over evolutionary time there is covariation in the independent adaptive demands placed by the environment on the organism (called here a *selective regime*), and a set of independent traits with shifting parameter values that are best responses to these demands, then one expects the evolutionary emergence of parameterized dimensions of covariation in the developmental expression for these formerly independent adaptations. There need be no logical coherence or functional necessity to the set of properties that are phenotypically scaled together: Just that the organism did better when these properties were increased (or decreased) together when an environmental variable (or covariant set of variables) moved together.

Dimensions of personality variation are potential candidates for adaptationist explanations of this kind. Although there ought to be individual differences caused by genetic noise permeating the human neurocomputational architecture, the consistent emergence (for some sets of individual differences) of a far smaller number of robust dimensions in personality suggest that patterns like the five factor model or the HEXACO model (Ashton et al., 2004) might be the product of adaptations to the covariant structure of selective regimes. In exploring this hypothesis, it is always preferable to begin with theoretically well-motivated theories of adaptive function, rather than simply constructing explanations after the fact.

Consider, for example, the hypothesis that the human anger program is a species-typical adaptation that evolved to orchestrate an individual's bargaining behavior in conflicts of interest so that they secure for themselves an advantageous resolution of the conflict (Sell et al., 2009). Power in bargaining comes from the ability to confer or withhold benefits, and the ability to inflict or refrain from inflicting harm. This theory predicts that individual differences in the ability to inflict harm (for example, by upper body strength) and the ability to confer or withhold benefits (for example, by attractiveness) should calibrate how successfully the individual will be able to incentivize better treatment for him- or herself using these advantages. Therefore, upper body strength and attractiveness were predicted to calibrate how readily the individual angers; how entitled they feel to better treatment; how successful they are in resolving conflicts of interest in their favor; (for strength) how useful they think force is in resolving disputes, and so on (these predictions were supported; Sell et al., 2009). This provides a case study of a theoretically derived, empirically supported adaptationist theory of some types of individual differences: Individual differences in inputs (strength, attractiveness, being male, being female) fed into the species-typical negotiative system then outputs advantageously calibrated behaviors and motivational settings. The species-typical adaptation creates a systematic and adaptively calibrated functional relationship between the magnitudes of some individual differences and the magnitudes of others. This is simultaneously consistent with the possibility of high heritability in anger proneness and entitlement (for example), because there is likely to be genetic variation in the factors that produce upper body strength and beauty (e.g., reactive heritability; Tooby & Cosmides, 1990b). These are processed by the organism just as if they were environmentally caused individual differences: The organism must respond adaptively to its own condition, however caused. Hence, a human-universal adaptation (the anger program) can, by taking in heritable inputs (individual differences in strength caused by individual differences in genes), produce functionally calibrated individual differences in anger proneness.

These results only scratch the surface of the potential ramifications of the evolved bargaining system on individual differences. Stronger and more attractive people will have less to fear from interacting with larger numbers of less familiar others, and because of the nature of social markets, will have more to gain. This predicts that there should be a functionally calibrated relationship between strength and attractiveness and the extraversion-introversion dimension. Lukaszewski and Roney (2011) did superb work testing this hypothesis in two studies, along with simultaneously investigating the contribution of specific genetic polymorphisms (the AR CAG repeat polymorphism) to extraversion. They found the relationship between strength and attractiveness and extraversion to be, as they predicted, high (and varying by sex in the expected directions). They also found that the AR CAG polymorphism accounted for some of the variance in extraversion.

So we know that at least some dimensions of personality variation are the product of parametric coordinative adaptations similar to, but more slowly changing than emotional states (e.g., strength persists far longer than a snake appearing in the path). Just as emotion programs involve adaptively coordinating multiple mechanisms within the architecture to the adaptive demands posed by an evolutionarily recurrent short term adaptive problem, personality factor (and especially subfactor) phenotypes are proposed to be parameterized coordinative adaptations to evolutionarily recurrent and longer-lasting selective regimes. That is, they are hypothesized to be best-bet deployments of the mechanisms in the psychological architecture and body, given the developmental adaptations' reading of the individual's location within the covariant structure of adaptive demands posed by the environment and the individual's own condition. These conditions may disappear over the lifespan (e.g., with loss of strength), but might last several generations (e.g., a high-warfare social ecology).

