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# From Evolution to Adaptations to Behavior

Toward an integrated  
evolutionary psychology

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## COMMENTS

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The lead article in this book is an extensive revision of a chapter originally published in John Dupré's (1987) edited volume on evolution and optimality theory, a collection that dealt mainly with theoretical issues relevant to human evolution. Although the skeleton of this article is drawn from the 1987 paper, most of the material has been revised to fit in with the theme of

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This chapter is based on several recent articles of ours, especially Cosmides and Tooby (1987) and Tooby and Cosmides (1990a, 1990b). As Don Symons is fond of saying, it is difficult to understand

this book. There are new sections on motivation, emotions as they relate to motivations, and why adaptations turn out to be species typical. Material and the ideas in this work provide a framework upon which the subsequent chapters are anchored. Although most of the authors did not specifically develop their chapters to fit in with the lead article, the substance of their works dovetails with the theme of that chapter. In the synopsis and comments that precede each chapter, I attempt to indicate the connections between ideas in the Cosmides and Tooby article and the chapter under discussion.

Although the main thrust of the Cosmides and Tooby chapter is on the value of evolutionary psychology for the understanding of human behavior, their arguments and proposals are equally cogent for the analysis of animal behavior. They regard a crucial link in the causal chain from evolution to behavior to be one involving innate psychological mechanisms. They focus on information-processing systems as prime examples of such mechanisms, and although the possibility was not explicit in that chapter, motivational mechanisms may also be involved in this link. Although information may be the key to the adaptive regulation of behavior, motivational factors are required for the expression of such regulation.

When applied to behavior, natural selection theory is regarded by the authors as more closely allied with the cognitive level of explanation than with any other level of proximate causation. This is because the cognitive level seeks to specify a psychological mechanism's function. Alternatively, one could argue that a motivational level of explanation also involves a specification of the mechanism's function. From a cognitive framework, Cosmides and Tooby propose that for important domains, animals should have evolved specialized learning mechanisms, called *Darwinian algorithms*, that organize experience into adaptively meaningful schemas or frames. When activated by appropriate environmental or proprioceptive information, these innately specified frame builders should focus attention and organize knowledge that will lead to domain-specific inferences, judgments, and choices. One may question what it is that activates this information; this is where motivational factors may enter into the picture.

The goal of evolutionary theory is to define the adaptive problems that or-

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what someone is saying until you know who they are arguing with. These papers were addressed to several distinct research communities: (a) those interested in taking an evolutionary approach to human behavior, but who are unfamiliar with cognitive science; (b) those skeptical of the value or possibility of taking an evolutionary approach to human behavior; and (c) cognitive psychologists, many of whom are unfamiliar with modern evolutionary functionalism. These papers were *not* addressed to behavioral scientists working on animal behavior, and this new chapter, built out of these earlier building blocks, unfortunately preserves the prior orientation. If we had had the time to address this new chapter to animal researchers, many things about it would be different, not least the presumptuous and hectoring tone. Animal researchers are in many respects far in advance of other communities in their focus on adaptive function, proximate mechanisms, and careful experimentation, and we suspect we are running the risk of telling animal researchers a great many things they already know. If so, we offer our apologies in advance. Another obvious flaw is that we did not have the time to bring the literature discussed fully up to date, and so have had to rely on the references that came to hand.

ganisms must be able to solve, while the goal of cognitive psychology is to discover the information-processing mechanisms that have evolved to solve them. It is reasonable to assume that both goals must be considered in the analysis of behavior. However, a more comprehensive analysis could also include motivational processes, unless one argues that an analysis incorporating evolutionary and cognitive mechanisms makes such an enterprise redundant.

The type of evolutionary psychology advocated by Cosmides and Tooby uses the methods of evolutionary biology as well as experimental psychology, particularly cognitive psychology, to study the naturally selected design of psychological mechanisms. Although the Darwinian algorithms are instantiated in neural hardware, Cosmides and Tooby argue that it is not necessary to understand the details of this hardware in order to analyze evolutionary adaptations. Hence the naturally selected design of the "mind" could be studied at the information-processing level. However, Crawford (1993) suggests that these mechanisms "come along with the computer": They are hard wired. If these algorithms were shaped by natural selection, then they can be changed only by natural selection, and then only through changes in DNA, which codes for enzymes that direct the construction of proteins. Such an inference implies that adaptive mechanisms may be analyzed at the biochemical or neural level. This type of analysis is presented in many of the subsequent chapters in this volume. However, Cosmides and Tooby assume that natural selection has fixed the alleles at loci mediating the development of Darwinian algorithms; thus, these adaptations can be studied without reference to DNA, biochemistry, or neuroanatomy. In addition to physiological analysis, then, most of the chapters in this book analyze motivational phenomena in terms of psychological mechanisms of the sort proposed by Cosmides and Tooby.

### References

- Crawford, C. B. (1993). The future of sociobiology: Counting babies or studying proximate mechanisms? *Trends in Ecology and Evolution*, 8, 183-186.
- Dupre, J. (1987). *The latest on the best: Essays on evolution and optimality*. Cambridge, MA: MIT Press.

### INTRODUCTION

Popular wisdom has it that arguments against new ideas in science typically pass through three characteristic stages, from

1. "It's not true," to
2. "Well, it may be true, but it's not important," to
3. "It's true and it's important, but it's not new—we knew it all along."

If the current state of the behavioral sciences is any indication, then the application of evolutionary biology to the understanding of human behavior has entered the "it's true but not important" stage.

Yet evolutionary biology is important for understanding human behavior, and not everyone knows it—in fact, those most involved in the scientific investigation of "human nature" are generally the most unaware of its implications. We shall argue that the reluctance of many behavioral scientists to appreciate or take advantage of the richness of the evolutionary approach is a direct consequence of a widespread tendency to overlook a crucial link in the causal chain from evolution to behavior: the level of evolved psychological mechanisms, functionally analyzed as adaptations, and described as information-processing systems. This level is pivotal, because it describes the mechanisms that actually link the evolutionary process to manifest behavior. It is these mechanisms that evolve over generations; within any single generation it is these mechanisms that, in interaction with environmental input, generate manifest behavior. The causal link between evolution and behavior is made through the psychological mechanism.

Efforts that skip this step in the evolutionary analysis of behavior, as valuable as they may be in other ways, have contributed to an erroneous caricature of the evolutionary approach to behavior as offering nothing more than post hoc compilations of correspondences between behavior and loosely reinterpreted evolutionary theory. But a rejection of the evolutionary approach based on such an incomplete and misleading characterization of its nature and valid possibilities is mistaken: As we shall discuss, the search for order in human behavior requires the application of the emerging principles of evolutionary psychology. We shall argue that an approach drawn from evolutionary psychology, consistently applied, can repair many of the deficiencies that have hampered progress in the social and behavioral sciences.

### **EVOLUTIONARY THEORY DOES NOT PREDICT INVARIANCE OR OPTIMALITY IN THE MANIFEST BEHAVIOR OF DIFFERENT INDIVIDUALS**

Sciences prosper when researchers discover the level of analysis appropriate for describing and investigating their particular subject: when researchers discover the level where invariance emerges, the level of underlying order. What is confusion, noise, or random variation at one level resolves itself into systematic patterns upon the discovery of the level of analysis suited to the phenomena under study. The lack of success the behavioral sciences have had since their founding has been explained either by the claim that no such science is possible (e.g., human complexity intrinsically transcends any attempt to discover fundamental patterns) or by the view we share, that progress has been slow because scientific efforts have not yet, for the most part, been framed using concepts and organizing principles suitable to the phenomena under study. Can such an appropriate level of inquiry be

found for a science of human behavior? Because humans are the product of the evolutionary process, the explanation for their characteristics must be sought in the evolutionary process: For a science of human behavior, the level of underlying order is to be sought in an evolutionary approach.

Using evolution as an informing concept is not enough, however. During the formative period of modern behavioral ecology in the 1970s, many researchers thought that evolutionary biology would revolutionize research in human behavior; this conviction spread after the publication of E. O. Wilson's *Sociobiology* drew widespread attention to the dramatic advances that were taking place in the application of evolution to behavior. Many thought that evolutionary theory would reveal the level of underlying order, that the apparent variation in human behavior would resolve itself into systematic patterns, that invariant relationships would be identified, and that a true social science would emerge. After more than a decade, however, this is a revolution still waiting to happen.

We suggest that the reason progress has been slow is that in the rush to apply evolutionary insights to a science of human behavior, many researchers have made a conceptual "wrong turn," leaving a gap in the evolutionary approach that has limited its effectiveness. This wrong turn has consisted of attempting to apply evolutionary theory directly to the level of manifest behavior, rather than using it as a heuristic guide for the discovery of evolved psychological mechanisms, that is, psychological adaptations.

The attempt to discover evolutionary structure directly in the behavioral level has created a series of difficulties, of which two should serve to illustrate: (a) the use of behaviorally uniform categories or behavioral universality as the signature of evolution, encouraging (among other things) forced typological approaches, and (b) using the "optimality" of manifest behavior (or the lack of it) as the measure of the success (or failure) of the evolutionary paradigm. The belief that evolutionarily structured behavior must be invariant across individuals, or inflexible in expression, has invited a brute force, typological approach to variation in, for example, cross-cultural studies and primate behavior (e.g., humans are monogamous, Hanuman langurs live in one-male groups, etc.). All too often, the researcher would take the observed variation, average it, and typify the species or group by that average (see Tooby & DeVore, 1987, for a more extensive discussion of this problem). The variation itself is considered noise, or an embarrassment to be explained away. Those social scientists skeptical that biology had anything to offer to an understanding of human behavior would dwell on the extraordinary complexity of human behavior, and its enormous and engaging variety, and counterpose this richness to the clear explanatory inadequacy of what they considered to be naive and reductive typological characterizations. Second, it is easy to catalog behaviors that appear absurdly nonoptimal, if the standard is fitness-maximization under modern conditions. Many have dismissed evolutionary approaches as weak or inapplicable to humans on the basis of this rich behavioral variation and the prevalence of obviously maladaptive behavior. Fitness-maximization does not seem to be the underlying logic that governs much of modern human behavior.

If these are the grounds for dismissing evolutionary approaches, however, they are poor ones. The theory of natural selection itself predicts that the manifest behavior of different individuals will vary enormously under many conditions according to principles hard to describe using behaviorally defined categories. Furthermore, it deductively implies that an individual's behavior will often appear far from "optimal," as, for example, when optimality is defined without respect to the individual's social environment, or without respect to the statistical distribution of situations to which a species has been exposed over its evolutionary history. In fact, difficulties emerge generally whenever optimality as a standard is applied to expressed behavior and not to the quality of the design of the mechanisms that generate it. A few of the reasons why looking for invariants or optimality at the behavioral level leads to difficulties are summarized by Tooby and DeVore (1987), in their discussion of hominid behavioral evolution. They include the following:

1. The fitness interests<sup>1</sup> of different individuals are often in conflict; in fact, much of modern evolutionary theory analyzes the conflicting fitness interests of different categories of individuals (e.g., self vs. kin [Hamilton, 1964], parent vs. offspring [Trivers, 1974], male vs. female [Trivers, 1972]) or even of different subsets of the genome within a single individual (Cosmides & Tooby, 1981). An interaction between individuals (or different traits within an individual) whose fitness interests conflict cannot, in principle, produce an outcome that is optimal for both individuals. The outcome will either be optimal for one party but not the other, or, very commonly, the conflict will result in an outcome that is nonoptimal for both.

2. Therefore, larger patterns of social behavior are not necessarily—or even usually—optimal for any individual or group of individuals. Instead, they will be the emergent result of the operation of evolved mechanisms situated in these interacting individuals—mechanisms selected to act in ways that reflect these con-

<sup>1</sup>The term *interests*, or *fitness interests* is a useful, but often misleading one, because it links a formal evolutionary concept to an implicit folk psychological concept, *self-interest*, without sufficiently flagging the profound differences between the two. Self-interest tends to be used to refer to conditions an individual desires to bring about because they reflect what he or she values, for whatever reason. On the other hand, the concept of *fitness interest* defines the set of potential outcomes for a specified set of genes in a specific organism that would maximally promote the replication of those genes. Because different subsets of genes in an individual are maximally replicated under different conditions, an individual cannot have a single unified fitness "interest" (see Cosmides & Tooby, 1981). Instead, only traits as defined by their genetic basis can. More significantly, selection acts on the basis of the statistical frequency of conditions, so fitness "interests" on any one occasion are important only to the extent that they reflect a large recurring class of situations that will correspondingly select for adaptations to address them. An even more serious pitfall involved in using the term *fitness interests* is that it invites teleological reasoning. Instead of viewing organisms as collections of mechanisms whose design features were selected for because under ancestral conditions they imposed behavioral outcomes that tended to correspond to fitness promotion, organisms are viewed as agents pursuing fitness as a goal. Organisms are adaptation executors, and not fitness pursuers. For many purposes, this distinction may not seem major, but in considering certain problems, it assumes major importance (see Tooby & Cosmides, 1990b, for discussion).

flicting fitness interests. Frequently, therefore, the behavior of an individual cannot be understood in isolation; its behavior will be the mutual result of adaptations selected to promote its own interests and the counterstrategies produced by the adaptations of others.

3. Organisms are selected to have adaptations that respond to features of their individual situation and social circumstances, and not simply to their local habitat ("the environment"). For example, an individual's best behavioral strategy may depend on its size, its health, its aggressive formidability, its facility at accruing resources, or the number of sibs it can rely on for support. This means that organisms will be selected to be facultative strategists (where appropriate) rather than inflexibly committed to the same behavior or morphology. Consequently, individuals equipped with the same species-typical set of evolved psychological adaptations will often manifest different behaviors in response to the different information they derive from assessing their own abilities, resources, and circumstances. Individual differences, behavioral variation, or "personality differences" that arise from exposing the same species-typical architecture and developmental programs to environmental differences relate individual differences to evolved functional design in a straightforward way. For this reason, much of the study of behavioral variation can be recast as the study of the underlying (and usually) universal psychological adaptations that generate variation in response to circumstantial input (see Tooby & Cosmides, 1990a).<sup>2</sup>

4. For certain social and reproductive behaviors, the favored strategy will depend on the distribution of other behaviors in the population, leading to complexly interactive dynamics. The prevailing analytic tool for dealing with this is game theory and evolutionarily stable strategies (Axelrod & Hamilton, 1981; Maynard Smith, 1982; Maynard Smith & Price, 1973). In such situations, selection can produce psychological mechanisms that are sensitive to information indicating the distribution of relevant behaviors in the local population and then respond accordingly. For example, under stable frequency-dependent conditions, behavioral strategies may be enduringly variable from individual to individual.

5. To be selected for, a trait need not be advantageous under every conceivable potential circumstance. It need only be of benefit *on balance*, against the

<sup>2</sup>Those researchers who are interested in applying an evolutionary perspective to individual differences can investigate the adaptive design of evolved species-typical mechanisms by seeing whether different manifest outputs are adaptively tuned to their corresponding environmental input: Does the algorithm that relates input to output show evidence of complex adaptive design? On the other hand, individual differences caused by genetic differences between individuals have to be analyzed differently and will generally be noise from a functional standpoint (Tooby & Cosmides, 1990a). Methodologically, the criterion of complex, functional design tends to segregate the two components: Complex adaptations will tend to be species-typical, or nearly so in species with a relatively open breeding structure, and so genetic differences will usually tend to be nonfunctional perturbations in species-typical (or at least population-typical) functional design.

statistical distribution of conditions encountered during its evolutionary history. This means that the frequency with which it was advantageous, scaled by the magnitude of the advantage, outweighed the frequency of disadvantage scaled by the cost. Thus, selection for a trait or mechanism has always occurred against a background statistical distribution of ancestral environmental conditions and cannot be understood when abstracted from this background. Nothing in the logic of selection precludes the emergence of designs that generate maladaptive choices under a subset of conditions, and even the most perfected, "optimal" strategy may involve producing many maladaptive acts as a by-product of producing advantageous behavior.

6. Therefore, natural selection cannot be expected to produce behavioral responses that maximize fitness under every imaginable circumstance. The situational specificity of an adaptation depends on the selective history of encountering similar situations (for discussion see Tooby & Cosmides, 1990b). The degree of situational adaptation manifested by individuals will be a matter of (a) how frequent in the species' evolutionary history that situation has been, (b) how long (in phylogenetic terms) it has been recurring, and (c) how large its fitness consequences are. Organisms will be well adapted to common, important situations, reasonably adapted to common less important situations and less common highly important situations, but not adapted to uncommon, unimportant situations.

7. The recognition that adaptive specializations have been shaped by the statistical features of ancestral environments is especially important in the study of human behavior. Our species spent over 99% of its evolutionary history as hunter-gatherers in Pleistocene environments. Human psychological mechanisms should be adapted to those environments, and not necessarily to the twentieth-century industrialized world. The rapid technological and cultural changes of the last several thousand years have created many situations, both important and unimportant, that would have been uncommon (or nonexistent) in Pleistocene conditions. Evolutionary researchers ought not to be surprised when evolutionarily unprecedented environmental inputs yield maladaptive behavior. Our ability to walk fails us hopelessly when we are chased off a cliff.

For these and other reasons, the search for scientifically analyzable order on the level of manifest behavior will meet with very limited success. Certain ingredients in behaviorism were, of course, a healthy and much needed antidote to attempts early in this century to base psychology on introspection and experientially derived descriptions and phenomena. Even cognitive psychologists would have to admit that in an important sense, we're all behaviorists now. But using behavioral data to test theories is not the same thing as restricting oneself to behavioral descriptive categories, and the marked emphasis by evolutionarily oriented researchers on behavior and behavioral categories has handicapped the integration of evolutionary biology with modern postbehaviorist psychology. Many (though not

all) psychologists have attempted to move ahead to describe the mechanisms responsible for behavior, whereas many (though not all) of the evolutionary community have remained focused on behavior. Trying to locate optimality in behavior (a weakness too often indulged by the evolutionarily oriented), or trying to use behavioral uniformity or inflexibility as particularly diagnostic of the "biological" (a weakness often characteristic of those hostile to evolutionary approaches) are both symptoms of a misdirected focus on behavior. These symptomatic problems are alleviated when attention turns from behavior to the mechanisms that generate behavior. Viewed from such a perspective, neither behavioral variation nor frequent departures from behavioral "optimality" are an embarrassment to an evolutionary perspective, but they are instead predictions of evolutionary theory, as applied to psychological mechanisms, viewed as adaptations.

When the appropriate level of analysis is found, variation becomes fuel in the search for order: Instead of averaging out variation, one looks for systematic relations among the different varying elements. What is variable at one level manifests order—that is, invariance—at another. Instead of lamenting the complex variations in human behavior, researchers can use patterns in behavioral variation positively, as clues to the nature of the psychological mechanisms that produce behavior. We think that the appropriate level is the analysis of psychological mechanisms, described in information-processing terms. Before turning to this, however, we need to address the controversy concerning whether evolution optimally designs organisms (Gould & Lewontin, 1979; Lewontin, 1978). After all, if natural selection is only a weak force, and organisms are random agglomerations of properties, why try to gain insights through attempting to analyze their functional designs?

## NOT OPTIMALITY BUT WELL-ORGANIZED DESIGN

The entire tortured debate on evolution and optimality founders on a central indeterminacy in its formulation that renders the controversy more of a distraction than an addition to our understanding of the utility of evolutionary approaches (see the papers in Dupré, 1987; Lewontin, 1978; Maynard Smith, 1978). The problem is that *optimality* is an undefined term unless all of the constraints on the problem to be solved are defined in advance. Is a given wing the best possible design for the new McDonnell-Douglas commuter jet, representing an optimal trade-off of all of the design requirements? That depends on what one considers to be possible, and what the design requirements are: How much money can be spent on the manufacturing phase? What materials are available to be used? Can the rest of the fuselage be modified as well, or are only the wings allowed to vary? What is the maximum load the plane has to carry, and the average load? How turbulent are the weather conditions it should be designed to withstand? What are the temperature conditions? Is passenger comfort a factor? And so on. Biological problems are almost always far too complex for every constraint on the possible to be identified and for every design requirement to be determined, which prevents *optimality* from

having any determinable meaning. To pick only one issue, no biologist ever has a complete historical record of the statistical properties of the range of environments a species evolved in: How then could one tell if the resulting design was optimally engineered for that range of environments?

