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80 Toward Mapping the Evolved Functional Organization of Mind and Brain

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ABSTRACT The human brain is a biological system produced by the evolutionary process, and thus, cognitive neuroscience is itself a branch of evolutionary biology. Accordingly, cognitive neuroscientists can benefit by learning about and applying the technical advances made in modern evolutionary biology. Among other things, evolutionary biology can supply researchers with (1) the biologically rigorous concept of function appropriate to neural and cognitive systems, (2) a growing list of the specialized functions the human brain evolved to perform, and (3) the ability to distinguish the narrowly functional aspects of the neural and cognitive architecture that are responsible for its organization from the much larger set of properties that are by-products or noise. With these and other tools, researchers can construct experimental stimuli and tasks that activate and are meaningful to functionally dedicated subunits of the brain. The brain is comprised of many such subunits: evolutionarily meaningful stimuli and tasks are far more likely than arbitrary ones to elicit responses that can illuminate their complex functional organization.

Nothing in biology makes sense except in the light of evolution.
– T. Dobzhansky

It is the theory which decides what we can observe.
– A. Einstein

Seeing with new eyes: Toward an evolutionarily informed cognitive neuroscience

The task of cognitive neuroscience is to map the information-processing structure of the human mind and to discover how this computational organization is implemented in the physical organization of the brain. The central impediment to progress is obvious: The human brain is, by many orders of magnitude, the most complex system that humans have yet investigated. Purely as a physical system, the vast intricacy of chemical and electrical interactions among hundreds of billions of neurons and glial cells defeats any straightforward attempt to build a comprehensive model, as one might at-

tempt to do with particle collisions, geological processes, protein folding, or host-parasite interactions. Combinatorial explosion makes the task of elucidating the brain's computational structure even more overwhelming: There is an indefinitely large number of specifiable inputs, measurable outputs, and possible relationships between them. Even worse, no one yet knows with certainty how computations are physically realized. They depend on individuated events within the detailed structure of neural microcircuitry largely beyond the capacity of current technologies to observe or resolve. Finally, the underlying logic of the system has been obscured by the torrent of recently generated data.

Historically, however, well-established theories from one discipline have functioned as organs of perception for others (e.g., statistical mechanics for thermodynamics). They allow new relationships to be observed and make visible elegant systems of organization that had previously eluded detection. It seems worth exploring whether evolutionary biology could provide a rigorous metatheoretical framework for the brain sciences, as they have recently begun to do for psychology (Shepard, 1984, 1987a, 1987b; Gallistel, 1990; Cosmides and Tooby, 1987; Pinker, 1994, 1997; Marr 1982; Tooby and Cosmides, 1992).

Cognitive neuroscience began with the recognition that the brain is an organ designed to process information and that studying it as such would offer important new insights. Cognitive neuroscientists also recognize that the brain is an evolved system, but few realize that anything follows from this second fact. Yet these two views of the brain are intimately related and, when considered jointly, can be very illuminating.

Why brains exist

The brain is an organ of computation that was built by the evolutionary process. To say that the brain is an organ of computation means that (1) its physical structure embodies a set of programs that process information, and (2) that physical structure is there *because* it embodies these programs. To say that the brain was built

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by the evolutionary process means that its functional components—its programs—are there *because* they solved a particular problem-type in the past. In systems designed by natural selection, function determines structure.

Among living things, there are whole kingdoms filled with organisms that lack brains (plants, Monera, fungi). The sole reason that evolution introduced brains into the designs of some organisms—the reason brains exist at all—is because brains performed computations that regulated these organisms' internal processes and external activities in ways that promoted their fitness. For a randomly generated modification in design to be selected—that is, for a mutation to be incorporated by means of a nonrandom process into a species-typical brain design—it had to improve the ability of organisms to solve adaptive problems. That is, the modification had to have a certain kind of effect: It had to improve the organisms' performance of some activity that systematically enhanced the propagation of that modification, summed across the species' range and across many generations. This means that the design of the circuits, components, systems, or modules that make up our neural architecture must reflect, to an unknown but high degree, (1) the computational task demands inherent in the performance of those ancestral activities and (2) the evolutionarily long-enduring structure of those task environments (Marr, 1982; Shepard, 1987a; Tooby and Cosmides, 1992).

Activities that promoted fitness in hominid ancestral environments differ in many ways from activities that capture our attention in the modern world, and they were certainly performed under radically different circumstances. (Consider: hunting *vs.* grocery shopping; walking everywhere *vs.* driving and flying; cooperating within a social world of ~200 relatives and friends *vs.* 50,000 strangers in a medium-sized city). The design features of the brain were built to specifications inherent in ancestral adaptive problems and selection pressures, often resulting in talents or deficits that seem out of place or irrational in our world. A baby cries—alerting her parents—when she is left to sleep alone in the dark, not because hyenas roam her suburban household, but because her brain is designed to keep her from being eaten under the circumstances in which our species evolved.

There is no single algorithm or computational procedure that can solve every adaptive problem (Cosmides and Tooby, 1987; Tooby and Cosmides, 1990a, 1992). The human mind (it will turn out) is composed of many different programs for the same reason that a carpenter's toolbox contains many different tools: Different problems require different solutions. To reverse-engineer the

brain, one needs to discover functional units that are native to its organization. To do this, it is useful to know, as specifically as possible, what the brain is for—which specific families of computations it was built to accomplish and what counted as a biologically successful outcome for each problem-type. The answers to this question must be phrased in computational terms because that is the only language that can capture or express the functions that neural properties were naturally selected to embody. They must also refer to the ancestral activities, problems, selection pressures, and environments of the species in question because jointly these define the computational problems each component was configured to solve (Cosmides and Tooby 1987; Tooby and Cosmides, 1990a, 1992).