Consider dimensions of the biotic and social ecology: Some environments will have higher rates of predation; some will have higher rates of warfare and/or within-group exploitation; some biotic and social ecologies impose zero-sum relationships between individuals and groups (where resource extraction by some intrinsically decreased resource extraction by others; some environments will be less abundant, or have periodic famines; some will have higher rates of disease; some individuals will be weaker or less attractive or have fewer kin). Optimal settings on anxiety, fear, thresholds for project abandonment in the face of risks or setbacks (i.e., proneness to discouragement or depression), vulnerability by gender, willingness to defer gratification, willingness to trust, rivalrousness, anger and so on should all shift depending on predictable features of the self, the social ecology, and the biotic ecology. These would provide a straightforward functional interpretation for the dimension of neuroticism, and for subfactors in agreeableness or HEXACO's honesty-humility.

This suggests an entirely different framework for research into personality. Instead of starting with empirical relationships of unknown functional significance and unknown ecological validity, it might be useful to (1) make or adopt models of adaptations that (2) need to take as inputs—in order to perform their function—locations along adaptively salient dimensions in ancestral environments and individual conditions, and (3) attempt to identify which adaptations should facultatively shift in response to movement along the same dimensions. By starting with specific adaptations and adaptive problems, and considering how sets of them should jointly vary by individual condition and ecology, one might be able to derive a principled series of empirically validated theories of personality variation. One might work upward, from specific adaptive problems and associated subscales, to larger sets of adaptations with more weakly associated responses to dimensions of ecological or phenotypic variation.

Indeed, there is no reason to attempt to force dimensions of personality variation to be statistically independent. On the contrary, one would expect from first principles that dimensions would derive from how the structure of variation in the environment drives demands for coordinated adaptive responses. There is no reason whatsoever to expect these dimensions of variation to all be orthogonal to each other (e.g., the degree to which social interactions in the social ecology are highly positive-sum might impact both agreeableness and honesty-humility, but neuroticism to a lesser degree). Also, researchers ought to be open to the discovery of major, previously unknown personality dimensions, since existing dimensions were empirically derived overwhelmingly in developed mass societies and abundant environments, rather than by (impossibly) censusing the range of fitness regimes that characterized the ancestral world.

For example, ancestrally, the fitness of individuals or sets of individuals might have been inversely related, unrelated, or positively related. Our normal intuitive expectations of rationality (characterized by a set of social orientations, emotional calibrations, ways of interpreting events, and motivated appetites forged in cooperative and positive sum social ecologies) we suspect is just one parameterization of a coordinative adaptive system capable of creating very different rationalities, including what might be called predatory rationality. In a fitness regime where those who socially interact are typically in intense negative sum or zero sum relationships with each other (because competition is local), win-win strategies are not seen to be best-bet responses; strength and aggressive formidability are highly prized and cultivated; there are no inhibitions on preying on the weaker; audacious predatory attacks and the extermination or humiliation of the antagonist is more attractive to the predatory-minded than to whose who have a cooperative orientation; cooperativeness, paranoia, generosity, revenge-proneness, envy, sensitivity to cues of fitness differentials and status differentials, propensity to exploit—all these are set at surprisingly different levels (Sznycer, et al, forthcoming; Tooby et al, forthcoming).

WHY MIGHT SOME COORDINATIVE CALIBRATIONS BE PARAMETERIZED BY ONTOGENETIC INPUTS, SOME BY QUANTITATIVE GENETIC INHERITANCE, AND SOME BY INHERITED EPIGENETIC INFORMATION?

For aspects of the world where the variance in the situation distribution is small (e.g., the geometry and physics of light), then a single design can uniformly develop (e.g., the visual system) to reliably improve the behavioral output of members of the species. In contrast, where variance in the situation distribution is large, a uniform expressed phenotype will rarely be the best solution. In such cases, fitness is enhanced to the extent that regulatory designs match their phenotypic outputs (e.g., mature early; invest in larger musculature; extend less credit in cultivating cooperative relationships) to the demands of actual conditions (e.g., greater extrinsic mortality; a social ecology of greater competition; a social ecology of lower payoffs to cooperation). In this case, the underlying uniform adaptation lies in the design of the regulatory machinery that parameterizes the expressed phenotypes to the particular situations that it will be facing.