Instead, of course, most evolutionary biologists tend to use the term *optimality* for far more modest purposes. Biologists have understood for the better part of a century that the evolutionary process includes random or function-blind elements such as mutation, drift, environmental change, developmental constraints, linkage, and so on, that act to reduce the match between evolved design and adaptive requirements. Despite these processes, organisms nevertheless display a high degree of complex functional organization, and biologists need a way to describe and investigate it. The sole known scientific explanation for this complex organic functionality is, of course, natural selection, which is the only component of the evolutionary process that is not blind to function. Selection constructs adaptations through a relentless hill-climbing process driven by the positive feedback of better replicating design features (Dawkins, 1986; see also Pinker & Bloom, 1990, for an excellent discussion of these issues; and Tooby & Cosmides, 1990b).

If one is to understand the functional dimension of organisms, one needs a way of referring to the solution of adaptive problems, however well or poorly grasped they may be by biologists in any specific case. Where adaptive problems can be modeled to some reasonable approximation and some of the most significant constraints identified, *optimality* is simply the name used to refer to the privileged part of the state space where one would expect the hill-climbing process to end up given static conditions and enough time. It allows the researcher to interpret organic structure in the light of functional analysis. Given that researchers have defined a specific problem, and identified a specific set of constraints as the only ones that will be considered in the analysis, then they can report how near or far the design of the organism happens to be from what their model identifies as optimal. The hotly contested question, How close to or far from optimality are organisms in general? is not only unknowable in practice, but in fact meaningless, because there is no privileged class of defined constraints and factors that could be applied to such an analysis.

Thus, one cannot meaningfully ask how close or far from perfection an organism's design is because there is no unique and logically coherent standard of perfection. But the question can be rephrased so that one asks, instead, How improbably functional is an adaptation in solving an adaptive problem? This question is answerable because although there is no unique and privileged standard of perfection, there are identifiable and usable standards for the other end of the scale, lack of perfection, or lack of functionality. Chance conditions unshaped by functionally organizing forces can be used as the entropic floor, so to speak, and this benchmark allows the biologist to recognize adaptations by virtue of how far biological organization departs from chance in the direction of incorporating features that contribute to the solution of known adaptive problems. Given a definition of an adaptive problem (e.g., vision, resistance to infection, providing nour-

ishment to offspring, predator evasion), functionality can be gauged by how improbably far from chance or some known prior condition an organ, mechanism, or adaptation goes toward manifesting functional properties (e.g., how much better is the eye for vision than is undifferentiated fetal tissue). By these criteria, many biological structures appear to be extremely well designed: The vertebrate eye or immune system may not be perfect (whatever that could mean), but they each involve sets of intricately coordinated elements that bring about otherwise improbable functionally exacting outcomes. Because this correspondence between evolved structures and functional requirements is astronomically unlikely to have come about by chance, we can confidently conclude that these functional systems were constructed by selection, the only evolutionary force not blind to function. Complex adaptations can be identified by the improbable degree of functional organization they show for solving an adaptive problem (Dawkins, 1986; Thornhill, 1991; Tooby & Cosmides, 1990b; Williams, 1966, 1985; see also Pinker & Bloom, 1990).

By using improbability of functional design as a standard rather than optimality, one can assess how widespread functional design is. For example, if designs are no better than chance, then chance rearrangements of their components will be as good as their present arrangements. Even on a simple biochemical level, of course, this is absurd. If one runs through the long list of complex organic molecules used in mammalian physiology, such as myoglobin, hemoglobin, ATP, RNA, DNA, serotonin, cysteine, and so on, and did the experiment of transmuting any one of these chemicals throughout the body into water, a nontoxic substance, the result would be devastating, and in most cases the organism would die. A number of other tests against random reorganization of components (in the brain, in physiology, in metabolic pathways, and so on) can be considered, all showing a marked interdependence of elements, combining to produce improbably good solutions to adaptive problems. The philosophically minded may wish to debate whether such a state of affairs represents perfection, or whether steel tubing might not be better than capillaries, but mammalian physiology and biochemistry inarguably reflect a well-coordinated functional design, whose parts fit together in an exceedingly intricate and exceedingly improbable mesh to bring about functional outcomes. To ignore the functional organization in organic structures is to miss the most important thing about them, and the primary thing that makes them intelligible.

So, instead of looking at the behavioral level, and trying to analyze whether it is optimal (fitness-maximizing, rational, or whatever), we suggest that researchers might more productively attempt to discover and map the structure of the psychological mechanisms that generate behavior. Where functional analysis is relevant and helpful in this enterprise (and we think it is often indispensable), the standard that should be used is the standard of improbably good design (based on the consequences of a mechanism's design features in conditions that resemble the species' environment of evolutionary adaptedness), rather than on the vague or indeterminate standard of optimality or perfection. Of course, assessing good design depends on carefully defining adaptive problems, an issue we will deal with later

in the chapter, after discussing the relationship between behavior, mechanisms, and evolution.

## FROM EVOLUTION TO PSYCHOLOGICAL DESIGN TO BEHAVIOR

To speak of natural selection as selecting for “behaviors” is a convenient shorthand, but it is misleading usage (for discussion, see Symons, 1989, 1992). The error is worth belaboring, because the failure to appreciate it has delayed the fruitful application of evolutionary theory to human behavior by years. When used too casually, this shorthand misleads because it obscures the most important level of proximate causation: the psychological mechanism.

Natural selection cannot select for behavior *per se*; it can only select for genes that guide developmental programs to construct mechanisms that produce behavior. There is nothing special about behavior in this regard; the same can be said, for example, of digestion. Natural selection can only spread rearrangements of patterns in molecules of DNA; these rearrangements have effects, and it is because they have these effects that they are selected for or not. Through this chain, natural selection gives us teeth, salivary amylase, a peristaltic esophagus, an acid-filled stomach, an absorptive colon: mechanisms that produce digestion. The operation of these mechanisms causes certain molecules to be extracted from plant and animal tissues and incorporated into our own tissues: an effect that we call digestion. Natural selection gives us food-processing machinery, and the operation of this machinery results in digestion, which is an effect of the functioning of mechanisms.

Behavior, like digestion, is an effect of the functioning of mechanisms. Natural selection can give you a reflex arc, and the functioning of this arc causes an effect: Your leg swings when your knee is tapped. But this effect cannot occur in the absence of a mechanism for producing it. Behavior cannot occur *sui generis*; behavior is an effect produced by a causal system: proximately, by psychological mechanisms. Although researchers would acknowledge these points as patently obvious, in practice, many simply methodologically leapfrog this level, with many unfortunate consequences.

One of the resulting confusions has to do with the nature of selection and its relationship to behavior in a given situation. Selection cannot directly “see” an individual organism in a specific situation and cause behavior to be adaptively tailored to the functional requirements imposed by the situation. Selection is a statistical process acting across generations, which “evaluates” the aggregate performance of alternative designs over the long run. This performance evaluation not only sums up design performance over the thousands of particular situations encountered by an individual over an individual lifetime, but indeed the trillions of situations encountered by millions of individuals over many generations. Because single events cannot cause designs to spread throughout the species, and be-

cause selection cannot anticipate unique events that an organism will encounter in the future, there are no adaptations specialized for single instances. Consequently, there is no way for behavior to be made specifically fitness-maximizing for each individual situation the organism encounters. More generally, design properties that are too particular in the conditions they address, and hence improve performance only in very rarely encountered situations, will be selected for only weakly—or not at all, if the frequency of their benefit does not offset their metabolic cost. Equally, the more common a particular type of situation, the more such situations will select for adaptations specialized to address them. Thus, the accumulating design of organisms over evolutionary time encounters individual events as instances of large recurrent classes: Individual events are in effect lumped into classes large enough to make it “worthwhile” to build situationally specific adaptations to deal with them. Because natural selection shapes mechanisms, and mechanisms in turn generate behavior, individual situations are treated by mechanisms only as instances of evolutionarily recurrent classes.

Thus, an adaptation is more than a mere collection of phenotypic properties, which, in a particular individual on a particular occasion, happen to have the effect of enhancing reproduction—winning the lottery, wearing parkas in Alaska, and irrigating fields are not adaptations. An adaptation must be a recurrent design that reappears across generations and across individuals (caused by the developmental interaction between stable features of the world and the relevant set of genes). For selection (as opposed to chance) to have manufactured a structure, the evolved design must have had repeated encounters with recurrent properties of the world. Those encounters constitute the history of selection for that design. If characteristics emerge uniquely every generation, or haphazardly from individual to individual, then selection cannot organize them.

This means that the phenotype of an individual organism must be carefully distinguished from the design of the phenotype. Natural selection manufactures design, defined as those properties that are stable across all individuals of the same genotype. As Williams says, “the central biological problem is not survival as such, but design for survival” (Williams, 1966, p. 159). The individual phenotype manifests innumerable transient properties, which disappear with the death of the phenotype or change idiosyncratically over the life span. Although some of these transient properties may promote reproduction, they are chance-produced beneficial effects, not adaptations (Williams, 1966). An important confusion (common in the evolutionary community) is the failure to distinguish between transient properties, which cannot be adaptations, and design properties, which can (Symons, 1989, 1992; Tooby & Cosmides, 1990b).

Thus, to understand the role of selection in behavior, one needs a description of the cross-generationally stable design of the phenotype: It is this that (potentially) has a functional explanation; it is this set of adaptations or mechanisms that brings about a correspondence between the adaptive demands of a situation and the functional patterns in behavior. The task of describing phenotypic design involves the process of redescribing the phenotypically variable and the transitory

in terms of the recurrent and the stable. This process of description is key: By choosing the wrong categories, everything about the organism can seem variable and transitory, to the extent that *plasticity* or *behavioral variability* can be seen as the single dominant property of an organism. By choosing the right categories—adaptationist categories—an immensely intricate species-typical architecture appears, with some limited additional layers of frequency-dependent or population-specific design as well. Discovering the underlying recurrent characteristics that generate the surface phenotypic variability is essential to the discovery of adaptations. To recover adaptive design out of behavioral or morphological observations, one needs to determine what is variable and what is invariant across individuals: Only the recurrent is a candidate adaptation. Adaptations may be variable in expression but must be uniform in design (Tooby & Cosmides, 1990a, 1990b). Because (holding genotype constant) behavior and physiology often do vary, underlying design will often have to be described in terms of conditional rules such as developmental programs or decision-making mechanisms. We have argued elsewhere for the importance of distinguishing adaptive design from its phenotypic expression (Tooby & Cosmides, 1990b). This is simply the equivalent in biological terms of distinguishing the mechanisms regulating behavior from behavior itself (Cosmides & Tooby, 1987; Tooby & Cosmides, 1989a).

By bypassing the level of mechanisms and focusing on behavior, one can easily lose sight of the distinction between the transient or variable and the recurring and stable. This has led to a research tradition of attempting to explain behavior in individual situations as tailored fitness-maximizing responses to the unique nature of each situation (e.g., How is Susan increasing her fitness by salting her eggs? Rather than: What is the nature of human salt preference mechanisms and how did they mesh with the physiological requirements for salt and the opportunities to procure salt in the Pleistocene?). Ironically, by focusing on behavior and not sifting for the stable features of the phenotype, many evolutionarily oriented researchers have thrown away one of the tools necessary to recognizing adaptations (Symons, 1989, 1992; Tooby & Cosmides, 1990b).

The motivation to finesse the level of mechanisms and move directly from evolution to behavior has two sources. The first is the rapid growth, over the last several decades, in the sophistication and power of modern evolutionary theory, especially in implications for behavior (Dawkins, 1976, 1982; Hamilton, 1964; Krebs & Davies, 1984; Maynard Smith, 1982; Trivers, 1972; Williams, 1966; Wilson, 1975). For many in the evolutionary community, the advances in evolutionary theory were so intoxicating and looked so powerful that it seemed as if the study of proximate mechanisms was unnecessary to build a science of behavior, and that their study could be postponed to some future date, as a kind of dotting of *i*'s and crossing of *t*'s.

Second, the widespread desire to avoid being entangled in the proximate level stems, in many cases, from the belief that the exploration of mechanisms means the exploration of the neurophysiological bases of behavior, a task that is genuinely thorny and arduous. Also, to be fair, at the present state of knowledge,

neuroscience seems limited to exploring only relatively simple kinds of behaviors, offering no purchase on many issues of interest, such as—to take a thoroughly random sample of topics interesting to behavioral ecologists—mate choice, reciprocation, assistance toward relatives, communication, inbreeding avoidance, small-group dynamics, habitat selection, foraging, and so on. Both of these reasons are misguided, however; evolutionary theory cannot be turned into a theory of psychology without building models of the adaptations (i.e., the proximate mechanisms) involved, and building models of proximate mechanisms need not always involve neurophysiological descriptions. There exists an alternative approach to the study of psychological mechanisms that can be pursued without waiting decades for the requisite advances in neuroscience. This is the cognitive analysis of psychological mechanisms, and it serves, among other things, to bridge the gap between neuroscience and evolutionary biology.

## LEVELS OF EXPLANATION: EVOLUTIONARY, COGNITIVE, AND NEUROPHYSIOLOGICAL

*Evolutionary psychology* relates evolutionary explanations in terms of adaptive function to psychological explanations in terms of proximate mechanisms (see, e.g., Buss, 1987, 1989; Cosmides, 1989; Cosmides & Tooby, 1987, 1989; Crawford, Smith, & Krebs, 1987; Daly & Wilson, 1981, 1988; Erickson & Zenone, 1976; Galef, 1990; Gallistel, 1990; Rozin & Schull, 1988; Shepard, 1984, 1987; Sherry & Schacter, 1987; Staddon, 1988; Symons, 1979, 1987, 1992; Tooby, 1985; Tooby & Cosmides, 1989a, 1990a, 1990b; and many others). The correct characterization of adaptive strategies gives precise meaning to the concept of function for proximate mechanisms. Reciprocally, a detailed analysis of the proximate mechanisms of a species gives rich insight into the past selective pressures that have acted to create and organize them. Psychological mechanisms constitute the missing causal link between evolutionary theory and behavior. Evolutionary theory frequently appears to lack predictive and explanatory value because many researchers skip this crucial predictive and explanatory level. Yet it is the proximate mechanisms that cause behavior that promise to reveal the level of underlying order for a science of behavior.

The psychology of an organism consists of the total set of proximate mechanisms that cause behavior. Natural selection, acting over evolutionary time, shapes these mechanisms so that the behavior of the organism correlates to some degree with its fitness. In the lifetime of any particular animal, however, it is the proximate mechanisms that actually cause behavior—not natural selection. If these proximate mechanisms can be understood, behavior can be predicted more exactly; understanding the fitness-promoting strategies studied by evolutionary theorists allows only approximate prediction. Behavior correlates exactly with proximate mechanisms, but only approximately with the fitness-promoting strategies that shaped those mechanisms. But in what descriptive language should proximate



mechanisms be described? Although the description of behavior in terms of adaptive strategies plays an important role in evolutionary theory and modeling (see, e.g., Maynard Smith, 1982), it cannot be used for describing proximate mechanisms: Other than a few impoverished terms such as *facultative* and *obligate*, it lacks a vocabulary and method for linking the results of evolutionary modeling to proximate mechanisms.

Psychological mechanisms, themselves, can be studied on different descriptive and explanatory levels. Most evolutionarily informed studies of proximate mechanisms have described psychological mechanisms in terms of their physiological or neurophysiological underpinnings, finding, for example, that birth spacing is mediated by lactation, which generates prolactin that suppresses ovulation; that testosterone levels change with shifts in dominance, thereby affecting agonistic behavior; or that vision is subserved by an array of retinotopic maps. Neurophysiological descriptions are certainly a valid and important descriptive level, and no account of proximate mechanisms can be considered complete until the neurophysiological dimension has been worked out.

But adaptationist approaches, so far, have made only limited contributions to the investigation of neurophysiology (Tooby & Cosmides, 1989b), and vice versa. This is because, in many cases, the descriptive languages that are convenient for describing evolutionary processes and their consequences and the descriptive languages that are convenient for neuroscientists are too far apart to be intelligibly related. More important, unless you know that a particular information-processing system exists and what its function is, it is very difficult to discover its physiological underpinnings. Likewise, it is difficult to discover a mechanism simply by trying to piece together the welter of neuroscientific results. Who would look for the neurophysiological mechanisms responsible for vision unless they first knew that the eyes existed and that their function is to gather information from light striking the retina? Until researchers have an inventory of the functions of the human mind—that is, the collection of information-processing tasks the brain evolved to solve—neuroscientific approaches will be limited to an unguided empiricism that gropes its way among a forest of incredibly complex phenomena, without any way of knowing how to group results so that larger scale functional systems can be recognized.

Although presently very valuable (and ultimately indispensable), neurophysiological studies by themselves do not usually address a crucial *functional* level of explanation, a level that describes what a mechanism does, rather than how it does it. As a result, both neuroscientists and evolutionarily oriented researchers into human behavior can profit by addressing the central level of proximate causation, needed to tie the other levels together: the cognitive level, analyzed in adaptationist terms. The investigation of adaptations, described as information-processing systems, will prove illuminating to both evolutionary biology and neuroscience. Moreover, both groups seem to be converging from different directions on this level—witness, for example, the growth of cognitive neuroscience as well as of mechanism-oriented behavioral ecology and evolutionary psychology. We will

argue that the cognitive level provides the previously missing common ground and conceptual tools necessary to forge richly informative relations between evolutionary biology and psychology, and then between an evolutionarily informed psychology and neuroscience.

The cognitive level is, of course, the characterization of psychological mechanisms in terms of their information-processing structure. This approach dovetails smoothly with evolution, because in the adaptive regulation of behavior, information is key. Behavior is not randomly emitted; it is elicited by information, which is gleaned from the organism's external environment, and, proprioceptively, from its internal states. Natural selection provided animals with information-processing machinery to produce behavior, just as it gave them food-processing machinery to produce digestion. This machinery selects—and frequently seeks—particular information from the environment; it manipulates such information according to structured procedures, extracts inferences from it, and stores some of it in memory in altered form; the machinery's output is used to make mental models, to inform other parts of the system, and to instruct the motor neurons responsible for behavior. Thus, behavior is one output of our information-processing machinery. Empirically, information-processing mechanisms can be explored because behavioral output differs with informational input; the information-processing machinery that maps informational input onto behavioral output is a psychological mechanism. In cognitive psychology, the term *mind* refers to an information-processing description of the operation of the brain—a description that, among other things, maps informational input onto behavioral output (Block, 1980; Fodor, 1981).

For these reasons, we suggest that the central organizing fact for psychology is that *the evolutionary function of the brain is to process information in ways that lead to adaptive behavior*. All adaptive behavior is predicated on adaptive thought: An animal must process information from its environment in ways that lead to fit behaviors while excluding unfit behaviors. Accordingly, characterizing proximate mechanisms in terms of their information-processing structure is not an arbitrary choice, but rather the most natural and appropriate course for psychologists to take. An information-processing framework provides a descriptive language excellently suited to capture the evolved design of proximate mechanisms. The cognitive level of explanation describes psychological mechanisms in functional terms, as programs that process information.

Traditionally, ethologists have—in effect—studied very simple cognitive programs: A newborn herring gull has a cognitive program that defines a red dot on the end of a beak as salient information from the environment, and that causes the newborn to peck at the red dot upon perceiving it. Its mother has a cognitive program that defines pecking at her red dot as salient information from her environment, and that causes her to regurgitate food into the newborn's mouth when she perceives its pecks.

Note that the descriptions of these simple programs are entirely in terms of the functional relationships among different pieces of information; they describe two simple information-processing systems. Naturally, these programs are instan-

tiated in neurological machinery, and it will be informative to work out eventually what the neural substrate is. But knowledge of how such programs are implemented physically is separate from an understanding of these programs as information-processing systems. Each is a separate kind of knowledge describing different features of the situation (see, for example, Block, 1980 or Fodor, 1981, for more discussion of the nature of cognitive explanations). Presumably, one could build a silicon-based robot that would produce the same behavioral output in response to the same informational input as the herring gull's do. The robot's cognitive programs would maintain the same functional relationships among pieces of information and therefore be identical (on an information-processing level) to the cognitive programs of the herring gull. The robot's "neural" hardware, however, would be totally different. The specification of a cognitive program constitutes a complete description of an important level of proximate causation, independent of any knowledge of the physiological mechanisms by which the program is instantiated. Through information-processing descriptions of the structure of mechanisms one can develop an understanding of the workings of the mind on a functional level; in subsequent research, this can be tied to a complementary description of how such mechanisms are neurobiologically implemented (see Pylyshyn, 1984, and Marr, 1982, for a discussion of functional versus neurobiological levels of description; see also Cosmides, Tooby, & Barkow, 1992, for their relationship to other kinds of description).

*When applied to behavior, the theory of natural selection is more closely allied with the cognitive level of explanation than with any other level of proximate causation. This is because the cognitive level seeks to specify a psychological mechanism's function, and the theory of natural selection is a theory about function.* The theory of natural selection specifies how an organism should respond to different kinds of information from its environment. It defines adaptive information-processing problems that the organism must have some means of solving. Cognitive programs are solutions to information-processing problems.

An evolutionary explanation for behavior or structure explains why a behavior pattern or structure was selected for (that is, why it was functional) or, in the absence of a selectionist explanation, how it otherwise evolved. An evolutionary approach to understanding the cognitive level of proximate causation asks, What kind of programming must an organism have if it is to extract and process information about its environment in a way that will lead to adaptive behavior? How does the organism use information from its environment to compute what constitutes the "right" behavior at the right place and the right time (Staddon, 1987)? A cognitive explanation provides an information-processing description of how the proximate mechanisms involved operate. And a neurophysiological explanation provides a description of how the cognitive mechanism or computational design is physically implemented in the organism. Each level illuminates different issues, offers and requires distinct arrays of tools for research, and has its unique set of relationships and links to the other levels. We think each level is indispensable and emphasize the cognitive level and its links to the evolutionary level pri-

marily because these relationships are, for too many research communities, a missing link on the path from evolution to behavior. Disregarding this level has proved crippling to many research efforts.

To understand these arguments it is important to keep clearly in mind what we mean by the cognitive or information processing level. Like all words, *cognitive* is used to mean many different things. For example, many psychologists use it in a narrow sense, to distinguish it as a kind of mental process distinct from others such as *emotion* or *motivation*—that is, as something that corresponds more or less to the folk concept of *thinking* while in a calm frame of mind. Many also associate it with so-called "higher" tasks, such as chess playing, mathematics, puzzle solving, and so on (of course, these were absent from our evolutionary history, and hence our ability to do them is an accidental by-product of evolved capacities). This characterization also builds on stereotypes; many cognitive psychologists study just these things: difficult, artificial tasks requiring deliberation and the application of culturally elaborated skills.

We are using the word *cognitive* in a completely unrelated sense, not as referring to any specific type of mental process, but rather as referring to a level of analysis and a descriptive language that can be applied to every psychological or indeed developmental process. Thus, one can have cognitive models of every aspect of an emotion (including associated physiological changes), of the regulation of breathing, or even of the development of calluses on hands (e.g., information derived from processes in the epidermal layer is procedurally evaluated to regulate whether growth rates should be increased and stabilized at a new thickness). Thus, *cognitive* in this usage is not a description of a type of process, but a method by which any regulatory process may be described—that is, in terms of functional relationships among units of information or contingent events. (One could even phrase it more abstractly: It is an explicit model of how a complexly contingent causal system interacts with a complexly contingent environment to produce predictable outcomes where both system and environment can temporally change.) Just as mathematics is an indispensable language for describing certain scientific models, procedural languages (of, for example, the kind used in computer programming) are precise descriptive languages for capturing how complex systems functionally interact with complex environments. Moreover, for reasons we will discuss, not only is this level of description methodologically convenient, but it allows the researcher to express in what is arguably the most appropriate and accurate terms the relationship between natural selection and the design of psychological mechanisms.

## EVOLUTION, FUNCTION, AND THE COGNITIVE LEVEL

It is nearly impossible to discover how a psychological mechanism processes information unless one knows what its function is, what it was "designed" or se-

lected to do. Trying to map out a cognitive program without knowing its function is like attempting to understand a computer program by examining it in machine language, without knowing whether it is for editing text, reconstructing three-dimensional images of the body from magnetic resonance data, or launching a space shuttle. It is perhaps conceivable that an inspired programmer may finally figure it out, but not probable, given that the programmer would not know what parts of the world its elements corresponded to, what was being regulated, what constituted successful or failing outcomes, and so on. If, on the other hand, the programmer knows that the program she is trying to map out is a text editor, she can begin by looking for a way of loading text, or for a command that will delete a word, or for a procedure that will move a whole paragraph. It is far easier to open up a black box and understand its architecture if one knows what it was designed to do.

Recognizing this, a number of cognitive scientists, such as Chomsky, Shepard, Fodor, and Marr, have argued that the best way to understand any mechanism, either mental or physical, is to first ask what its purpose is, what problem it was designed to solve (e.g., Chomsky, 1975; Fodor, 1983; Marr & Nishihara, 1978; Shepard, 1981).

This is exactly the question that evolutionary theory allows one to address. It allows one to pinpoint the kinds of problems the human mind was “designed” (that is, selected) to solve and consequently should be very good at solving. And although it cannot tell one the exact structure of the cognitive programs that solve these problems, it can suggest what design features they are likely to have. It allows one to develop a *computational theory* for that problem domain: a theory specifying the problem and therefore what functional characteristics a mechanism capable of solving that problem must have (Marr, 1982; Marr & Nishihara, 1978).

Many cognitive psychologists assume that the human mind is a general-purpose computer with domain-general, content-independent processes (Cosmides, 1989). From an evolutionary point of view, this is a highly implausible and unparsimonious assumption, and, in fact, one logically impossible to sustain. For virtually any vertebrate species (at least), there are domains of activity for which the evolutionarily appropriate information-processing strategy is complex, and deviations from this strategy result in large fitness costs. An organism that relied on the vagaries of, for example, trial-and-error learning for such domains would be at a severe selective disadvantage (see also Shepard, 1981). The more general and content-independent the process, the more alternatives there are to compute, and combinatorial explosion fatally cripples such systems (Cosmides, 1989; Cosmides & Tooby, 1987; Tooby & Cosmides, 1989a, 1990b).

Instead, for such domains, animal species should have evolved *Darwinian algorithms*—specialized mechanisms that organize experience into adaptively meaningful schemas or frames (Cosmides, 1985, 1989; Cosmides & Tooby, 1987). When activated by appropriate environmental or proprioceptive information, these innately specified “frame-builders” should focus attention, organize perception and

memory, and call up specialized procedural knowledge that will lead to domain appropriate inferences, judgments, and choices. Like Chomsky’s language acquisition device, these inference procedures allow the organism to “go beyond the information given” in experience—to behave adaptively even in the face of incomplete or degraded information (Bruner, 1973). Such mechanisms constitute phylogenetically supplied structure designed to supply what is absent from the information available through experience, so that the two in concert can accomplish what either alone could not: the adaptive regulation of behavior.

What we call *Darwinian algorithms* have been called (sometimes with related but somewhat distinct meanings) *adaptive specializations* by Rozin (1976) *modules* by Fodor (1983), *cognitive competences* or *mental organs* by Chomsky (1975), or, more generally, psychological or cognitive adaptations. In our view such evolved mechanisms have two defining characteristics: (1) They are (usually) most usefully described on the cognitive level of proximate causation, and (2) they are evolved adaptations. We have used the term *Darwinian algorithm* when addressing certain research communities because it emphasizes both characteristics.

There are many domains of human and nonhuman activity that should have Darwinian algorithms associated with them. Aggressive threat, mate choice, sexual behavior, parenting, parent–offspring conflict, friendship, kinship, resource accrual, resource distribution, disease avoidance, predator avoidance, and social exchange are but a few. The dynamics of natural selection shape the patterns of behavior that can evolve in such domains and therefore provide insights into the structure of the cognitive programs that produce these patterns.

## COMPLEX ADAPTIVE PROBLEMS SHOULD BE DEFINED IN COMPUTATIONAL THEORIES

The signal lesson lurking beneath the surface of modern evolutionary biology is that adaptive behavior requires the solution of many information-processing problems that are highly complex—far more complex than is commonly supposed. The cognitive programs that allow the newborn herring gull to gain sustenance from its mother are relatively simple: They directly connect the perception of an environmental cue with an adaptively appropriate behavioral response. But not all adaptive problems are so easily solved, and many complex adaptive problems can be solved only by complex cognitive programs.

Discovering the structure of complex cognitive programs requires a great deal of theoretical guidance. A series of hunt-and-peck experiments may uncover a few simple cognitive programs, but it is unlikely that a research program that is blind to function will ever uncover the structure of a complex information-processing system, such as the human mind—or even an insect mind. Simple combinatorial explosion assures this result. If you analogize the structure of a psychological mechanism to a computer program, or try to write a computer program that

duplicates what a psychological mechanism does, one will rapidly discover that it takes a large number of programming instructions to accomplish what even a simple psychological mechanism does. Complex psychological mechanisms might be likened to computer programs with thousands or even hundreds of thousands of lines of code. If the researcher has nothing to assist her aside from a pure faith in empiricism, the sheer number of alternative possibilities will almost always defeat the discovery of the architecture of the more complex psychological mechanisms. Without some valid expectations about what is to be found guiding the design of experiments and the strategy of investigation, psychological research will fail to capture or even to detect the complex psychological mechanisms responsible for regulating many rich domains of behavior. Thus, it has been no accident that the more theory-agnostic empirical research programs have tended to defend the position that all psychological phenomena can be explained by invoking a few, simple, general principles. Because of their research strategy, they could not have discovered more.

So, if theoretical guidance is necessary for a successful research program, what form should it take? In his pioneering studies of visual perception, David Marr argued that *computational theories* of each information-processing problem must be developed before progress can be made in experimentally investigating the cognitive programs that solve them (e.g., Marr, 1982; Marr & Nishihara, 1978). A computational theory is a task analysis; it specifies the nature of an information-processing problem. It does this by incorporating “constraints on the way the world is structured—constraints that provide sufficient information to allow the processing to succeed” (Marr & Nishihara, 1978, p. 41). A computational theory is an answer to the question, What must happen if a particular function is to be accomplished?

For example, the information-processing problem that Marr wanted to understand was how an organism reconstructs three-dimensional objects in the world from a two-dimensional retinal display. As you walk around a table with a square top, for example, light reflected from the tabletop hits your retina, projecting upon it a two-dimensional trapezoid of changing dimensions. Yet you do not perceive an ever-deforming, two-dimensional trapezoid. Instead, your cognitive programs use these data to construct a “percept” of a stable, three-dimensional, square tabletop.

To understand how we compute solid objects from data like these, Marr and his colleagues first examined relevant constraints and relationships that exist in the world, like the reflectant properties of surfaces. They considered the discovery of such constraints the “critical act” in formulating a theory of this computation, because these constraints must somehow be used by and embodied in any cognitive mechanism capable of solving this problem (Marr, 1982; Marr & Nishihara, 1978). Marr called the specification of such constraints, together with their deductive implications, a computational theory of an information-processing problem.

Natural selection, in a particular ecological situation, defines and constitutes “valid constraints on the way the world is structured,” and therefore can be used

to create computational theories of adaptive information-processing problems. Such constraints can be drawn from the structure of selection pressures, from the statistical structure of ancestral environments, or from their combination. For example, cognitive programs that are designed to regulate the disposition of benefits on kin will be selected to conform to the [cost to self in terms of forgone reproduction < (benefit to kin member in terms of enhanced reproduction) weighted by (the probability of sharing a gene at a random locus identical by descent with the kin member)] constraint of kin selection theory (Hamilton, 1964). The more a cognitive program violates this constraint, the more it is selected against. Equally, the more closely a cognitive program instantiates this constraint, the more strongly it will be selected for. This constraint is inherent in the dynamics of natural selection, and thus should apply to any species from any habitat at any time during evolutionary history. For various reasons, members of a species may be precluded from conferring benefits on their relatives, but if they regularly do, then understanding this constraint will help to discover the structure of the cognitive programs responsible.

The production of behavior that respects constraints imposed by the evolutionary process is a cognitive program’s *adaptive function*—that is, it was the reason it was selected for. In other words, the production of behavior that more closely conforms to favored adaptive strategies is the criterion by which alternative designs for cognitive programs are filtered, so that the program (out of the alternatives that appear) that most closely implements these design requirements is the one that most often spreads through the population to become a species-typical trait.

The specification of constraints imposed by the evolutionary process—the specification of an adaptive function—does not, in itself, constitute a complete computational theory. These constraints merely define what counts as adaptive behavior. Cognitive programs are the means by which behavior—adaptive or otherwise—is produced. The important question for a computational theory to address is: What kind of cognitive programs must an organism have if it is to produce behavior that meets these adaptive criteria?

Natural selection theorists do not usually think of their theories as defining information-processing problems, yet this is precisely what they do. For example, kin selection theory raises and answers questions such as, How would a well-designed psychological architecture treat the information that individual *X* is its brother, and how should it regulate decisions about helping him? How should its assessment of the cost to it of helping its brother, versus the benefit to the brother of receiving help, affect the decision? Should the information that *Y* is a cousin alter the decision on the allocation of assistance between its newborn and its brother? In general, how should a good design treat information about relatedness and the costs and benefits of actions on individuals in order to improve its decision making?

As these questions show, an organism’s behavior cannot fall within the bounds of the constraints imposed by the evolutionary process unless it is guided

by cognitive programs that can solve certain information-processing problems that are very specific. To confer benefits on kin in accordance with the constraints of kin selection theory, the organism must have cognitive programs that allow it to extract certain specific information from its environment: Who are its relatives? Which kin are close and which distant? What are the costs and benefits of an action to itself and to its kin? The organism's behavior will be random with respect to the constraints of kin selection theory unless (a) it has some means of extracting information relevant to these questions from its environment, and (b) it has well-defined decision rules that use this information in ways that instantiate the theory's constraints. A cognitive system can generate adaptive behavior only if it can perform specific information-processing tasks such as these.

The fact that any organism capable of conferring benefits on its kin must have cognitive programs capable of solving these information-processing problems does not imply that different species will solve each problem via the same cognitive program. There are many reasons why such programs may differ. For example, different environmental cues may have different reliabilities and accessibilities for different species. Moreover, each species occupies a different ecological niche, and hence the value of particular actions will differ across species: The cognitive programs of a baboon will assign a different value to social grooming than will the cognitive programs of a whale. But cognitive programs that perform the same function in different species may differ in more profound ways. For example, the cognitive programs for recognizing kin might operate through phenotype matching in one species, but through early imprinting in another species (Holmes, 1983). Both programs will accomplish the same important adaptive function. Yet they will embody radically different information-processing procedures, and they will process different information from the environment. For this and other reasons, in constructing a computational theory or task analysis, it is usually not enough simply to know the relevant evolutionary theory.

### **COMPUTATIONAL THEORIES SHOULD CONTAIN AN ANALYSIS OF THE STRUCTURE OF THE ENVIRONMENT**

Usually, in building a task analysis, understanding the relevant evolutionary theory is a necessary starting point. This may involve both a basic familiarity with models of the evolutionary process (including such things as definitions of fitness, selection, adaptation, genes, the role of stochastic factors) and the available models of the selection pressures relevant to the problem under study (such as descriptions of the selectional principles governing such domains as kin-directed altruism, reciprocation, sexual recombination, and sexual selection). But such models will rarely be sufficient, in themselves, to build a model of the task facing the organism. Almost always, it will be necessary to analyze how these principles were manifested as a species-specific array of selection pressures, refracted

through the specific ecological, social, genetic, phylogenetic, and informational circumstances experienced along a given species' evolutionary history (Tooby & Cosmides, 1990b; Tooby & DeVore, 1987). This is the characterization of ancestral conditions, sometimes referred to as the *environment of evolutionary adaptedness* or EEA.

Selection acts so that the properties of evolved psychological and developmental mechanisms tend to mesh together with the recurrent structure of the world so that their interaction produces functional outcomes. Theories of selection pressures provide definitions of what counts as a functional outcome. And because of this mesh between environment and mechanism, an analysis of the recurrent structure of the world—or that portion of it relevant to the problem or problem-solving mechanism—is a rich source of information about the mechanism. For this reason, the analysis of the structure of the ancestral world is a critical part of the construction of a computational theory.

Often, of course, because most of the properties of the world stay the same, the modern world provides a satisfactory laboratory for the analysis of the structure of many ancestral environments and conditions. For example, in understanding how color vision works, or in studying the ontogeny and regulation of bipedal locomotion, the relevant parts of the modern world provide an adequate model. For many animal species studied in the field, modern conditions are doubtless as representative of these species' EEA as anything additional inference could contrive. For humans, however, many aspects of the world have changed dramatically, and so the reconstruction of hominid ancestral conditions is more necessary. The structure of cues and events in modern suburban environments, for example, is not a good model for how predators impinged on our hominid ancestors, and in such cases models of ancestral conditions must be reconstructed from the array of available sources (see Tooby & Cosmides, 1990b; Tooby & DeVore, 1987, for discussion). And as informative as evolutionary theory is, it cannot substitute for a model of ancestral conditions. Evolutionary theory cannot tell you such things as how often individual variance in foraging success was substantially greater than band-wide variance, important in understanding the psychology of hominid reciprocation (Cosmides & Tooby, 1992); nor can it tell you the mean ecological frequency of hominid-menacing predators, how far off they can be spotted in various landscapes, or what types of naturally occurring refuges were typically available (see Orians & Heerwagen, 1992, for a discussion of human habitat selection).

In developing such descriptions, it is important to remember that the environment of evolutionary adaptedness (EEA) is not a place or a habitat, or even a time period. Rather, it is a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and fitness-consequences. For example, how often was the cue of a snake-shape linked to a venomous bite? The properties used to build the composite are selected out of all possible environmental properties as those that actually interacted with the existing design of the organism during the period of evolution. Whether or not these things are observable by the organism,

they can be “known” (that is, reflected) in the structure of the mechanisms because natural selection will select those mutant designs whose structure conforms to these otherwise unobservable features of the world. Thus, organisms can act far more appropriately than can be explained by “experience,” through the action of specialized mechanisms that reflect the structure of evolutionarily recurrent situations. Domain-general mechanisms, which must reflect equally the structure of every possible situation, can thus supply no specialized guidance in the solution of particular families of problems.