What is key is that there be a principled guidance system whose evolved architecture decides on and then implements those targeted phenotypic modifications that correctly close the gap between the needed phenotype (in a given situation) and the realized phenotype, over the range of situations the species typically faces (Tooby & Cosmides, 1992). Success in the game of matching phenotype to circumstances would be impossible for the architecture unless there existed (1) information that (with computation) systematically predicted which circumstances the organism was going to face, (2) a repertoire of phenotypic alternatives that encoded the phenotypic modifications that would be needed for the organism to develop a high-performing response for those circumstances, and (3) a function that mapped the information about circumstances to the best bet phenotypic alternative. Fortunately for organisms, there are many such systematic relationships that natural selection has exploited to build developmental or facultative adaptations that successfully solve these problems (e.g., skin darkening in response to sun exposure).

The two key questions governing how these systems evolve are (Tooby, 1976; Tooby & Cosmides, 2003; Tooby, Cosmides, & Barrett, 2003):

1. When does the information become available that is needed to decide on the best-bet phenotype?; and,
2. How much lead time does the organism need to generate or construct the best-bet phenotype in time for it to discharge its function?

For the startle reflex, the information needed to protect the eyes does not become available until a few hundred milliseconds before impact; but the system needs around 50 milliseconds to begin to respond. So flinching is linked to rapid looming (and if it is faster than that, you are out of luck). It would make no sense to determine the time of the flinch minutes, hours, days, or years in advance, because time the flinch is needed could not be known to sufficient precision earlier. The best design (where possible) is one in which response selection can be cost-effectively postponed until the environmental demand can be assayed with high reliability (e.g., through perception); and only then is the phenotypic response selected and implemented. To take a more interesting example, some fish species change sex based on their relative size and the death of the dominant local male (Warner, 1989). Humans and other mammals, in contrast, use a genetic sex determination system, presumably because you can build a better woman or man if you start very early in development differentiating the adaptations of the two phenotypes, long before there any is useful information about the adult sex ratio will be at maturation. We have to place our gender bets before we have information (so genetic sex determination flips a coin). For systems involving major tissue differentiation, intricate wiring, and/or long-term nutrient flow (like becoming female or male), construction needs to begin very early. Similarly, to acquire large databases of intricately patterned information (as in acquiring a skill given a sexual division of labor), the human child also may not be able to afford to wait too long. It seems likely that there exist developmental adaptations whose function is to make predictive inferences about the adult fitness regime by sampling self and world early in life, and then using these predictions to calibrate life history (see, e.g., Griskevicius et al., 2011). However, for many traits, early life does not predict the best bet later in life, either because the correlation is too low, or the sample is too brief and unrepresentative to be useful.

What then? It must often be the case that there is a correlation of conditions among adjacent generations in certain respects (e.g., if a mother faces an exceptionally competitive, predatory, or food limited environment, then there is an increased probability that offspring will too—and with some decay function, that subsequent generations will as well). If this information exists, it is available long before development even begins. Such cases would select for coopting non-DNA-based systems of inheritance that could transmit regulatory signals from one or more generations to the next. Although several of these systems have been suspected or known for decades (Cosmides & Tooby, 1981; Tooby, 1976; Tooby et al., 2003), only recently have they become a focus of interest (see Jablonka & Lamb, 2005, for review).

We believe that cross-generational epigenetic effects are not simply accidental byproducts, but that they are evolved adaptations with functions. Most generally, the function of these signals is to parameterize individual development so it goes along pathways that better suit it to the conditions it is likely to face across its life. Given the operation of such systems, individual differences in phenotypes would be partly calibrated from environmental cues during ontogeny (conditions less far away in time should be more diagnostic); partly epigenetically inherited (i.e., frequencies of events summed over multiple generations are going to provide an independent method of improving predictive validity); these systems should cause heightened parent–offspring phenotypic similarity in a way not attributable to DNA-sequence differences. Indeed, these additional systems of inheritance would be selected to use nonDNA-based mechanisms, because DNA sequence transmission is too high fidelity to be useful for tracking rapid changes across multiple generations.