Thus, statistical and structural regularities define the EEA. The conditions that characterize the EEA are usefully decomposed into a constellation of specific environmental regularities that had impact on fitness and that endured long enough to work evolutionary change on the design of an adaptation. For convenience, we have called these statistical regularities *invariances*. Invariances need not be conditions that were absolutely unwavering, although many, such as the properties of light or chemical reactions, were. Rather, an invariance is a single descriptive construct, calculated from the point of view of a selected adaptation or design of a given genotype at a given point of time. No matter how variable conditions were, they left a systematically structured average impact on the design, and that systematic impact needs to be coherently characterized in terms of the statistical and structural regularities that constituted the selection pressure responsible. These invariances can be described as sets of conditionals of any degree of complexity, from the very simple (e.g., the temperature was always greater than freezing) to a two-valued statistical construct (e.g., the temperature had a mean of 31.2C and standard deviation of 8.1), to any degree of conditional and structural complexity that is reflected in the adaptation (e.g., predation on kangaroo rats by shrikes is 17.6% more likely during a cloudless full moon than during a new moon during the first 60 days after the winter solstice if one exhibits adult male ranging patterns). Thus, as a composite, it is necessarily “uniform” in the abstract sense, although that uniform description may involve the detailed characterization of any degree of environmental variability—which may, in fact, have selected for mechanisms that can track such variability and respond accordingly.

Of course, from the point of view of an adaptation or mechanism, important parts of the structure of the world include not just the external physical, biological, and social environment, but also the regularities presented by the other mechanisms in the brain and body, as well as in others’ minds and bodies. The lungs are part of the EEA to the heart, and cross-cultural regularities in emotional expression or grammatical structure are part of the EEA to face interpretation mechanisms and the language acquisition device, respectively.

Thus, a computational theory of an adaptive problem is defined by the recurrent structure of the world, the structure of selection pressures, and how these combine to create demands for certain kinds of information processing. These must be directly reflected in the design of any mechanism that solves the adaptive problem, when it is expressed in information-processing terms. As we shall discuss, such computational theories are invaluable as heuristic guides for psycho-

logical research. This is true even though there may be many possible information-processing structures that could potentially solve the adaptive problem. (Moreover one of course needs evidence that the organism actually does regularly solve the adaptive problem under EEA-like conditions more often than would be expected by chance.) In the likely event that there is more than one possible mechanism design that could solve the adaptive problem, then experimentation is needed to discover which design the organism actually has.

## THE IMPORTANCE OF COMPUTATIONAL THEORIES

A computational theory is a description of the specific information-processing problems and subtasks regularly encountered by a species during its evolutionary history, including the ecological, informational, social, and physiological conditions in which the problems were regularly embedded. These problems should be catalogued and made explicit, for they are the building blocks of psychological theories. There are two reasons why this is so.

The first is obvious. These computational theories supply a great deal of the theoretical guidance necessary to construct experiments and studies, saving the researcher from groping along on blind empiricism alone. They provide suggestions about the kinds of mechanisms an organism is likely to have, about the kinds of information from the environment a mechanism subserving a given function will be monitoring, about what the goals of the mechanism are (that is, what functional outcomes it is designed to produce), and so on. Knowing, for example, that an organism—because of its ancestral social environment and inclusive fitness theory—must have some means of distinguishing kin from nonkin may not uniquely determine the structure of a cognitive program, but it does help narrow hypotheses. The cognitive program responsible must be sensitive to environmental cues that correlate with kin but do not correlate with nonkin. In most cases, very few cues from the species’ environment of evolutionary adaptedness will be sufficiently reliable or accessible, and the researcher can in due course discover which are used by the organism’s cognitive programs. Discovering which cues are used will illuminate other of the program’s information-processing procedures: Early exposure suggests an imprinting process, whereas facial similarity suggests phenotype matching procedures. Step by step, deduction by deduction, experiment by experiment, the cognitive programs responsible for kin recognition can be mapped. In the meantime, the researcher who is blind to function will not even be looking for a program that guides kin recognition, let alone figure out which environmental stimuli it monitors, what representations are constructed from these cues, and what procedures act on these representations to regulate behavior.

The second reason why a fully elaborated computational theory is useful is less obvious, but perhaps equally important. The computational theory allows a test of adequacy that any proposed psychological theory must be able to pass. The test is this: *Is the hypothesized system of cognitive programs powerful enough to*

realize the computational theory? That is, is the proposed mechanism capable of solving the adaptive problem? This allows one to rule out certain theoretical approaches without having to test each one of an infinitely expandable list of hypotheses. Many can be eliminated simply by seriously inquiring what computational architecture is being assumed by the hypothesis and analyzing its performance capabilities.

Any proposed cognitive system must be powerful enough to produce adaptive behaviors while *not* simultaneously producing too burdensome a set of maladaptive behaviors. (One can equally well use this test with a less controversial standard: Any hypothesized mechanism advanced as being responsible for certain behavioral phenomena must be powerful enough to produce the observed behavior while *not* simultaneously producing too large a set of behaviors that are not observed.) Not just any cognitive program will do: Our cognitive programs must be constructed in such a way that they somehow lead to the adaptive results specified by evolutionary theory on the basis of the information available. This test of computational sufficiency (see Pinker, 1979, 1984, 1989) or solvability (see Tooby & Cosmides, 1992) often allows researchers to eliminate whole categories of hypotheses. In particular, current research in cognitive psychology and artificial intelligence suggests that many of the general-purpose learning theories that are widely accepted by social and behavioral scientists are not powerful enough to solve even artificially simplified computational problems, let alone the complex information-processing problems regularly imposed by selective forces operating over evolutionary time. Because of the survival of extant species into the present, we know for a fact that they can successfully solve an entire suite of problems necessary to reproduction, and we need to develop theories of the architecture of the information-processing mechanisms—the cognitive adaptations—that allow them to do it.

Researchers involved in empirical debates are all too conscious of the fact that there are an inexhaustible set of alternative hypotheses that can be invented by the ingenious to avoid having to dispose of cherished intellectual positions. Therefore, the empirical testing of each hypothesis in turn from this potentially inexhaustible set cannot by itself be a practical research strategy. One must be able to integrate these empirical findings with other sources of valid inference to be able to draw larger and more interesting conclusions. For psychologists, the analysis of computational performance is one approach to doing this.

## THE ANALYSIS OF COMPUTATIONAL PERFORMANCE

Thirty years ago, Noam Chomsky inaugurated a new era in cognitive psychology when he explored psychological questions by analyzing the capacities of well-specified computational systems (Chomsky, 1957, 1959). He was attempting to evaluate the adequacy of behaviorist accounts of language, such as Skinner's *Ver-*

*bal Behavior* (1957). To perform such an analysis, Chomsky needed models descriptions of two components of the question. The first model essentially corresponded to what Marr subsequently called a computational theory—a task analysis defining the problem to be solved, which specifies things such as what counts as success, what are the conditions under which the candidate mechanisms must perform, what information is available to the mechanism, and so on. Language was an excellent choice for such a test of behaviorist accounts of psychological phenomena, because language—particularly syntax—involved complex but clearly specifiable patterns of behavior. Within this domain, one could define without ambiguity and with great exactitude criteria for recognizing what behavioral patterns humans could and did routinely produce and, therefore, what any mechanism hypothesized to account for this behavior had to produce as well. (In these early analyses, Chomsky focused not on the issue of whether conditioning processes could account for the initial learning of language, but on the far more restricted question of whether behaviorist mechanisms, having complete access to grammatical rules in whatever fashion they could be represented within the system, could be made to produce as output a defined subset of grammatical English sentences.)

The second description or model Chomsky needed was a formalization, computational or information-processing terms, of the hypothesis being tested—in this case, stimulus-response (S-R) learning theory. This marked an important departure from the then widespread practice, still endemic in psychology, of failing to specify the computational architecture of the mechanism being proposed, and instead simply positing a black box described solely in terms of its assumed ability to produce certain consequences. To actually see whether a mechanism is capable of solving a problem, one needs a well-specified description of the information-processing structure of the mechanism being hypothesized. Whenever a hypothesis about a psychological mechanism is being advanced, one needs to carefully investigate what computational architecture for the mechanism is being assumed or is entailed. In this case, Chomsky (following others) settled on finite state devices as natural implementations of Hullian learners, along with some other background assumptions necessary for the analysis to proceed.

The third step in such an analysis is to apply the model of the mechanism to the model of the task and thereby explore how the proposed computational system performs, given the conditions and the goals as defined in the computational theory. What parts, if any, of the problem can the hypothesized mechanism solve? What are the strengths and weaknesses of the mechanism's performance? What information or environmental conditions does the mechanism need to be present in order to succeed? Does it require infinite memory, or immensely long periods of computation, or certain specific cues? Of course, the most basic question is, Is the design of the candidate mechanism computationally sufficient to solve the problem (Pinker, 1979, 1984, 1989)? That is, can the computational system solve the problem? If not, of course, the hypothesis can be ruled out.

In this case, for Chomsky's general analysis, the computational theory was the grammar of the English language as it is known by ordinary speakers: all the

grammatical sentences of English, such as “the child seems asleep,” but not the indefinitely larger set of ungrammatical sentences, such as “the child seems to sleeping.” The information-processing problem to be solved was the production or recognition of sentences that conformed to this set. The question Chomsky addressed was: Can these sentences be produced by a finite state device similar to the mechanisms proposed by the behaviorists of the time? By using this approach, and related, more informal arguments, Chomsky was able to persuade many psychologists and linguists that finite state devices (and their incarnation in psychology, behaviorist theories of conditioning) were not tenable explanations for human language competence because they were incapable of solving many language-related tasks in any plausible fashion. Given realistic assumptions about memory, the total number of states allowable to the system, and similar considerations, the general-purpose, S-R learning mechanisms proposed by the behaviorists were not powerful enough to generate the set of sentences that conformed to English grammar—that is, they were not powerful enough to produce many grammatical sentences while simultaneously precluding the production of large classes of ungrammatical sentences. As one part of this analysis, Chomsky formally demonstrated that finite state grammars were completely incapable of generating a well-defined subset of grammatical English sentences. Perhaps more significant for subsequent research, Chomsky sketched other difficulties this family of mechanisms had in dealing with issues of acquisition, generalization, phonology, semantics, and so on. By performing this kind of analysis, Chomsky showed that S-R learning mechanisms could not plausibly account for the fact that people speak English. Given, of course, that some people do speak English, his computational analysis allowed Chomsky to eliminate a whole class of hypotheses for language competence: those invoking mechanisms that embody finite state grammars (Chomsky, 1957, 1959). Moreover, if there was at least one class of behaviors that could not be accounted for by standard conditioning theory, then S-R mechanisms could not therefore be a complete account of the mind. This pointed to the possibility that there might be a large array of mental mechanisms that did not operate according to S-R principles.

Chomsky’s pioneering analysis, despite some controversy about the generality of its conclusions, initiated a vigorous research program into the cognitive mechanisms underlying the human language faculty. Subsequently, many researchers have worked on constructing nonbehaviorist psychological theories of language that include more powerful and more specialized computational machinery (for a review, see Wanner & Gleitman, 1982). Of more lasting significance, however, is the general strategy that continues to guide some of this work: Many psycholinguists and linguists have tended to pursue their research through (a) the empirical investigation of natural language production, acquisition, perception, and comprehension, including the structure it displays and the computational problems it poses, and (b) the use of this knowledge to construct increasingly sophisticated models of various components of the human language faculty, often through exploring and evaluating the performance of the various candidate

computational mechanisms hypothesized to manage these tasks. By approaching the psychology of language in this way, psycholinguists have been able to make substantial progress in exploring one of the most complex phenomena facing psychologists.

We suggest that there are a series of lessons to be drawn from these developments in psycholinguistics that might be productively applied elsewhere in psychology. The first lesson is to focus on the mechanisms responsible for generating behavioral phenomena, and not just on the behavioral phenomena themselves. The second is to insist that these hypotheses about mechanisms be made computationally explicit, that is, that a cognitive or information-processing model of the mechanism be supplied. This element, though sometimes laborious, has become far easier given the widespread accessibility of computers and easy programming languages, as well as the broad array of other tools for formal analysis. The third lesson is the value of constructing careful computational theories or task analyses of the problem being addressed by the mechanism. And, finally, the last lesson is the value of combining these elements in order to evaluate the performance of alternative candidate mechanisms in solving the tasks or generating the observed patterns of behavior. In short, it is very productive for behavioral scientists to analyze phenomena from a cognitive, information-processing, or computational perspective. We should move beyond the hand-waving stage of theorizing, in which black boxes are endowed with miraculous abilities through the bestowal of labels. Instead, we should investigate explicitly described computational architectures and the performance they can be expected to generate. In so doing, the field of psychology has everything to gain and nothing to lose.

## LEARNABILITY AND DOMAIN-SPECIFICITY

The emergence of this form of analysis in psycholinguistics serves to illustrate the value of the analysis of computational performance, and we suggest that this tool can provide an equally effective tool for psychologists in other areas, assisting in the investigation of the mechanisms responsible for generating the behavioral phenomena they study. The investigation of “learnability” in the study of language acquisition may prove particularly instructive for psychologists, because its analysis mixes two issues of widespread applicability throughout psychology. Many tasks successfully faced by organisms are complex and also involve “learning,” that is, the modification of a specific competency using information derived from encounters with the world. In fact, for many social and behavioral scientists, “learning” is treated as a key explanation for many phenomena. What lessons are there in the study of language acquisition about the issue of learning?

The purpose of a learnability analysis is to evaluate whether a proposed information-processing mechanism is capable of learning to solve the problem that its advocates claim it can solve, given the information that is available to it in the



environment (Pinker, 1979, 1984, 1989). In short, it is the question of computational sufficiency applied to models of learning mechanisms (Pinker, 1984). For example, to learn to solve a given problem, different information-processing mechanisms require different kinds of environmental information. If the information necessary for a given mechanism to work does not exist in the environment, yet the organism being studied solves the problem, then one knows that the mechanism under consideration is not the one that is responsible for the organism's performance. Instead, an alternative design is required, which, for example, may supply the missing information that is necessary for the learning process to succeed through the evolved structure of its procedures.

Learnability analyses have been most fully developed in psycholinguistics, where they have been used to evaluate, reject, or suggest modifications in hypotheses about how a child acquires the grammar of the language spoken by its adult community (Pinker, 1979, 1982, 1984, 1989; Pinker & Prince, 1988; see also Grimshaw, 1981; Wexler & Culicover, 1980). For example, some hypotheses about the information-processing mechanisms responsible for grammar acquisition require that adults provide reliable feedback when the child makes a grammatical error. Yet lengthy transcripts of parent-child interactions have been collected and analyzed, and these show that adults rarely correct children's grammatical errors (Pinker, 1989). In fact, children acquire grammar normally even in cultures in which adults do not regularly converse with very young children, where overheard streams of adult-adult speech constitute the only informational input available to the child's learning mechanisms (Heath, 1983; Pinker, 1991). Consequently, one can reject any hypothesis that posits the existence of a learning mechanism that will work only if the child reliably gets negative feedback when he or she makes a grammatical error.

The rise of Chomskyan psycholinguistics (especially learnability analysis) constituted an important turning point in the development of modern psychology. Up until that point, psychology had been overwhelmingly dominated by general-purpose learning and cognitive theories. These theories were *domain-general*: The same process was supposed to account for learning in all domains of human activity, from suckling at the breast to the most esoteric feat of modern technology. General-purpose mechanisms are still the favored kind of hypothesis throughout the social and behavioral sciences (Tooby & Cosmides, 1992). Yet by specifying what actually needs to be accomplished in order to acquire grammar, psycholinguists have shown that a task routinely mastered by four-year-old children was too complexly structured to be accounted for by, for example, S-R learning theory.

Of course, modern incarnations of domain-general explanations of language acquisition have fared no better against the battery of specialized computational problems posed by language than did their behaviorist predecessors. When each new computational technology appears in psychology (from telephone switching systems to holograms to computers to new programming languages), in the heady excitement of exploring the potentialities of the new technology the crippling weaknesses of associationism are forgotten. This pattern was most recently re-

enacted with the advent of connectionism, which was initially taken by many to be a computational model of a domain-general associationism that could work. Yet, in the careful application of this family of models to actual adaptive problems real organisms solve, all of the same difficulties reappear. For example, through careful learnability and computational performance analyses, Pinker and Prince (1988; Pinker, 1991) were able to show that the existing domain-general connectionist model for the acquisition of the past tense in English was computationally insufficient to solve the problem and can (at most) reflect only part of the relevant mechanisms. Many of the reasons the model failed were not specific to the particular connectionist model proposed, but instead were general to domain-general connectionist models (Fodor & Pylyshyn, 1988). Of course, connectionist designs—like every other possible architecture—run into such logically inescapable problems as combinatorial explosion and the need for “innately supplied” specialized structure, meaning that functional connectionist architectures that solve real adaptive problems will also turn out to require domain-specific designs (see, e.g., Jacobs, Jordan, & Barto, 1990; Miller & Todd, 1990; Todd & Miller, 1991, 1991b). Thus, while connectionist models provide an interesting and important addition to the range of computational systems available for modeling psychological processes, they do not provide any escape from domain-specificity.

Work on language learnability has convinced many psychologists that a general-purpose learning mechanism would be powerful enough to permit the acquisition of the grammar of a natural language under natural conditions. But what kind of learning mechanism would have the requisite power? The conclusion has been that the acquisition of a natural language grammar requires cognitive programming that is not only complex, but specialized. Chomsky argued that just as the body has many different organs, each of which is specialized for performing a different function—a heart for pumping blood, a liver for detoxifying poisons—the mind can be expected to include many different “mental organs” (Chomsky, 1980). A mental organ is an information-processing system that is specialized for performing a specific cognitive function. A mental organ instantiates learning theories that are *domain-specific*: Its procedures are specialized for quick and efficient learning about an evolutionarily important domain of activity. Chomsky argues that the acquisition of a grammar could be accomplished only through a highly structured and complex *language acquisition device* (LAD): a functionally distinct mental organ that is specialized for learning a language.

The problem posed by the child's acquisition of the local grammar is that there are an indefinitely large set of grammars that can, in principle, generate whatever subset of adult language the child hears. Only one of them is correct, and the child picks the correct one, even though an infinity are logically possible. Despite the fact that the data available to the child are insufficient by themselves, the child must induce which of these grammars in fact generated that sample. This cannot be done unless the design features of the evolved mechanisms that allow the child to learn language place constraints on the child's hypothesis space that reflect actual adult grammar. If the mechanisms were content-independent and d

main-general, they would have no information about the nature of adult grammar that could allow the mechanisms in the child to decide among alternatives. Only mechanisms that came specifically equipped with this “knowledge” could determine which adult grammar is actually being spoken. Where does this “knowledge”—perhaps in the form of procedures or other structural features in the mechanisms—come from? The Chomskian argument is inherently adaptationist: Nothing, apart from selection, can endow the LAD with just those adaptive specializations necessary to supply the information regularly missing from adult speech samples, coordinating the two so that the local adult grammar can be uniquely determined (Pinker & Bloom, 1990; see also Tooby & Cosmides, 1990c). The evolved procedures of a child’s language acquisition device depend for their success upon stable and enduring species-typical regularities of the grammar-producing mechanisms of adults.

In this history, there are several increasingly familiar lessons. The first is that it pays to develop explicit models of the mechanisms proposed. The second is that adaptive problems, when dissected, usually turn out to be far more complex than is commonly appreciated. The third is that this complexity tends to require corresponding specialization in the psychological machinery in order to address the unique features of the specific problem type—that is, mechanisms capable of solving adaptive problems will frequently be domain-specific. Fourth, the structure of the world needs to be studied (or at least that part of it relevant to the problem to be solved), because the mechanism evolved to mesh with this structure to produce the functional consequence. And finally, the fact that a psychological phenomenon falls under the heading of “learning” makes no difference—one still needs a model of the environment, the mechanism, and their interaction.

Learnability analyses can, and should, be applied to all adaptive problems involving “learning,” that is, that involve the modification of competences based on encounters with the world. Of course, no hypothesis about an information-processing device can be evaluated unless it has been made sufficiently explicit. Black boxes labeled “capacity to learn what foods have the highest number of calories per unit of toxin,” “ability to learn how to be a good parent,” “capacity for culture,” “capacity to learn to maximize inclusive fitness,” and so on do not qualify: A label is not a substitute for a hypothesis. A computational system (such as we are) cannot be given abilities through magical fiat, and to understand such a system one needs to go through the explicit enumeration of all the causal steps necessary to produce behavior. Of course, it is a laborious task to detail actual procedures for even relatively simple tasks. But it is a standard that exposes hand-waving, as well as hypotheses that depend on the operation of previously unrecognized miracles. There is a traditional lament among junior military officers who have just been given orders: Nothing is impossible for the person who doesn’t have to do it. In the social and behavioral sciences, no model of a species’ psychological architecture seems impossible when its proponents do not have to specify by what methods it generates the necessary behavior. In particular, domain-general, content-independent “learning” and cognitive processes have gotten

a free ride by having been left unspecified as to computational architecture. They seem attractive hypotheses because being unspecified, nothing can be impossible to them.

Many psychologists think of the dispute over Chomsky’s language acquisition device as a controversy about innateness, but, as we shall see later, it was not. “Innate” is not the “opposite” of “learned.” Every coherent learning theory—even Hume’s associationism or Skinner’s brand of behaviorism—assumes the existence of innate cognitive mechanisms that structure experience. A “blank slate” will stay forever blank: Without innate cognitive mechanisms, learning is impossible (e.g., Hume, 1977/1748; Kant, 1966/1781; Quine, 1969; Popper, 1972). As Herrnstein (1977) points out, Skinnerian learning theorists were able to avoid discussion of the innate cognitive mechanisms governing generalization and discrimination only by ignoring the problem of which dimensions, out of uncountable possibilities, are used by the organism. Instead, the controversy in psycholinguistics was important because it highlighted the weakness in the most central explanatory concept in the history of psychology: learning.

### “LEARNING” IS NOT AN “ALTERNATIVE HYPOTHESIS”

Many common concepts in the behavioral and social sciences are used as if they were hypotheses and explanations, when in fact they are not. “Learning” stands out as one of these: It is a concept that many people believe is heavily freighted with explanatory power. Analytically, however, the only meaning operationally coupled to the word “learned” is “environmentally influenced.” As a hypothesis to account specifically and causally for mental or behavioral phenomena, it is nearly devoid of meaning.

Processes categorized as “learning” are accomplished through information-processing mechanisms, of course, and what matters is the discovery of the specific structures of these mechanisms. Their architectures may be (and arguably are) completely different from each other, and the application of the same label—learning—to describe all of them conceals this fact. Thus, such mechanisms may be simple or complex, domain-general or domain-specific, present from birth or late developing, and so on. An organism may be endowed with many different learning mechanisms, or just a few. The ubiquitous belief that the human mind, for example, contains only one domain-general cognitive process that results in “learning”—whether “induction” or “hypothesis testing” or “conditioning” or “imitation” or “rationality”—is nothing but conjecture conventionally accepted in many research communities as a fact (see Tooby & Cosmides, 1992). It has no empirical basis at all and in cognitive psychology appears to be a metatheoretical holdover from the heyday of behaviorism.

In reality, the controversy in psycholinguistics was over whether the evolved learning mechanisms that allow humans to acquire a grammar are simple and do-

main-general or complex and domain-specific (e.g., Atherton & Schwartz, 1974; Chomsky, 1975; Katz, 1975; Marshall, 1981; Pinker, 1979; Putnam, 1967). The behaviorists thought that the simple, domain-general processes of classical and operant conditioning were plausible accounts for language; Chomsky and his successors showed that they were not and proposed the existence of learning mechanisms that were complex and domain-specific. Both camps agreed that language is "learned" (i.e., requires exposure to language environments); they disagreed about *how* it is learned (i.e., about what the nature of the evolved mechanisms is).

The failure to grasp this point leads to enormous conceptual confusion in the behavioral sciences. The common belief that "learning" is an alternative hypothesis to an evolutionary theory of adaptive function is a category error. Learning is a label for a family of cognitive processes (defined solely by the fact that they modify some aspect of the behavioral control system in interaction with the world). An adaptive function is not a cognitive process; it is a problem that is solved by a cognitive process. Learning is accomplished through psychological mechanisms (whose nature is most often not understood), and these were created through the evolutionary process, which includes natural selection. Consequently, the issue can never sensibly be whether a particular behavior is the result of natural selection "or" learning. The issue is: What is the evolved information-processing structure of the learning mechanisms involved in producing a particular behavior? More generally, one might ask: What kinds of learning mechanisms does natural selection tend to produce?

As Symons has cogently argued, this has been the substance of the nature–nurture controversy—which could not have genuinely been about innateness at all, since all (coherent) participants must acknowledge the reliable development of some evolved structure in the psychological architecture (Symons, 1987). Instead the debate is really about whether the innate mechanisms are few and domain-general, or many and functionally specialized. Thus, when behavioral scientists are arguing about whether aggression is "innate," the substance of the debate (however they may put it to themselves) is whether there are any features of the psychological architecture that evolved specifically to regulate aggression, or whether aggression is purely a result of the same few domain-general learning mechanisms that are putatively responsible for nonsense syllable memorization or domino matching. So, one question to ask is: Are the mechanisms that constitute the human psychological architecture few and general, or do they include many specialized mechanisms for food choice, foraging decisions, mate choice, incest avoidance, aggression regulation, social exchange regulation, sexual jealousy, parental care, and so on?

As discussed, when models of cognitive programs become sufficiently well specified to actually account for empirical results, they almost always turn out to be complex and domain-specific. When researchers present such well-specified models together with the empirical results that support them, they are often met with the counterclaim that "people might just learn to think that way." Yet, the invocation of an unspecified learning process does not constitute a valid alternative

hypothesis. Suggesting that "learning" is an alternative hypothesis is comparable to claiming that an alternative hypothesis to a well-specified theory of vision, such as Marr's (1982), is "light hits the retina and this causes the organism to see three-dimensional objects." This is not an explanation; it is a description of the phenomenon to be explained. All the intervening steps are missing: It does not count as an "alternative hypothesis" because no one has bothered to specify the nature of the cognitive programs that cause it to happen.

"Learning" designates the phenomenon to be explained. A complex, domain-specific cognitive program is a learning mechanism; how, then, can "learning" be construed as an "alternative hypothesis"?

The claim that a behavior is the product of "culture" is not an "alternative hypothesis" either. It entails nothing more than the claim that surrounding or preceding individuals are an environmental factor that has influenced the behavior under discussion in some way. It leaves the learning mechanisms that allow humans to acquire and generate culture completely unspecified (Tooby & Cosmides, 1989a, 1992).

Interestingly, evolutionary researchers are often subject to a reciprocal species of error (see discussion in Tooby & Cosmides, 1990b). Many seem to operate from the implicit premise that an organism can "decide" which course of action, however complex, will promote its inclusive fitness simply by inspecting the environment. These researchers interpret the fact that humans were produced by the evolutionary process to mean that humans must be maximizing their inclusive fitness in all situations, or at least attempting to do so, even in evolutionarily unprecedented modern environments. This view makes sense only if one believes that the organism has a cognitive program that says "do that which maximizes your inclusive fitness." Yet this is merely a veiled way of claiming that the organism "learns" what to do to maximize its fitness. It is not a hypothesis. It leaves "learning" a mysterious, omniscient, and utterly unspecified process.

It is improper to invoke an undefined process as an explanation. "Learning" should not be invoked to explain other phenomena at this point in the development of psychology, because it is itself a phenomenon that requires explanation. The nature of the cognitive processes that allow learning to occur are far from understood.

The tendency to assume that learning is accomplished only through a few simple domain-general mechanisms lingers in many branches of psychology, including cognitive psychology. We believe this metatheoretical stance is seriously flawed, and persists only because psychologists and evolutionary biologists have not joined forces to create computational theories that catalog the specific and detailed information-processing problems entailed by the need to track fitness under Pleistocene or ancestral conditions. Later, we join Daly and Wilson (1988), Gallistel (1990), Pinker and Bloom (1990; see also Pinker, 1991), Rozin (1976), Shepard (1981), Symons (1987), and many others in arguing that a consideration of such problems suggests that natural selection has produced a great many cognitive programs that are complex and highly domain-specific.

## INNATENESS, SPECIES-TYPICAL DESIGN, AND INDIVIDUAL DIFFERENCES

Before discussing why evolutionary considerations suggest that most psychological adaptations will be domain-specific, that is, functionally specialized, we should briefly discuss the use of the word *innate* and several related issues. In this chapter, we are using this frequently misunderstood word as cognitive psychologists often use it: to describe reliably developing species-typical properties of the organism. We are not using it to refer to expressed phenotypic properties that are present from birth; human teeth provide an example of something that develops reliably, according to a species-typical design, that is absent at birth. “Innate” features of the human species-typical architecture could appear through maturation at any time throughout the life-cycle. We often use another phrase, *evolved*—as in evolved structure—in certain contexts as a synonym. That is, for a complex functional structure to have evolved, it needed to have appeared often enough in phenotypes to have been the target of selection.

More significantly, we do not mean to imply by using the word *innate* that something is immutable or impervious to modification or elimination by sufficiently ingenious ontogenetic intervention. Every feature of every phenotype is fully codetermined by the interaction of the organism’s genes, its initial package of zygotic cellular machinery, and its “environment”—meaning everything else that impinges on it. But simply pointing to the interaction between the two misses something important: that natural selection acts on the species’ set of genes so that the result of the usual interaction between the genes and the environment is to produce a stabilized, improbably functional design. Thus, developmental mechanisms are themselves adaptations, shaped to buffer environmental perturbation by ignoring dimensions of the world that were variable during the EEA and shaped to employ in their processes of organismic construction the stably recurring structure in the world. The usual result is a successfully produced complex architecture, most aspects of which are species-typical, although (depending on the breeding structure of the species), some may be population-typical or frequency-dependent.

Consequently, every individual really has two inheritances: its genes, which may be perturbed by mutations, and the environmental invariances or regularities that its developmental processes depend on. Selection acts on genes that regulate developmental programs to suppress perturbation from genetic and environmental sources. Thus, gene–environment interactionism is quite compatible with stably recurrent evolved design (Crawford & Anderson, 1989). It is this recurring structure that we are referring to when we use terms such as *innate* or *evolved* or *reliably developing* or *design*. Obviously, developing organisms are vulnerable and complex dynamic systems, and environmental intervention can change almost everything about them, so these terms entail assumptions about spontaneous development in normal or EEA-like environments. When the organism develops in environments that deviate from that to which the genotype is adapted, its phenotype may also deviate from those aspects of its design that were targets of selec-

tion. This divergence of past and present environments sometimes introduces complications for the researcher, particularly those who study humans.

## WHY SHOULD DARWINIAN ALGORITHMS BE SPECIALIZED AND DOMAIN-SPECIFIC?

Nature has kept us at a great distance from all her secrets, and has afforded us only the knowledge of a few superficial qualities of objects; while she conceals from us those powers and principles, on which the influence of these objects entirely depends. Our senses inform us of the colour, weight, and consistence of bread; but neither sense nor reason can ever inform us of those qualities, which fit it for the nourishment and support of a human body.

—David Hume, 1977/1748, p. 21

Genes coding for psychological mechanisms that promote the inclusive fitness of their bearers will outcompete those that do not and tend to become fixed in the population. The promotion of inclusive fitness is an evolutionary “end”; a psychological mechanism is a means by which that end is achieved. Can the human mind be comprised primarily of domain-general and content-independent psychological mechanisms and yet realize this evolutionary end? We argue that natural selection could not have produced such a psychological architecture, nor could such a hypothetical design successfully promote fitness (i.e., regulate behavior adaptively).

Consider how Jesus explains the derivation of the Mosaic code to his disciples:

Jesus said unto him, “Thou shalt love the Lord, thy God, with all thy heart, and with all thy soul, and with all thy mind. This is the first and great commandment. And the second is like it, Thou shalt love thy neighbor as thyself. *On these two commandments hang all the law and the prophets.*”

—Matthew 22:37–40 (emphasis added)

Jesus has given his disciples a domain-general, content-independent decision rule to be used in guiding their behavior. But what does it mean in practice? Real life consists of concrete, specific situations requiring specific decisions out of an infinite set of alternatives. How, from this rule, do I infer what counts as “loving my neighbor as myself” when, to pick a standard Biblical example, my neighbor’s ox falls into my pit? Should I recompense him, or him me? By how much? How should I behave when I find my neighbor sleeping with my spouse? Should I fast on holy days? Should I work on the Sabbath? What counts as fulfilling these commandments? How do I know when I have fulfilled them?

In what sense does all the law “hang” from these two commandments?

These derivations are not obvious or straightforward. That is why the Talmud was written. The Talmud is a “domain-specific” document: an interpretation

of the “law” that tells you what actions fulfill the injunctions to “love God” and “love your neighbor” in the concrete, specific situations you are likely to encounter in real life. The Talmud solves the *frame problem* (e.g., Boden, 1977; Fodor, 1983) posed by a domain-general rule like Jesus’.

A domain-general decision rule such as “Do that which promotes your inclusive fitness” cannot guide behavior in ways that actually do promote fitness, because what counts as fit behavior differs from domain to domain. Therefore, like the Talmud, psychological mechanisms governing evolutionarily important domains of human activity must be domain-specific.

The easiest way to see that Darwinian algorithms must be domain-specific is to ask whether the opposite is possible: In theory, could one construct a domain-general, content-independent decision rule, that, for any two courses of action, would evaluate which better serves the end of promoting inclusive fitness? (For additional discussion on why the answer is no, see Tooby & Cosmides, 1990b.)

First, such a rule must include a criterion for assessing inclusive fitness: There must be some observable environmental variable against which courses of action from any domain of human activity can be measured. As the promotion of inclusive fitness means differential representation of genes in subsequent generations, the time at which the consequence of an action can be assessed is remote from the time at which the action is taken. For simplicity’s sake, let us drop collateral fitness components and assume that number of grandoffspring produced by the end of one’s life is an adequate assessment of fitness. Using this criterion, the decision rule can be rephrased more precisely as, “Choose the course of action that will result in more grandoffspring produced by the end of one’s life.”

But how could one possibly evaluate alternative actions using this criterion? Consider a simple, but graphic example: Should one eat feces or fruit? Will trial and error (or operant conditioning, induction, hypothesis testing, imitation, etc.—the argument is general to any system that lacks specialized procedures to deal with the stable structure of the world) work? Clearly, no individual has two parallel lives to lead for purposes of comparison, identical except that he or she eats feces in one life and fruit in the other. Each life is a single, uncontrolled experiment. The individual who eats feces is far more likely to contract parasites or infectious diseases, thereby incurring a large fitness cost. And if this individual instead eats fruit and leaves a certain number of grandoffspring, he or she still does not know whether eating feces would have been better: For all that individual knows, feces could be a rich food source (as they are for some species) that would increase fecundity.

Does learning from others constitute a solution to the problem? Imitation is useless unless those imitated have themselves solved the problem of the adaptive regulation of behavior. If the blind leadeth the blind (to retain our Biblical orientation), they shall both fall into the ditch. Imitation, as a strategy, can only supplement systems that have already solved the primary problem of the adaptive regulation of behavior.

If, however, others are monitored not as role models for imitation but instead as natural experiments, this does allow the comparison of alternative courses of action, in a limited fashion. The number of hypotheses that can be tested is a function of the number of individuals under observation and the comprehensiveness of the observation. Nevertheless, each individual life is subject to innumerable uncontrolled and random influences that rapidly outstrip the population size and that any observer would have to keep track of to make valid inferences. If the observer watches some people eat fruit and others eat feces and waits to see which will have a larger number of grandoffspring, how would the observer know whether these individuals’ differential fitness was caused by their diet or by one of the millions of other things they experienced in the course of their lives? Of course, the most major problem is that of time delay between action and the cue used to evaluate the action: grandoffspring produced. It is fundamentally impractical to have to wait two generations (or even any substantial fraction of one) to determine the value of choices that must be made today—learning latencies tend to be very short because of this problem of combinatorial explosion. Moreover, where would the population of individuals living by trial and error, which supports the observer’s adaptive regulation system, come from? Obviously, although social observation can and does supplement other psychological processes (e.g., Galef, 1990), potential role models would have to have solved the problem of the adaptive regulation of behavior by some other method if observing them is to provide any benefit.

Can the use of perceptual cues solve the problem? The individual could decide to eat what smells good and avoid what smells bad. This method works, of course, because such criteria are design features of evolved, domain-specific mechanisms. Nothing smells intrinsically bad or good; the smell of feces is attractive to dung flies. Admitting smell or taste preferences is admitting domain-specific knowledge or procedures. Admitting the inference that foul-smelling or foul-tasting entities should not be ingested is admitting a domain-specific innate inference.

Even if it were somehow possible to learn the fruit-eating preference using domain-general mechanisms, an individual equipped with appropriate domain-specific mechanisms would enjoy a selective advantage over one who relied on “trial and possibly fatal error” (Shepard, 1987). The tendency to rely on trial and error in this domain would be selected out; domain-specific Darwinian algorithms governing food choice would be selected for and become a species-typical trait.

There is also the problem of deciding which courses of action to evaluate, an instance of the widespread information-processing problem of combinatorial explosion. The possibilities for action are infinite, and the more truly domain-general a mechanism is, the more it would be restricted to generating random possibilities to be run through the inclusive fitness decision rule. When a tiger charges, what should your response be? Should you smile winningly? Do a cartwheel? Sing a song? One has the intuition that running randomly generated response possibilities through the decision rule would not be favored by selection. And again, on what basis and by what procedures would psychological mecha-

nisms compute which possibility would result in more grandchildren? An alternative design that includes Darwinian algorithms specialized for predator avoidance seems reasonable, with design features such as a tendency to trade an increase in false positives in predator detection in for an increase in hits, and procedures that, upon detecting a potential predator, restrict response alternatives to flight, fight, or concealment, and orchestrate among them.

The domain-general “grandchildren produced” criterion fails even in these simple situations. How, then, could it work in more complicated learning situations—for example, when an action that increases fitness in one domain decreases it in another? Suppose the hypothetical domain-general learning mechanism somehow reached the inference that sexual intercourse is a necessary condition for producing offspring. Should the individual, then, have sex at every opportunity?

An evolutionarily well-designed organism would not, of course. There are, for example, large fitness costs associated with incest (e.g., Shepher, 1983). Given a potential partner with cues (evaluated by domain-specific mechanisms: see Buss, 1987, 1989, 1991a, 1992, 1994; Symons, 1979) that would normally elicit sexual desire, EEA-reliable cues indicating that the potential partner is a family member should inhibit sexual impulses.

How could a regulatory system like this be induced by a general purpose system? If a female engages in incest, then loses her baby after a few months, how could a domain-general mechanism identify what caused the miscarriage? Each life is a series of many events (perhaps including sex near the time of conception with nonkin as well as kin), any one of which is a potential cause. Why conclude that sex with one individual, who physically and psychologically resembles other members of his sex in many respects, caused the loss of the baby? Why not reject everyone of the same eye color, or stop having sex at a particular time of day, or start eating within six hours of having sex, and so on, ad infinitum? Even assuming that a domain-general system did settle on the “kin versus nonkin” dimension, a design that had to learn this evolutionarily stable contingency between mating with family members and fitness reduction would be rapidly replaced by a design that came equipped with specialized mechanisms that solved the problem.

Indeed, where could the correct dimensions of discrimination and generalization come from (Herrnstein, 1977)? There are an infinite number of dimensions that could be used to carve the environment into categories; there is no assurance that a general-purpose information-processing system would ever isolate those useful for creating the kin/nonkin categorization scheme, and the “grandchildren produced” criterion cannot guide such a system toward the appropriate dimensions. (In contrast, domain-specific kin recognition mechanisms can exploit evolutionarily recurring statistical regularities that link cues with kinship, such as being raised by the same caretaker.)