To take a hypothetical example, if the mother is made repeatedly fearful by exposure to predators in an enduringly predator-rich environment, then signals transmitted by methylation, in utero, or in early maternal care to the offspring could be designed to cause it to develop a predator-cautious phenotype usefully in advance of experiencing attacks by local predators. Depending on the temporal structure of the environmental change, these systems could be designed to be passed on signals according to a multigenerational decay function to subsequent generations. That is, by including (say) three generations of information gathering on the frequency of droughts, the system could make better predictions than if it simply used one. Similarly, if the parents (and/or other close lineal ancestors) are food limited, and such a condition often persists across generations, then the offspring would benefit by developing a more frugal metabolism, selecting for an inheritance system that regulates metabolism and life-history across generations. To take a third case, if the parents are in an exceptionally competitive environment, then offspring would benefit by developing a more aggressive, territorial, competitive phenotype, with a greater tendency to emigrate, delayed maturation, and a greater tendency to bias uterine sex ratio toward the more dispersing sex. Not only have many of these empirical relationships been observed (Clark & Galef, 1995; Clark, Karpiuk, & Galef, 1993; Francis, Diorio, Liu, & Meaney, 1999), but they fit elegantly into an evolutionary psychological theory of functional development.

From this theoretical vantage point, cross-generational inheritance effects are not only unsurprising but are instead predicted for traits whose value depends on conditions (a) that frequently endure across more than one generation; or (b) whose probability of occurrence in the upcoming generation can be better estimated using their incidence over multiple recent generations; and (c) that repeatedly cycle along dimensions of variation across generations (Tooby, 1976; Tooby et al., 2003). We predict that such inheritance systems should be be especially prominent in regulating traits that are used starting early in the life cycle (e.g., frugal metabolism, predator-evasion tactics, physiology tuned to local conditions; affiliativeness to coalitions; ecological incidence of positive vs. zero-sum/negative sum interactions) or that are less costly or more effective if the organism begins to develop them prior to directly detecting the conditions it will be facing (e.g., life history trajectory, competitive ability, size reduction and heightened fat stores for better survive food interruptions).

One might also expect that the sex that disperses less would be selected to engage in more epigenetic inheritance, since the correlation of environments of parent and offspring would be higher (Tooby, 1976).

In sum, these systems should evolve and regulate development cross generationally when (1) the dimensional covariation they track is autocorrelated on time scales longer than a generation—i.e., conditions persist long enough in the environment (or in the lineage); (2) when the optimal developmental coordinative response or strategy is dependent on being parameterized by information about the position of the system in its dimensions of variation; (3) for developmental processes such as physiological adjustment or expertise acquisition that need to begin early in development (or at least before the task environment that must be prepared for can be directly perceived). It is important to recognize that not just physical features of the environment (e.g. climate) fit these criteria. Local social ecologies (cooperative hunting; warfare; intensity of individual competition) and biotic ecologies (disease, food abundance, predation) fit these criteria, as do individual heritable somatic features such as strength, reflexes, or genetic impairment.Finally, it bears noting that the methods used by behavior geneticists would tend to misattribute systems of epigenetically regulated individual differences in behavior to genetic differences. Epigenetic states, like the genes they adhere to, are passed down from parents to offspring, and make family members more similar to each other that they would be to nonrelatives. Since these are the sources of data that behavior geneticists use to compute heritability it is indeed possible that a great proportion of the variance in individual behavioral (and somatic) phenotypes that has been attributed to DNA sequences are instead due to epigenetic systems. This would make particular sense for dimensional systems of personality variation which may well be the product of parameterized coordinative adaptations. This would explain why it has been so difficult to track down and identify many DNA sequences that can be shown to explain observed behavioral differences. If epigenetic systems can process information more rapidly that selection acting on quantitative genetic variation (which they can), and if they can efficiently parameterize coordinative adaptations so phenotypes are better matched to ontogenetic conditions (which seems likely), then behavior genetics findings may mostly be behavior epigenetics findings. An examination of the subtly discordant empirical models of heritability across different familial pathways might be more consistent with more rapidly mutating epigenetic transmission. One might predict that traits that turn out to be determined by quantitative genetic variation will be ones where the temporal structure of successive environments cannot be better predicted by sampling over small numbers of generations (that is, environmental autocorrelation is too low to be useful), and the best that can be done is to sample randomly quantitative genetic variation from the broader population.