A general purpose system would have to solve the infinite dimensions problem not only if it is to categorize events, but also if it is to apply the knowledge acquired to new situations. Suppose the architecture had somehow correctly in-

ferred that avoiding sex with kin had positive fitness consequences. How should one generalize this knowledge about the kin/nonkin categorization scheme to other domains of human activity? Should one, for example, avoid any interaction with kin? This would be a mistake; selectively avoiding sex with kin has positive fitness consequences, but selectively avoiding helping kin has negative fitness consequences (given a certain envelope of circumstances; Hamilton, 1964).

Thus, not only must the acquisition of the kin/nonkin categorization scheme be guided by domain-specific Darwinian algorithms, but its adaptive use for guiding behavior is also domain-specific. In the sexual domain, kin must be avoided; in the helping domain, they must be helped; when one needs help, kin are a likely source from whom to solicit it (Hamilton, 1964); when one is contagiously ill, one should avoid infecting kin to the extent this is consistent with the solicitation of help. Domain-general learning is inadequate not only because it is costly, slow, and unreliable in practice, but because in principle there is no domain-independent variable for discriminating success from error. In the sexual domain, error = sex with kin. In the helping domain, error = not helping kin given the appropriate envelope of conditions. In the disease domain, error = infecting kin. What is the common criterion of success in mate selection, predator avoidance, and foraging? One cannot escape the conclusion that motivational systems—if nothing else—driven by the evaluation of consequences must contain domain-specific features. The only general criterion of success is fitness itself, which is inherently unobservable at the time decisions must be made.

In short,

1. There is no domain-general definition of what counts as success and failure that correlates with fitness.
2. Adaptive courses of action can be neither deduced nor learned by general criteria because they depend on statistical relationships between features of the environment, behavior and fitness that emerge over many generations, and are therefore not observable during a single lifetime.
3. Combinatorial explosion cripples any insufficiently content-structured mechanism, as there are an infinite number of potential category dimensions, an infinite number of possible relations, an infinite number of potential hypotheses, and an infinite number of potential behaviors.

For these reasons, exclusively domain-general architectures are computationally insufficient to solve many adaptive problems. And even where they might be sufficient, they cannot solve them as efficiently as architectures equipped with functionally specialized mechanisms, because sets of procedures designed to take advantage of the recurrent features of defined adaptive problems will, by their nature, be more efficient than any alternative design lacking this information.

Given the complexity of the world, and the complexity of the total array of adaptive tasks faced by living organisms, the psychological architecture of any real species must be permeated with domain-specific structure. The psychological architecture appears to be more complexly specialized than anyone ever suspected.

## DARWINIAN ALGORITHMS SOLVE THE “FRAME PROBLEM”

Researchers in artificial intelligence have found that trial and error is a good procedure for learning only when a system already has a well-specified model of what is likely to be true of a domain, a model that includes a definition of what counts as error. More generally, they have found that whenever they try to build a system that can tackle a real problem, they have to build in large amounts of “domain-specific” programming structure about the problem-space. Artificial intelligence researchers call this the *frame problem* (e.g., Boden, 1977; Fodor, 1983), and it arises because general-purpose computational systems have the problems discussed earlier. To move an object, make the simplest induction, or solve a straightforward problem, the computer must already have a sophisticated model of the domain in question: what counts as an object or stimulus, what counts as a cause, how classes of entities and properties are related, how various actions change the situation, what goal is to be achieved. Unless the learning or problem domain is severely circumscribed and the procedures highly specialized and content-dependent—unless the programmer has given the computer what corresponds to vast quantities of “innate knowledge”—the computer can move nothing, learn nothing, solve nothing. The frame problem is a concrete, empirical demonstration of the philosophical objection to the *tabula rasa*. It is also a cautionary tale for advocates of domain-general, content-independent learning mechanisms.

Unfortunately, the lessons from AI have been lost on many. Although most cognitive psychologists realize that their theories must posit some innate cognitive architecture, a quick perusal of textbooks in the field will show that these still tend to be restricted to content-independent operating system characteristics: short-term stores, domain-general retrieval and storage processes, imagery buffers. Researchers who do insist on the necessity of positing content-dependent schemas or frames (e.g., Minsky, 1977; Schank & Abelson, 1977) seldom ask how these frames are built. Their approach implicitly presumes that frames are the product of experience structured only by domain-general learning mechanisms. For example, Cheng and Holyoak (1985) cite “induction” as the process that builds their content-dependent “pragmatic reasoning schemas.” Yet the building of frames must also be subject to the frame problem: Where do the situation-specialized procedures or information come from that “know” how to build appropriate as opposed to the infinite set of inappropriate frames?

The chain has to begin somewhere and, as we have seen, domain-general processes alone cannot accomplish the task. What can? The conclusion seems inescapable: For the organism’s cognitive architecture to solve adaptive problems, or to “learn” adaptively, it must have domain-specific procedures, that is, content-specialized Darwinian algorithms. These Darwinian algorithms can be seen as schema or frame *builders*: as cognitive mechanisms that structure experience along adaptive dimensions in a given domain and define useful problem spaces and, in general, supply the other necessary specificity to structure the developing psychol-

ogical architecture so that it is equipped to frame problems adaptively. Phylogenetically supplied Darwinian algorithms solve the frame problem for the organism, just as the programmer solves it for the artificially intelligent system.

## THE FRAME PROBLEM AND SO-CALLED “CONSTRAINTS” ON LEARNING

Biologists and psychologists have an unfortunate tendency to refer to the properties of domain-specific (but not domain-general) mechanisms as “constraints.” For example, the one-trial learning mechanism, discovered by Garcia and Koelling (1966), that permits a rat to associate a food taste with nausea several hours later is frequently referred to as a “biological constraint on learning.” Reviews or treatments of domain-specific elements in psychological systems frequently have titles such as *Biological Boundaries of Learning* (Seligman & Hager, 1972), *Constraints on Learning* (Shettleworth, 1972), or even *The Tangled Wing: Biological Constraints on the Human Spirit* (Konner, 1982). This terminology is seriously misleading, because it incorrectly implies that “unconstrained” learning mechanisms are a theoretical possibility; it implicitly denies the existence of the frame problem.

All constraints are properties, but not all properties are constraints. Calling a property a “constraint” implies that the organism would have a wider range of abilities if the constraint were to be removed. Are a bird’s wings a “constraint on locomotion”? Obviously, such usage would be absurd: Wings expand the bird’s capacity to locomote. On the other hand, a thick rubber band placed in such a way that it pins a bird’s wings to its body is a constraint on the bird’s ability to locomote, constraining the bird to walking. If anything, wings should be called “enablers,” because they enable an additional form of locomotion.

Equally, there is no evidence that the domain-specific mechanisms that permit one-trial learning of an association between taste and nausea are “constraints on learning.” Removing the specific properties that allow the efficient learning of this particular association would not expand the rat’s capacity to learn; it would reduce it. Not only would the rat be unable to associate a food taste with an electric shock; it would also be unable to associate a food taste with nausea.

The tendency to refer to such evolved structures as “constraints on learning” shows the durability of the mistaken notion that a *tabula rasa* is possible and, more specifically, that learning is possible in the absence of a great deal of domain-specific structure. If the “constraint” language were accurate in its implications, then a property that “prepares” an organism to associate a taste with nausea might preclude it from associating a taste with an electric shock. However, if an organism with this prepared association also had a domain-general associative mechanism, there is no a priori reason why that mechanism should not work to pair taste with electric shocks. In order to call the prepared association a “constraint” on the learning caused by the general-purpose mechanism, one would have to demon-

strate empirically that the activation of the prepared association by the presence of food somehow causes the general-purpose mechanism to shut down. Rozin and Schull (1988) have pointed out another way in which the terminology of constraints is misleading: It implies that the human mind was "built down" from a more general-purpose cognitive system present in our ancestors. Yet such a phylogenetic history seems far from likely: It presumes that our primate ancestors had a capacity to learn that was broader and more powerful than our own.

The rich, functionally specialized information-processing structures present in the psychologies of organisms should be affirmatively characterized as adaptations, rather than as constraints. They should not be characterized, implicitly or explicitly, by how far they deviate from the ideal of a nonexistent—and indeed, impossible and incoherent—general-purpose architecture. It is true that psychologies differ in the breadth of situations to which they can respond appropriately. The fact that humans can improvise an amazing and elaborate range of behaviors, from composing symphonies to piloting aircraft to writing *The Idiot* indicates a generality of achieved problem solving that is truly breathtaking. But we know from the reality of combinatorial explosion and its progeny in various fields that this cannot be the result of mechanisms that are solely domain-general, content-independent, and free of procedures poised to exploit the structure of the world. Most of all, "generality" is a description of what an architecture lacks: It means that it lacks anything particular (such as information or procedures) that suits it for some situations over others. For this reason, generality of accomplishment is not achieved, and could not be achieved, by generality of design. General designs are inherently weak designs, while specialized designs are inherently more powerful, though at the price of addressing a narrower range of problems. The solution, for an architecture that must be both powerful, yet somewhat general, is the bundling of specialized mechanisms together, so that in aggregate, they address a large range of problems and do so powerfully. Moreover, mechanisms that are "general purpose" to some degree can be embedded in this guiding matrix of functional specialization to supplement them and broaden the range of solvable problems still further. Thus, in the human case (for example), one has mechanisms incorporating (highly structured) social observation, imitation, operant conditioning, and so on that (conjointly with an expanded array of specialized mechanisms) increase the range of situations that can be responded to appropriately. It is time for behavioral scientists to turn from a nearly exclusive focus on these more general-purpose mechanisms to the crucial, and largely neglected, encompassing superstructure of evolved domain-specific functional specializations.

## FUNCTIONAL SPECIFICITY IN MOTIVATION

Within this tradition of emphasizing general-purpose architectures, the field of motivation has played a subversive role (Tooby & Cosmides, 1992). As was clear from the previous analysis, motivation is the most obviously difficult thing to

make general, because what counts as adaptively successful behavior for the organism differs completely from domain to domain. There is simply no uniform element in sex, eating, drinking, staying warm (but not overheating), and so on, that could be used to build a general architecture that could learn to accomplish these behaviors. Any architecture that can do these tasks requires something functionally specialized to address them. What many psychologists did was to make motivation the repository of the inescapable minimum of functionally specialized regulatory structure, while making the rest of their hypothesized architectures as general as possible. Despite the admission of functional specialization into psychological processes, the tendency has been to keep these elements restricted to as small a class as possible and to view them as external to the "important" central learning or cognitive processes. They are incorporated as, for example, reinforcers operating by drive reduction.

Modern mainstream cognitive psychologists have continued in this tradition, for the most part, and have labored to keep any such content-influenced elements extrinsic to the primary cognitive machinery. Indeed, they have usually avoided addressing how functional action—such as mate choice, food choice, or effort calculation—takes place at all. The principles of concept formation, of reasoning, of remembering, and so forth have traditionally been viewed as uninfected prior to experience with any content, their procedures lacking features designed for dealing with particular types of content. (The recent emergence of modular or domain-specific cognitive psychologists constitutes a dissenting subcommunity.)

Given this division of labor (i.e., with motivation the keeper of the functionally specific, and learning theory the keeper of the general laws of mind), much of great value was learned. However, because of the powerful prejudice against content-sensitivity or functional specialization harbored by many learning theorists, a great deal more could have been learned, even within this Procrustean framework. An attempt could have been made to comprehensively survey the list of primary reinforcers, and the conditions and contexts within which they were reinforcing. Unfortunately, the pretheoretical preference was to keep this list as short as could be accepted as credible (with credibility depending on what kinds of animal behavior one knew about). To keep this short list credible, one had to keep research organisms outside ecologically valid circumstances, away from biologically significant stimuli and, indeed, in highly stimulus-impooverished circumstances (Beach, 1955; Breland & Breland, 1961; Lockard, 1971).

Ethology (or sociobiology or behavioral ecology or animal behavior—the names have been changed to protect the innocent) has played an important corrective role in this regard (Daly & Wilson, 1984; Krebs & Davies, 1984; Lorenz, 1965; Tinbergen, 1951; Wilson, 1975). These fields have provided carefully documented, functionally interpretable behaviors that lie far outside anything that drive reduction theory and a short list of motivations could explain. Thus, one has the effort male ring doves will go to monitor the sexual behavior of their mates (Erickson & Zenone, 1976). One has reports from an entire range of species—from langurs to lions to rodents—of newly resident males killing the infants of



their predecessors and thereby accelerating ovulation (Hrdy, 1977; for reviews see Hausfater & Hrdy, 1984). The now well-known selection pressure of kin selection has led to the search for and documentation of an enormous array of kin-directed altruistic acts—behaviors completely undreamt of in drive theory's philosophy (Hamilton, 1964; Williams & Williams, 1957; for review see Krebs & Davies, 1984). Similarly, the complex conditions under which reciprocation is and is not engaged in are hard to account for using traditional notions of what reinforcers are and what, exactly, it is that they reinforce (e.g., Wilkinson, 1988, 1990).

Evolutionary studies of humans similarly bristle with documented phenomena that cannot be accounted for with general architectures and a short list of drives, rewards, or reinforcers (see Tooby & Cosmides, 1992, for discussion, and the papers in Barkow, Cosmides, & Tooby, 1992, for examples). Buss's and Symons's important work in the area of human mate choice and sexuality shows that the "sex drive" is a construct completely inadequate to cope with the structural richness of the factors involved in the differentiated sexual psychologies of males and females (Buss, 1987, 1989, 1991a, 1992, 1994; Symons, 1979). Some of our own work has focused on the complex evolved structure of the inference mechanisms and associated motivations linked to human reciprocation (Cosmides, 1989; Cosmides & Tooby, 1989, 1992). Finally, Daly and Wilson have explicitly been exploring the issue of the complexity and functional subtlety of the human motivational system and how it conforms to expectations drawn from a broad array of selectionist theories (Daly & Wilson, 1981, 1982, 1984, 1987a, 1987b, 1988; Daly, Wilson, & Weghorst, 1982; Wilson & Daly, 1985, 1987, 1992). They have explored the motivational structure recoverable from such phenomena as risk taking, violence, sexual jealousy and proprietariness, parental care (and its lack), spousal abuse, and their regulation by such factors as gender, age, kinship, reproductive value, and various situational factors. Work such as Buss's, Symons's, and Daly and Wilson's leads to the conclusion that the human mind contains evolved motivational mechanisms that are specifically targeted to address adaptive problems involved in mate selection, aggression, mate guarding, discriminative child care, and so on, and that these psychological mechanisms recalibrate themselves depending on the age, sex, number of children, and so on, of the individual they are in. That is, humans have motivations specifically "about" the sexual behavior of their spouses, "about" those identified by cues as genetic kin, "about" how much to care for a sick child, and so on that are not derived from a shorter list or culturally variable socially learned "values."

Information-processing descriptions of motivational questions provide a rich language for characterizing this expanding range of behavioral phenomena. For example, the cognitive architecture of bumblebees appears to contain psychological specializations for foraging (Real, 1991). These mental organs embody rules of relevance, drawing the animal toward some aspects of its environment and not others. These rules cause the animal to search for certain kinds of environmental patterns—such as flower-shaped objects—and, upon finding these patterns, to engage in adaptively appropriate activities—such as sampling the nectar from the flower.

Its rules cause the animal to compute certain functions—such as nectar reward per unit time per flower—and use the computed value to decide which color flowers to forage on (Real, 1991). The animal might continue to forage until some consummatory function—perhaps a calculation of total nectar consumed—deactivates the mental organ and thereby causes the foraging behavior to cease. Mental organs may be arranged in hierarchical fashion, in such a way that a bee might forage as long as the predation risk is sufficiently low, but when environmental cues indicate the presence of a predator, the foraging mechanisms are deactivated and the predator avoidance programs activated.

Once one has a map of the information-processing programs that govern behavior, motivational questions can be discussed with great precision. For example, bumblebees are risk-averse foragers; given two different flower patches that have the same expected nectar payoff but different variances, they concentrate their foraging on the low variance patch (Real, 1991). Describing the bumblebee's behavior as the expression of cognitive rules encourages one to ask very specific questions about those rules, such as: Do these rules cause the bee to prefer the more variable patch if its average reward is higher? How much higher does the average reward have to be? Do the bee's decision rules compute reward as a function of time for one flower at a time, or are these values averaged over two or more flowers? Does the bee's past history with a flower of a specific color affect its foraging decisions? and so on (Real, 1991). Once one has specified all the cognitive rules that govern the bumblebee's foraging—what kinds of information these rules take as input, what transformations they perform on that information, and what behaviors they generate as output—one has a very complete and specific description of the bumblebee's motivational programs in the domain of foraging.

Theories of adaptive function, in their ranking of outcomes in terms of fitness promotion, inherently help in analyzing the design of motivational mechanisms. Moreover, computational theories that include models of ancestral conditions as well as selection pressures will provide clues as to what cues and outcomes should be rewarding, how to define goal states, and how to model an equivalence and relative value in a mental or information-processing currency of cued consequences (so-called *fitness tokens*; Daly & Wilson, 1988). Of course, the most important implication is that it will often be more productive to consider motivational mechanisms as subcomponents in separate domain-specific mechanisms, rather than as a single unitary system crosscutting through every domain. That is, one should consider a pluralism of motivational mechanisms, without expecting that the motivational dimension should operate according to the same rules from problem-solving system to problem-solving system. In such models, motivation may show up, for example, as a series of differentiated regulatory variables embedded in separate problem-solving mechanisms whose magnitudes play roles in decisions and procedure activation. Of course, given that every organism needs to arbitrate between activities, there will need to be an encompassing integrative and arbitrative motivational system that addresses the issue of task switching. This raises the issue of the organization of the entire psychological architecture, and with it, emotion.

## EMOTIONS AS ADAPTATIONS TO PHYLOGENETICALLY RECURRING SITUATIONS

All adaptations evolved in response to the repeating elements of past environments, and their structure reflects in detail the recurrent structure of ancestral environments. This ability to “know about” and exploit the complex structure of the world, based on cues that identify recurring situations, is one of the things that give domain-specific mechanisms such an edge in producing adaptive behavior. Given that animal minds consist of collections of evolved mechanisms in a world in which situations reappear from generation to generation, a functional description of emotion naturally emerges (Tooby, 1985, Tooby & Cosmides, 1990b). One simply needs to shift the focus from considering how an individual mechanism matches the environmental structure of its particular problem type to addressing how sets of mechanisms might advantageously be coordinated when dealing with evolutionarily reappearing situations.

Of course, each psychological mechanism can operate in a number of alternative ways, each of which will be more or less useful in dealing with a given situation. Taken together in their interaction with the other mechanisms in the architecture, some configurations will deal better than others with specific situations. For this reason, selection can have been expected to have shaped the system architecture to structure interactions among the different mechanisms so that they function particularly harmoniously when confronting commonly recurring (across generations) adaptive situations. Fighting, engaging in sex, needing nourishment, falling in love, escaping predators, confronting sexual infidelity, and so on, have each recurred innumerable times in evolutionary history, and each requires that a certain subset of the psychological architecture’s behavior-regulating algorithms function together in a particular way to guide behavior adaptively through that type of situation. This structured functioning together of mechanisms is a mode of operation for the mind and can be meaningfully interpreted as an emotional state. Each emotion state—fear of predators, guilt, sexual jealousy, rage, grief, and so on—corresponds to an integrated mode of operation that functions as a solution designed to take advantage of the particular structure of the recurrent situation these emotions correspond to. The characteristic feeling that accompanies each such mode is the signal that activates the specific constellation of mechanisms appropriate to solving that type of adaptive problem.

To make this concrete, let us briefly describe in these terms what might happen to a hypothetical human hunter-gatherer when a distant lion becomes visible. The recognition of this predator triggers the internal “broadcast” that we call the feeling of fear; this broadcast acts as a signal to all of the diverse mechanisms in the psychological architecture. Upon detecting this signal, they each switch into the “fear mode of operation”—that is, the mode of operation most appropriate to dealing with the danger presented by a predator. The mechanism maintaining the hunger motivation switches off and cognitive activity involved in reasoning about the discovery of food is stopped, neither being appropriate. A different set of mo-

tivational priorities is created. Mechanisms regulating physiological processes issue new “instructions” making the person physiologically ready for the new sort of behaviors that are now more adaptive: fighting or, more likely, flight. Inferential activity switches to representations of the local terrain, estimates of probable actions by the lion, sources of help and protection from the lion, and so on. The primary motivation becomes the pursuit of safety—a concept specially defined by this emotion state. The modes of operation of the perceptual mechanisms alter radically: Hearing becomes far more acute; danger-relevant stimuli become boosted while danger-irrelevant stimuli are suppressed. The inferential networks underlying the perceptual system interpret ambiguous stimuli (i.e., shadows, masking noise) in a threatening way, creating a higher proportion of true predator detections at the cost of a higher rate of false alarms. Attention-directing mechanisms become fixed on the danger and potential retreats. Similarly, discovering one’s mate in a sexual liaison signals a situation that threatens future reproduction and present investment allocation; this cue should therefore activate sexual jealousy (Daly, Wilson, & Weghorst, 1982; Daly & Wilson, 1988; Buss, 1992). 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 violence; the goal of deterring, injuring, or murdering the rival emerges; the goal of punishing or deserting the mate appears; the desire to make oneself more competitively attractive emerges; memory is activated to reanalyze the past; and so on.

In this view, emotion and “thinking” (i.e., consciously accessible inference) are not parallel processes; rather, emotional states are specific modes of operation of the entire psychological architecture (and, indeed physiological architecture), including whatever inferential processes may be going on. Each emotional state manifests regulatory features “designed” to solve particular families of adaptive problems, whereby the psychological mechanisms assume a unique configuration. Using this approach, each emotional state can be mapped in terms of its characteristic configuration and the particular mode each identifiable mechanism adopts (motivational priorities, inferential algorithms, perceptual mechanisms, physiological mechanisms, attentional direction, emotion signal and intensity, prompted cognitive contents, etc.).

Of course, ever since Darwin (1871, 1872), emotions have been seen as the product of the evolutionary process, and usually, although not always, as functional adaptations (Arnold, 1960, 1968; Chance, 1980; Daly et al., 1982; Darwin, 1872; Eibl-Eibesfeldt, 1975; Ekman, 1982; Frijda, 1986; Hamburg, 1968; Izard, 1977; Otte, 1974; Plutchik, 1980; Tomkins, 1962, 1963; and many others). In fact, much of the best work in evolutionary psychology to date stems from an evolutionary-functional approach to emotions (e.g., Bowlby, 1969; Daly et al., 1982; Ekman, 1982). The particular interpretive framework advanced here (Tooby, 1985; Tooby & Cosmides, 1990b; see also 1990a) is consistent with much of the vast literature on emotion. It is simply an attempt to integrate into a modern adaptation-

ist framework: (a) the idea that the mind consists primarily of a collection of evolved function-specific information-processing mechanisms with such views as that (b) emotions are coordinated systems (Arnold, 1960, 1968; Frijda, 1986; Izard, 1977; Lazarus, Kanner, & Folkman, 1980; Plutchik, 1980), that (c) organize action (Frijda, 1986; Lazarus, 1966) appropriate to situations (Arnold, 1960; Frijda, 1986; Lazarus et al., 1980; Tolman, 1932; see especially Nesse's, 1990, excellent discussion).

To characterize an emotion as an adaptation in information-processing terms, one must identify the following properties of environments and of mechanisms:

1. *A situation*—a recurrent structure of environmental and organismic properties, characterized as a complex statistical composite of how such properties covaried in the environment of evolutionary adaptedness. Examples of situations are being in a depleted nutritional state, competing for maternal attention, being chased by a predator, being about to ambush an enemy, having few friends.
2. *The adaptive problem*—the identification of which organismic states and behavioral sequences will lead to the best average functional outcome, given the situation. For example, what to do given you are being chased by a predator; what to do given you are in a depleted nutritional state.
3. *Cues that signal the presence of the situation*—for example, low blood sugar signals a depleted nutritional state; the looming approach of a large fanged animal signals the presence of a predator; seeing your mate having sex with another signals sexual infidelity; finding yourself consistently alone or avoided by others signals that you have few friends.
4. *Algorithms that monitor for situation-defining cues*—including perceptual mechanisms, proprioceptive mechanisms, and situation-modeling memory.
5. *Algorithms that detect situations*—these mechanisms take the output of the monitoring algorithms in (4) as input, and through integration, probabilistic weighting, and other decision criteria identify situations as either present or absent (or present with some probability).
6. *Algorithms that assign priorities*—a given world-state may correspond to more than one situation at a time, for example, you may be nutritionally depleted *and* in the presence of a predator. The prioritizing algorithms define which emotion modes are compatible (e.g., hunger and boredom), which are mutually exclusive (e.g., feeding and predator escape). Depending on the relative importance of the situations and the reliability of the cues, the prioritizing algorithms decide which emotion modes to activate and deactivate, and to what degree.
7. *An internal communication system*—given that a situation has been detected, the internal communication system sends a situation-specific signal to all relevant mechanisms; the signal switches them into the appropriate adaptive emotion mode.
8. *A set of algorithms specific to each mechanism that regulates how it responds to each specialized emotion state*—these algorithms determine whether the mechanism should switch on or switch off, and if on, what emotion-specialized performance they will implement.

Any controllable biological process that, by shifting its performance in a specifiable way, would lead to enhanced average fitness outcomes should come to be partially governed by emotional state (see [8] above). Such processes include:

*Goals.* The cognitive mechanisms that define goal-states and choose among goals in a planning process should be influenced by emotions. For example, vindictiveness—a specialized subcategory of anger—may define “injuring the offending party” as a goal state to be achieved. (Although the functional logic of this process is deterrence, this function need not be represented, either consciously or unconsciously, by the mechanisms that generate the vindictive behavior.)

*Motivational priorities.* Mechanisms involved in hierarchically ranking goals, or for nonplanning systems, other kinds of motivational and reward systems should be emotion-dependent. What may be extremely unpleasant in one state such as harming another, may seem satisfying in another state (e.g., aggressive competition may facilitate counterempathy).

*Information-gathering motivations.* Because establishing which situation you are in has enormous consequences for the appropriateness of behavior, the process of detection should in fact involve specialized inference procedures and specialized motivations to discover whether certain suspected facts are true or false. What one is curious about, what one finds interesting, what one is obsessed with discovering should all be emotion-specific.

*Imposed conceptual frameworks.* Emotions should prompt construals of the world in terms of concepts that are appropriate to the decisions that must be made. If in an angry mood, domain-specific concepts such as social agency, fault, responsibility, and punishment will be assigned to elements in the situation. If hungry, the food–nonfood distinction will seem salient. If endangered, safety-categorization frames will appear. The world will be carved up into categories based partly on what emotional state an individual is in.

*Perceptual mechanisms.* Perceptual systems may enter emotion-specific modes of operation. When fearful, acuity of hearing may increase. Specialized perceptual inference systems may be mobilized as well: If you've heard rustling in the bushes at night, human and predator figure-detection may be particularly boosted, and not simply visual acuity in general. In fact, nonthreat interpretations may be depressed, and the same set of shadows will “look threatening”—that is, given a specific threatening interpretation such as “a man with a knife”—or not, depending on emotion-state.

*Memory.* The ability to call up particularly appropriate kinds of information out of long-term memory will be influenced. A woman who has just found strong evidence that her husband has been unfaithful may find a torrent of memories about small details that seemed meaningless at the time but that now fit into an interpretation of covert activity. We also expect that what is stored about present experience will also be differentially regulated, with important or shocking events, for example, stored in great detail.

*Attention.* The entire structure of attention, from perceptual systems to the contents of high-level reasoning processes, should be regulated by emotional state. If you are worried that your spouse is late and might have been injured, it is hard to concentrate on other ongoing tasks.

*Physiology.* Each organ system, tissue, or process is a potential candidate for emotion specific regulation, and “arousal” is doubtless insufficiently specific to capture the detailed coordination involved. Changes in circulatory, respiratory, and gastrointestinal functioning are well-known and documented, as are changes in levels of circulating sex hormones. We expect thresholds regulating the contraction of various muscle groups to change with certain emotional states, reflecting the probability that they will need to be employed. Similarly, immune allocation and targeting may vary with disgust, with the potential for injury, or with the demands of extreme physical exertion.

*Communication processes.* What individuals communicate, whether “voluntarily” or “involuntarily,” will be influenced by emotion state. The role of emotional expression as a form of functional communication of situation (including intentions) goes back to Darwin and is widely appreciated (Darwin, 1872; Ekman, 1982).

*Behavior.* All psychological mechanisms are involved in the generation and regulation of behavior, so obviously behavior will be regulated by emotion state. More specifically, however, mechanisms proximately involved in the generation of actions (as opposed to processes like face recognition that are only distally regulatory) should be very sensitive to emotion state. Not only may highly stereotyped behaviors of certain kinds be released (as during sexual arousal or rage, or as with species-typical facial expressions and body language), but more complex action-generation mechanisms should be regulated as well. Specific acts and courses of action will be more available as responses in some states than in others, and more likely to be implemented. Emotion mode should govern the construction of organized behavioral sequences that solve adaptive problems.

*Specialized inference.* Emotion mode should be one factor that governs the activation of specialized inferential systems, such as cheater detection (Cosmides, 1985; Cosmides, 1989; Cosmides & Tooby, 1989), bluff detection, and so on.

*Reflexes.* Muscular coordination, tendency to blink, threshold for vomiting, shaking, and many other reflexes should be regulated by emotion mode.

*Learning.* Emotion mode will also regulate learning mechanisms. What someone learns from stimuli will be greatly altered by emotion mode, because of attentional allocation, motivation, situation-specific inferential algorithms, and a

host of other factors. Emotion mode will cause the present context to be divided up into situation-specific functionally appropriate categories so that the same stimuli and the same environment may be interpreted in radically different ways, depending on emotional state. For example, which stimuli are considered similar should be different in different emotional states, distorting the shape of the individual’s psychological “similarity space” (Shepard, 1987).

*Hedonic evaluation of acts, events, and stimuli.* A behavioral sequence is composed of many acts. Each of these acts can be thought of as an intermediate “factor” in the production of a behavioral sequence. Determining which course of action are worthwhile and which are not is a major informational problem. The payoff of each “factor of production”—of each act in the sequence—must be computed before one can determine whether the whole sequence is worthwhile. Every time there is a change in the world that affects the probable payoff of an act or new information that allows a better evaluation of payoffs, this value needs to be recomputed. Evaluating entire chains as units is not sufficient, because each item in a chain (staying behind from the hunt, making a tool, borrowing materials from a friend, etc.) may be used in another unique sequence at a later time. Therefore, effort, fitness token-payoffs (rewards), risks, and many other components of evaluation need to be assigned continually to classes of acts. For this reason, there should be mechanisms that assign hedonic values to acts, tallied as intermediate weights in decision processes. Our stream of actions and daily experiences will be affectively “colored” by the assignment of these hedonic values. If our psychological mechanisms were not using present outcomes to assign hedonic weights to classes of acts, there would be no function to suffering, joy, and so on. Emotion mode obviously impacts the assignment of hedonic values to acts.

*Energy level and effort allocation.* Overall metabolic budget will of course be regulated by emotion, as will specific allocations to various processes and facilitation or inhibition of specific activities. The effort that it takes to perform given tasks will shift accordingly, with things being easier or more effortful depending on how appropriate they are to the situation reflected by the emotion. Thus, fear will make it more difficult to attack an antagonist, while anger will make it easier. The confidence with which a situation has been identified should itself regulate the effortfulness of situation-appropriate activities. Confusion should inhibit the expenditure of energy on costly behavioral responses and should motivate more information gathering and information analysis.

For a more extended discussion of emotions as architecture-organizing psychological adaptations, and how to relate them to the cue structure of ancestral environments, see Tooby and Cosmides (1990b).

## INDIVIDUAL DIFFERENCES

Of course, mapping a universal evolved psychology would be an empty project if every member of a species had a fundamentally different one. But complex adaptations, including complex psychological adaptations, should tend to be nearly species-typical for humans or any species with an open-breeding system, and at least population-endemic for species with more closed population structures (Tooby & Cosmides, 1990a). Evolutionary constraints on how adaptations must be implemented, as well as recent developments in the theory of the evolution of sexual reproduction and genetic systems can help here: They show how genetic differences can exist within the shared superstructure of universal, complex, adaptively organized psychological mechanisms.

The argument is straightforward (see Tooby & Cosmides, 1990a; see also, Tooby, 1982): (a) A species is a group of organisms defined by their ability to interbreed and form offspring that can equally well reproduce. (b) To survive and reproduce in a complex world, the organism needs complex mechanisms (complex adaptations). (c) Complex adaptations require complex blueprints at the genetic level. This means that they require coordinated gene expression, involving hundreds or thousands of genes to regulate their development. (d) If the genes involved in complex adaptations differed in ways that significantly impacted the design of the component parts, from individual to individual, then, (e) every sexual generation (which breaks apart old combinations and randomly generates new ones) would lead to the break down of complex adaptations. (f) Sexual recombination makes it improbable that all of the necessary genes for a complex adaptation would be together in the same individual if the genes coding for components of complex adaptations varied substantially between individuals. Therefore, (g) humans, and other complex organisms, cannot vary significantly in those genes that underlie their complex adaptations. This applies with equal force to psychological adaptations: Even relatively simple cognitive programs or “mental organs” must contain a large number of interdependent processing steps, limiting the nature of the variation that can exist without violating the functional integrity of psychological adaptations.

These conclusions are well supported by observations on human and non-human physiology. One can flip open *Gray's Anatomy* to any page and discover it describes down to fine detail the architecture of any normal human from anywhere on the planet. The “architecture” or physiological and neurobiological design of humans is both distinctively species-specific and species-typical. When one examines the organs, with their complex design and interlocking architecture, one finds (within an age and sex, and to a large extent between sexes) monomorphism of design: Everyone has two lungs, one neck, blood, hemoglobin, insulin, and so on. And, although there is a great deal of superficial variation—no two hands are exactly the same size—each organ system has the same basic design: The locations and connections between organs are topologically the same, and the internal tissue structures and physiological processes have a uniformity of structure and func-

tional regulation. One has to descend to specific enzymatic pathways before design differences—as opposed to quantitative variation—start showing up: Individual proteins may indeed differ due to genetic differences between individuals, but genetically specified, coordinated functional variation in biochemical pathways between individuals of the same sex and age is very rare.<sup>3</sup>

In short, although there is a large amount of variation among humans concerning single or quantitative characteristics of specific organ systems, there is almost *no variation* among humans in what organs exist, or the basic design of each organ system. Everyone has a heart, and a liver, and so on, and everyone's heart and liver function in much the same way. We expect that this pattern holds for “mental organs” as well. Such variation, whether it is of “physical” or “mental” organ systems, can modify the functioning of these systems between individuals—sometimes drastically. Phenylketonuria is the result of a single gene modification. Nevertheless, such variation must be recognized as modifications of a design whose integrity is largely intact and is not likely to consist of a wholly different design, differing “from the ground up.” We find implausible, on the basis of population genetics considerations, the notion that different humans have fundamentally different and competing cognitive programs, resting on wholly different genetic bases. For this reason, individuals should be slightly noisy versions of species-typical designs, perturbed in many minor fashions by genetic noise in superficial properties. Consequently, heritable psychological differences are not themselves likely to be complex psychological adaptations. Thus, we believe that behavioral scientists can most effectively devote most of their early research effort to elucidating the most commonly shared and basic design features of a species' cognitive programs. (For further development of this argument, and its application to the study of both species-typical design and individual differences, see Tooby & Cosmides, 1990a.)

In this view, individual differences are primarily explained by different environmental factors being fed into the same species-typical design: a standard psychological view. This is why regularities must be found at the level of mechanisms, and not behavior itself. For example, individual differences may be caused when wholly different cognitive programs become activated in different individuals, although they exist latently in all individuals, based on a species-typical genetic basis. Such facultative programs can be differentially activated early in the life cycle (setting individuals along different developmental tracks), by short-term situational elicitation, or even as the result of superficial (in the sense discussed earlier) genetic differences in other parts of the genome (e.g., constitutional differences or gender).

<sup>3</sup>Nonetheless, it is well established that there is a remarkable amount of genetic diversity in humans, and other similar species. What is it doing there? There seems to be good reason to believe that it is there in order to create variation that is superficial from the point of view of functional architecture but that enhances defenses against infectious disease (see, e.g., Hamilton & Zuk, 1982; Tooby, 1982). That is, it seems likely to be the result of parasite-driven frequency-dependent selection for biochemical individuality, supplemented by other by-products of the evolutionary process, such as mutations and selectively neutral variants drifting through the population.

## CONCLUSIONS

Many evolutionary biologists seem to think that once they have identified an adaptive function, their job is done: Specifying how the organism accomplishes the function is a trivial matter. This is comparable to thinking that once Einstein had derived the equation  $E = mc^2$ , designing a nuclear power plant was a trivial matter. Understanding what properties a cognitive program must have if it is to accomplish an adaptive function is far from trivial—it is one of the most challenging problems facing modern researchers. But it is an illuminating enterprise.

There is emerging a new approach, usually called evolutionary psychology, which is made possible by the simultaneous maturation of behavioral ecology, evolutionary biology, paleobiology, cognitive psychology, and neuroscience. Together, these disciplines allow the discovery and principled investigation of the set of evolved information-processing adaptations that constitute one important description of human and nonhuman psychological architecture. We propose that they be combined according to the following guidelines:

1. Use the principles of natural selection as a starting point to develop models of the adaptive problems that the species of interest had to solve.
2. Attempt to determine how these adaptive problems would have manifested themselves in the species' environment of evolutionary adaptedness, insofar as this is possible. Recurrent environmental features relevant to the adaptive problem, including constraints and relationships that existed in the social, ecological, genetic, and physical situation of the species should be specified; these constitute the conditions in which the adaptive problem arose and further define the nature of the adaptive problem. Such features and relationships constitute the only environmental information available to whatever cognitive program evolved to solve the adaptive problem. The structure of the cognitive program must be such that it can guide behavior along adaptive paths given only the information available to it in these conditions.
3. Integrate the model of the selection pressures with available knowledge of the relevant ancestral conditions, drawing whatever valid and useful implications can be derived from this set of constraints. Catalog the specific information-processing problems that must be solved if the adaptive function is to be accomplished. This constitutes a computational theory of the adaptive information-processing problem. The computational theory is then used as a heuristic for generating testable hypotheses about the structure of the cognitive programs that solve the adaptive problem in question.
4. Use the computational theory to (a) determine whether there are design features that any cognitive program capable of solving the adaptive problem must have, and (b) develop candidate models of the structure of the cognitive programs that the species in question might have evolved to solve the adaptive problem. Be sure the model proposed is, in principle, powerful enough to solve the problem defined in the computational theory.
5. Eliminate alternative candidate models with experiments and field observation. Cognitive psychologists have already developed an impressive array of concepts and experimental methods for tracking complex information-processing systems—these should be used to full advantage. The end result is a validated model of the cogni-

tive programs in question, together with a model of what environmental information, and other factors, these programs take as input.