How could this make sense of dimensions of personality variation? In the first place, one would expect that—just as selection has merged independent traits into allometric growth fields so that the species or population responds to selection more rapidly—selection would have done the same to quantitative settings in sets of psychological adaptations that would benefit from being adjusted together. If, cross-generationally, ecologies shift periodically into conditions where male-male competition is more intense, then all of the parameterizations of psychological adaptations that improve performance in male competition might be linked together so the dial can be turned up or down (leading to parameterizations of, e.g., the shame-honor system). Initially, this would select for systems of quantitative genetic variation in such a dimension. Similarly, where extrinsic mortality is high, this might link fear-anxiety sensitivity to a lower propensity to defer gratification (e.g., showing up in personality psychology as psychoneuroticism). Second, where reliable information exists during development, then cues may parameterize the coactivation of adaptations functionally. Third, where the parameterization bet can be improved by information transmitted from previous generations, epigenetic systems would be one adaptive calibrational system that natural selection could construct. So personality variation would be the functional product of the program architecture of psychological adaptations, as calibrated by cues during development; heritable differences in other parts of the organism (e.g., strength) being functionally responded to by these adaptations (e.g., bargaining power, anger); epigenetic signals sent from past generations, which improve the ability of the developmental system to bet on the best parameterizations of adaptations for the organism; or, failing that, falling back of quantitative genetic variation responding slowly to recent selection on the population.

THE FUTURE OF EVOLUTIONARY PSYCHOLOGY AND A UNIFIED SOCIAL SCIENCE

The amazingly high levels of functional order that are found in evolved systems is so dazzlingly intricate, that originally the machinery of life clearly seemed to be the handiwork of an omniscient transcendental craftsman, who built physical systems far beyond human comprehension. Since Darwin's discovery of how blind causality can push replicating systems uphill against the physical tendency of ordered systems to deteriorate, and the other natural sciences made rapid strides in understanding micro-scale causation, we now have an emerging skeletal framework around which to organize our understanding of life forms. Yet it remains important to recognize that at every scale and level of organization, the structure of biological systems is so labyrinthine and sophisticated that what that we so far understand is merely the nearest edge of a vast space of unseen and uncharted evolved organization.

Therefore, we are only at the beginning of an age of extraordinary discovery, and we should be open to surprising transformations and additions to our knowledge. To judge by the systems (like the visual system) we understand to some limited degree, natural selection produces exquisitely subtle and sophisticated functional complexity that may be likened to a high technology developed by extraterrestrials millions of years ahead of us. The key idea is that natural selection tends to build subtle adaptations out of the enduring structure of the world, the information ecology provided by that structure, and by the computational or regulatory power provided wherever biological structure can be hijacked to provide it. So, we can expect many unexpected and major discoveries about how these are woven together functionally. For example, the DNA and RNA machinery inside individual cells provide all the elements necessary for each cell to function as an assemblage of Turing machines. It seems unlikely that selection would have left this vast computational power untapped, which means that a great deal of computation might be taking place within and not just between neurons. So we expect that the neuron—once regarded as a mere on-off switch—will eventually be found to be something much more like an integrated circuit. Similarly, we expect that the epigenetic machinery underlying cellular differentiation in ordinary development has also been hijacked to transmit and process information across generations through the genetic machinery in gametes and other biologically active molecules provided by parents to offspring. Similarly, the immune system is both capable of recognizing immense numbers of proteins, and simultaneously monitoring various components of health, and so we consider it likely that this has been conscripted as a powerful organ of perception and dietary regulation.

Finally, 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 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 by integrating information from across these systems to manufacture a flexibly deployable array of tools to attack novel problems (e.g., the concept of causation in the object mechanics system provided the core concept that was used to develop modern science).

The evolved architecture of the mind includes specialized mechanisms that permit offline, decoupled cognition. These include metarepresentations, imagery, and a scope syntax, which together can interact with the outputs of domain-specific mechanisms to allow counterfactual and suppositional thinking that is basic to human evaluation, decision-making, and causal reasoning (Cosmides & Tooby, 2000a; Leslie, 1987; Sperber, 1994). Decoupled cognition may have evolved to help calibrate or recalibrate mechanisms through experiencing evaluative feedback from imagined or planned outcomes, infer other people's mental contents, or imagine solutions to social, tool use, or other ancestral problems. But it seems likely that, whether as byproducts 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 four or five decades, as a large scale collaborative program 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. These in turn can then inform models of social interactions and culture, providing a foundation for a more rigorous and integrated social science. It will be a fundamental advance for our species once we have constructed a true, natural science of humanity.

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