6. Finally, compare the model against the patterns of manifest behavior that are produced by modern conditions. Informational inputs from modern environments should produce the patterns of manifest behavior predicted by the model of the cognitive programs already developed.

As previously discussed, some who adopt the evolutionary perspective attempt to leap directly from Step 1 to Step 6, neglecting the intermediate steps, searching only for correspondences between evolutionary theory and modern manifest behavior. However, because they leave the causal chain by which evolution influences behavior vague and unspecified, such attempts have sown the widespread confusion that (in the human case) hypotheses about economics, culture, consciousness, learning, rationality, social forces, and so on, constitute distinct alternative hypotheses to evolutionary or “biological” explanations. Instead, such hypotheses are more properly viewed as proposals about the structure of evolved cognitive programs and the kinds of information they take as input. They contain implicit theories about how these evolved cognitive programs interact with information derived from modern environments.

Cognitive psychology and evolutionary biology are sister disciplines. The goal of evolutionary theory is to define the adaptive problems that organisms must be able to solve. The goal of cognitive psychology is to discover the information-processing mechanisms that have evolved to solve them. Alone, each is incomplete for the understanding of behavior. Together, applied as a unified research program, they offer the promise that the level of analysis appropriate for describing and investigating behavior has, at last, been found.

## REFERENCES

- Arnold, M. B. (1960). *Emotion and personality*. New York: Columbia University Press.
- Arnold, M. B. (1968). *The nature of emotion*. London: Penguin Books.
- Atherton, M., & Schwartz, R. (1974). Linguistic innateness and its evidence. *The Journal of Philosophy*, 71, 6.
- Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, 211, 1390–1396.
- Barkow, J. H., Cosmides, L., & Tooby, J. (Eds.). (1992). *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press.
- Beach, F. A. (1955). The snark is a boojum. *American Psychologist*, 5, 115–124.
- Block, N. (1980). What is functionalism? In N. Block (Ed.), *Readings in philosophy of psychology*. Cambridge, MA: Harvard University Press.
- Boden, M. (1977). *Artificial intelligence and natural man*. New York: Basic Books.
- Bowlby, J. (1969). *Attachment and Loss, Volume 1*. New York: Basic Books.
- Breland, K., & Breland, M. (1961). The misbehavior of organisms. *American Psychologist*, 16, 681–684.
- Bruner, J. S. (1973). *Beyond the information given*. (J. M. Anglin, Ed.). New York: Norton.
- Buss, D. M. (1987). Sex differences in human mate selection criteria: An evolutionary perspective. In C. B. Crawford, M. F. Smith, & D. L. Krebs (Eds.), *Sociobiology and psychology*. Hillsdale, NJ: Erlbaum.

- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12, 1–49.
- Buss, D. M. (1991). Evolutionary personality psychology. *Annual Review of Psychology*, 42, 459–491.
- Buss, D. M. (1992). Mate preference mechanisms: Consequences for partner choice and intrasexual competition. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press.
- Buss, D. M. (1994). *The evolution of desire*. New York: Basic Books.
- Cheng, P. W., & Holyoak, K. J. (1985). Pragmatic reasoning schemas. *Cognitive Psychology* 17, 391–416.
- Chance, M. R. A. (1980). An ethological assessment of emotion. In R. Plutchik & H. Kellerman (Eds.), *Emotion: Theory, research, and experience* (pp. 81–111). New York: Academic Press.
- Chomsky, N. (1957). *Syntactic structures*. The Hague: Mouton & Co.
- Chomsky, N. (1959). Review of Skinner's "Verbal Behavior." *Language*, 35, 26–58.
- Chomsky, N. (1975). *Reflections on language*. New York: Random House.
- Chomsky, N. (1980). *Rules and representations*. New York: Columbia University Press.
- Cosmides, L. (1985). Deduction or Darwinian algorithms?: An explanation of the "elusive" content effect on the Wason selection task. Doctoral dissertation, Department of Psychology and Social Relations, Harvard University, Cambridge, MA.
- Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, 31, 187–276.
- Cosmides, L., & Tooby J. (1981). Cytoplasmic inheritance and intragenomic conflict. *Journal of Theoretical Biology* 89, 83–129.
- Cosmides, L., & Tooby, J. (1987). From evolution to behavior: Evolutionary psychology as the missing link. In J. Dupre (Ed.), *The latest on the best: Essays on evolution and optimality*. Cambridge, MA: MIT Press.
- Cosmides, L., & Tooby, J. (1989). Evolutionary psychology and the generation of culture, Part II. Case study: A computational theory of social exchange. *Ethology & Sociobiology*, 10, 51–97.
- Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press.
- Cosmides, L., Tooby, J., & Barkow, J. (1992). Evolutionary psychology and conceptual integration. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press.
- Crawford, C. B., Smith, M. F., & Krebs, D. L. (Eds.). (1987). *Sociobiology and psychology*. Hillsdale, NJ: Erlbaum.
- Crawford, C. B., & Anderson, J. L. (1989). Sociobiology: An environmentalist discipline? *American Psychologist*, 44(12), 1449–1459.
- Daly, M., & Wilson, M. (1981). Abuse and neglect of children in evolutionary perspective. In R. D. Alexander & D. W. Tinkle (Eds.), *Natural selection and social behavior*. New York: Chiron.
- Daly, M., & Wilson, M. (1982). Homicide and kinship. *American Anthropologist*, 84, 372–378.
- Daly, M., & Wilson, M. (1984). A sociobiological analysis of human infanticide. In G. Hausfater & S. Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp. 487–502). New York: Aldine de Gruyter.
- Daly, M., & Wilson, M. (1987a). Evolutionary psychology and family violence. In C. B. Crawford, M. F. Smith, & D. L. Krebs (Eds.), *Sociobiology and psychology*. Hillsdale, NJ: Erlbaum.
- Daly, M., & Wilson, M. (1987b). The Darwinian psychology of discriminative parental solicitude. *Nebraska Symposium on Motivation*, 35, 91–144.
- Daly, M., & Wilson, M. (1988). *Homicide*. New York: Aldine.
- Daly, M., Wilson, M., & Weghorst, S. J. (1982). Male sexual jealousy. *Ethology and Sociobiology*, 3, 11–27.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: Murray.
- Darwin, C. (1872). *The expression of emotion in man and animals*. London: Murray.
- Dawkins, R. (1976). *The selfish gene*. New York: Oxford University Press.
- Dawkins, R. (1982). *The extended phenotype*. San Francisco: W. H. Freeman.
- Dawkins, R. (1986). *The blind watchmaker*. New York: Norton.
- Dupre, J. (Ed.). (1987). *The latest on the best: Essays on evolution and optimality*. Cambridge, MA: MIT Press.

- Eibl-Eibesfeldt, I. (1975). *Ethology: The biology of behavior* (2nd ed.). New York: Holt, Rinehart and Winston.
- Ekman, P. (Ed.). (1982). *Emotion in the human face* (2nd ed.). Cambridge, UK: Cambridge University Press.
- Erickson, C. J., & Zenone, P. G. (1976). Courtship differences in male ring doves: Avoidance of cuckoldry? *Science*, 192, 1353–1354.
- Fodor, J. A. (1981). The mind-body problem. *Scientific American*, 244(1), 124–133.
- Fodor, J. A. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.
- Fodor, J. A., & Pylyshyn, Z. (1988). Connectionism and cognitive architecture: A critical analysis. *Cognition*, 28, 3–71.
- Frijda, N. H. (1986). *The emotions*. London: Cambridge University Press.
- Galef, B. G. (1990). An adaptationist perspective on social learning, social feeding, and social foraging in Norway rats. In D. Dewsbury (Ed.), *Contemporary issues in comparative psychology*. Sunderland, MA: Sinauer.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Garcia, J., & Koelling, R. A. (1966). Relations of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123–124.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian program: A critique of the adaptationist programme. *Proceedings of the Royal Society of London*, 205, 281–288.
- Grimshaw, J. (1981). Form, function, and the language acquisition device. In C. L. Baker & J. J. McCarthy (Eds.), *The logical problem of language acquisition*. Cambridge, MA: MIT Press.
- Hamburg, D. A. (1968). Emotions in the perspective of human evolution. In S. L. Washburn & P. C. Jay (Eds.), *Perspectives on human evolution* (pp. 246–257). New York: Holt.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology* 7, 1–52.
- Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, 218, 382–387.
- Hausfater, G., & Hrdy, S. (Eds.). (1984). *Infanticide: Comparative and evolutionary perspectives*. New York: Aldine de Gruyter.
- Heath, S. B. (1983). *Ways with words: Language, life, and work in communities and classrooms*. New York: Cambridge University Press.
- Hermstein, R. J. (1977). The evolution of behaviorism. *American Psychologist*, 32, 593–603.
- Holmes, W. G. (1983). Kin recognition in animals. *American Scientist*, 71, 46–55.
- Hrdy, S. B. (1977). *The langurs of Abu*. Cambridge, MA: Harvard University Press.
- Hume, D. (1977). *An enquiry concerning human understanding* (E. Steinberg, Ed.) Indianapolis: Hackitt. (Original work published 1748)
- Izard, C. E. (1977). *Human emotions*. New York: Plenum.
- Jacobs, R. A., Jordan, M. I., & Barto, A. G. (1990). *Task decomposition through competition in a modular connectionist architecture: The what and where vision tasks* (COINS Technical Report 90-27). Dept. of Computer & Information Science, University of Massachusetts, Amherst, MA 01003.
- Kant, I. (1966). *Critique of pure reason*. New York: Anchor Books. (Original work published 1781)
- Katz, J. J. (1975). Innate ideas. In S. P. Stich (Ed.), *Innate ideas*. Berkeley: University of California Press.
- Konner, M. (1982). *The tangled wing: Biological constraints on the human spirit*. New York: Holt, Rinehart and Winston.
- Krebs, J., & Davis, N. (1984). *Behavioural ecology: An evolutionary approach* (2nd ed.). Oxford: Blackwell Scientific Publications.
- Lazarus, R. (1966). *Psychological stress and the coping process*. New York: McGraw-Hill.
- Lazarus, R., Kanner, A., & Folkman, S. (1980). Emotions: A cognitive-phenomenological analysis. In R. Plutchik & H. Kellerman (Eds.), *Emotion: Theory, research and experience: Vol 1. Theories of emotion* (pp. 189–217). New York: Academic Press.
- Lewontin, R. (1978). Adaptation. *Scientific American*, 239, 157–169.
- Lockard, R. (1971). Reflections on the fall of comparative psychology: Is there a message for us all? *American Psychologist*, 26, 22–32.
- Lorenz, K. (1965). *Evolution and the modification of behavior*. Chicago: University of Chicago Press.

- Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: W. H. Freeman.
- Marr, D., & Nishihara, H. K. (1978, October). Visual information processing: Artificial intelligence and the sensorium of sight. *Technology Review*, pp. 28–49.
- Marshall, J. C. (1981). Cognition at the crossroads. *Nature*, 289, 613–614.
- Maynard Smith, J. (1978). Optimization theory in evolution. *Annual Review of Ecology and Systematics*, 9, 31–56.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.
- Maynard Smith, J., & Price, G. A. (1973). The logic of animal conflict. *Nature* (London), 246, 15–18.
- Miller, G. F., & Todd, P. M. (1990). Exploring adaptive agency: I. Theory and methods for simulating the evolution of learning. In D. S. Touretski, J. L. Elman, T. J. Sejnowski, & G. E. Hinton (Eds.), *Proceedings of the 1990 Connectionist Models Summer School* (pp. 65–80). San Mateo, CA: Morgan Kaufman.
- Minsky, M. (1977). Frame-system theory. In P. N. Johnson-Laird & P. C. Wason (Eds.), *Thinking: Readings in cognitive science*. Cambridge, UK: Cambridge University Press.
- Nesse, R. M. (1990). Evolutionary explanations of emotions. *Human Nature*, 1, 261–289.
- Orians, G., & Heerwagen, J. (1992). Evolved responses to landscapes. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 555–579). New York: Oxford University Press.
- Otte, D. (1974). Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics*, 5, 385–417.
- Pinker, S. (1979). Formal models of language learning. *Cognition*, 7, 217–283.
- Pinker, S. (1982). A theory of the acquisition of lexical interpretive grammars. In J. Bresnan (Ed.), *The mental representation of grammatical relations*. Cambridge, MA: MIT Press.
- Pinker, S. (1984). *Language learnability and language development*. Cambridge, MA: Harvard University Press.
- Pinker, S. (1989). *Learnability and cognition: The acquisition of argument structure*. Cambridge, MA: MIT Press.
- Pinker, S. (1991). Rules of language. *Science*, 253, 530–535.
- Pinker, S., & Bloom (1990). Natural language and natural selection. *Behavioral and Brain Sciences*, 13(4), 707–784. (Reprinted in J. Barkow, L. Cosmides, & J. Tooby [Eds.], *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press.)
- Pinker, S., & Prince, A. (1988). On language and connectionism: Analysis of a parallel distributed processing model of language acquisition. *Cognition*, 28, 73–193.
- Plutchik, R. (1980). *Emotion: A psychoevolutionary synthesis*. New York: Harper & Row.
- Popper, K. R. (1972). *Objective knowledge: An evolutionary approach*. London: Oxford University Press.
- Putnam, H. (1967). The “innateness hypothesis” and explanatory models in linguistics. *Synthese*, 17, 12–22.
- Pylyshyn, Z. W. (1984). *Computation and cognition: Toward a foundation for cognitive science*. Cambridge, MA: MIT Press.
- Quine, W. V. O. (1969). *Ontological relativity and other essays*. New York: Columbia University Press.
- Real, L. A. (1991). Animal choice behavior and the evolution of cognitive architecture. *Science*, 253, 980–986.
- Rozin, P. (1976). The evolution of intelligence and access to the cognitive unconscious. In J. M. Sprague & A. N. Epstein (Eds.), *Progress in psychobiology and physiological psychology*. New York: Academic Press.
- Rozin, P., & Schull, J. (1988). The adaptive-evolutionary point of view in experimental psychology. In R. C. Atkinson, R. J. Herrnstein, G. Lindsey, & R. D. Luce (Eds.), *Stevens's handbook of experimental psychology*. New York: Wiley.
- Schank, R., & Abelson, R. P. (1977). *Scripts, plans, goals, and understanding*. Hillsdale, NJ: Erlbaum.
- Seligman, M. E. P., & Hager, J. L. (1972). *Biological boundaries of learning*. New York: Meredith.
- Shepard, R. N. (1981). Psychophysical complementarity. In M. Kubovy & J. R. Pomerantz (Eds.), *Perceptual organization*. Hillsdale, NJ: Erlbaum.
- Shepard, R. N. (1984). Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychological Review*, 91, 417–447.
- Shepard, R. N. (1987). Evolution of a mesh between principles of the mind and regularities of the world. In J. Dupre (Ed.), *Evolution and information*. Cambridge, MA: MIT Press.
- Shepher, J. (1983). *Incest: A biosocial view*. New York: Academic Press.
- Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. *Psychological Review*, 94, 439–454.
- Shettleworth, S. J. (1972). Constraints on learning. In D. S. Lehrman, R. A. Hinde, & E. Shaw, (Eds.), *Advances in the study of behavior* (vol. 4). New York: Academic Press.
- Skinner, B. F. (1957). *Verbal behavior*. New York: Appleton.
- Staddon, J. E. R. (1987). Optimality theory and behavior. In J. Dupre (Ed.), *Evolution and information*. Cambridge, MA: MIT Press.
- Staddon, J. E. R. (1988). Learning as inference. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning*. Hillsdale, NJ: Erlbaum.
- Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.
- Symons, D. (1987). If we're all Darwinians, what's the fuss about? In C. B. Crawford, M. F. Smith, & D. L. Krebs (Eds.), *Sociobiology and psychology* (pp. 121–146). Hillsdale, NJ: Erlbaum.
- Symons, D. (1989). A critique of Darwinian anthropology. *Ethology and Sociobiology*, 10, 131–144.
- Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 137–159). New York: Oxford University Press.
- Thornhill, R. (1991). The study of adaptation. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and explanation in the study of behavior*. Boulder, CO: Westview Press.
- Tinbergen, N. (1951). *The study of instinct*. New York: Oxford University Press.
- Todd, P. M., & Miller, G. F. (1991a). Exploring adaptive agency: II. Simulating the evolution of associative learning. In J. A. Meyer & S. W. Wilson (Eds.), *From animals to animats: Proceedings of the First International Conference of Simulation of Adaptive Behavior* (pp. 306–315). Cambridge, MA: MIT Press.
- Todd, P. M., & Miller, G. F. (1991b). Exploring adaptive agency: III. Simulating the evolution of habituation and sensitization. In H. P. Schwefel & R. Manner (Eds.), *Parallel problem solving from nature* (pp. 307–313). Berlin: Springer-Verlag.
- Tolman, E. C. (1932). *Purposive behavior in animals and men*. New York: Appleton-Century-Crofts.
- Tooby, J. (1982). Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology*, 97, 557–576.
- Tooby, J. (1985). The emergence of evolutionary psychology. In D. Pines (Ed.), *Emerging syntheses in science*. Proceedings of the Founding Workshops of the Santa Fe Institute. Santa Fe, NM: The Santa Fe Institute.
- Tooby, J., & Cosmides, L. (1989a). Evolutionary psychology and the generation of culture: Part I. Theoretical considerations. *Ethology & Sociobiology*, 10, 29–49.
- Tooby, J., & Cosmides, L. (1989b). Adaptation versus phylogeny: The role of animal psychology in the study of human behavior. *International Journal of Comparative Psychology*, 2(3), 105–118.
- Tooby, J., & Cosmides, L. (1990a). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*, 58, 17–67.
- Tooby, J., & Cosmides, L. (1990b). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375–424.
- Tooby, J., & Cosmides, L. (1990c). Toward an adaptationist psycholinguistics. *Behavioral and Brain Sciences*, 13(4), 760–762.
- Tooby, J., & Cosmides, L. (1992). Psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.
- Tooby, J., & DeVore, I. (1987). The reconstruction of hominid behavioral evolution through strategic modeling. In W. Kinzey (Ed.), *Primate models of hominid behavior* (pp. 183–237). Albany, New York: SUNY Press.
- Tomkins, S. S. (1962). *Affect, imagery, consciousness* (Vol. I). New York: Springer.
- Tomkins, S. S. (1963). *Affect, imagery, consciousness* (Vol. II). New York: Springer.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man 1871–1971*. Chicago: Aldine.
- Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14, 249–264.



- Wanner, E., & Gleitman, L. R. (1982). *Language acquisition: The state of the art*. Cambridge, UK: Cambridge University Press.
- Wexler, K., & Culicover, P. (1980). *Formal principles of language acquisition*. Cambridge, MA: MIT Press.
- Wilkinson, G. S. (1988). Reciprocal altruism in bats and other mammals. *Ethology and Sociobiology*, 9, 85–100.
- Wilkinson, G. S. (1990, February). Food sharing in vampire bats. *Scientific American*, pp. 76–82.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Harvard University Press.
- Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology*, 6, 59–73.
- Wilson, M., & Daly, M. (1987). Risk of maltreatment of children living with step-parents. In R. Gelles & J. Lancaster (Eds.), *Child abuse and neglect: Biosocial dimensions* (pp. 215–232). New York: Aldine de Gruyter.
- Wilson, M., & Daly, M. (1992). The man who mistook his wife for a chattel. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 289–322). New York: Oxford University Press.
- Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton, NJ: Princeton University Press.
- Williams, G. C. (1985). A defense of reductionism in evolutionary biology. *Oxford Surveys in Evolutionary Biology*, 2, 1–27.
- Williams, G. C., & Williams, D. C. (1957). Natural selection of individually harmful social adaptations among sibs with special reference to social insects. *Evolution*, 17, 249–253.