For these reasons, evolutionary biology, biological anthropology, and cognitive psychology (when integrated, called *evolutionary psychology*) have the potential to supply to cognitive neuroscientists what might prove to be a key missing element in their research program: a partial list of the native information-processing functions that the human brain was built to execute, as well as clues and principles about how to discover or evaluate adaptive problems that might be proposed in the future.

Just as the fields of electrical and mechanical engineering summarize our knowledge of principles that govern the design of human-built machines, the field of evolutionary biology summarizes our knowledge of the engineering principles that govern the design of organisms, which can be thought of as machines built by the evolutionary process (for overviews, see Daly and Wilson, 1984; Dawkins, 1976, 1982, 1986; Krebs and Davies, 1997). Modern evolutionary biology constitutes, in effect, a foundational “organism design theory” whose principles can be used to fit together research findings into coherent models of specific cognitive and neural mechanisms (Tooby and Cosmides, 1992). To apply these theories to a particular species, one integrates analyses of selection pressures with models of the natural history and ancestral environments of the species. For humans, the latter are provided by hunter-gatherer studies, biological anthropology, paleoanthropology, and primatology (Lee and DeVore, 1968).

First principles: Reproduction, feedback, and the entropic construction of organic design

Within an evolutionary framework, an organism can be described as a self-reproducing machine. From this perspective, the defining property of life is the presence in a system of “devices” (organized components) that cause the system to construct new and similarly reproducing

systems. From this defining property—self-reproduction—the entire deductive structure of modern Darwinism logically follows (Dawkins, 1976; Williams, 1985; Tooby and Cosmides, 1990a). Because the replication of the design of the parental machine is not always error free, randomly modified designs (i.e., mutants) are introduced into populations of reproducers. Because such machines are highly organized so that they cause the otherwise improbable outcome of constructing offspring machines, most random modifications interfere with the complex sequence of actions necessary for self-reproduction. Consequently, such modified designs will tend to remove themselves from the population—a case of negative feedback.

However, a small residual subset of design modifications will, by chance, happen to constitute improvements in the design's machinery for causing its own reproduction. Such improved designs (by definition) cause their own increasing frequency in the population—a case of positive feedback. This increase continues until (usually) such modified designs outreproduce and thereby replace all alternative designs in the population, leading to a new species-standard design. After such an event, the population of reproducing machines is different from the ancestral population: The population- or species-standard design has taken a step “uphill” toward a greater degree of functional organization for reproduction than it had previously. This spontaneous feedback process—natural selection—causes functional organization to emerge *naturally*, that is, without the intervention of an intelligent “designer” or supernatural forces.

Over the long run, down chains of descent, this feedback cycle pushes designs through state-space toward increasingly well-organized—and otherwise improbable—functional arrangements (Dawkins 1986; Williams, 1966, 1985). These arrangements are functional in a specific sense: the elements are improbably well organized to cause their own reproduction in the environment in which the species evolved. Because the reproductive fates of the inherited traits that coexist in the same organism are linked together, traits will be selected to enhance each other's functionality (however, see Cosmides and Tooby, 1981, and Tooby and Cosmides, 1990a, for the relevant genetic analysis and qualifications). As design features accumulate, they will tend to sequentially fit themselves together into increasingly functionally elaborated machines for reproduction, composed of constituent mechanisms—called *adaptations*—that solve problems that either are necessary for reproduction or increase its likelihood (Darwin, 1859; Dawkins, 1986; Thornhill, 1991; Tooby and Cosmides, 1990a; Williams, 1966, 1985). Significantly, in species like humans, genetic processes ensure that complex adaptations virtu-

ally always are species-typical (unlike nonfunctional aspects of the system). This means that *functional* aspects of the architecture will tend to be universal at the genetic level, even though their expression may often be sex or age limited, or environmentally contingent (Tooby and Cosmides, 1990b).¹

Because design features are embodied in individual organisms, they can, generally speaking, propagate themselves in only two ways: by solving problems that increase the probability that offspring will be produced either by the organism they are situated in or by that organism's kin (Hamilton, 1964; Williams and Williams, 1957; however, see Cosmides and Tooby, 1981, and Haig, 1993, for intragenomic methods). An individual's relatives, by virtue of having descended from a recent common ancestor, have an increased likelihood of having the same design feature as compared to other conspecifics. This means that a design modification in an individual that causes an increase in the reproductive rate of that individual's kin will, by so doing, tend to increase its own frequency in the population. Accordingly, design features that promote both direct reproduction and kin reproduction, and that make efficient trade-offs between the two, will replace those that do not. To put this in standard biological terminology, design features are selected to the extent that they promote their inclusive fitness (Hamilton, 1964).

In addition to selection, mutations can become incorporated into species-typical designs by means of chance processes. For example, the sheer impact of many random accidents may cumulatively propel a useless mutation upward in frequency until it crowds out all alternative design features from the population. Clearly, the presence of such a trait in the architecture is not explained by the (nonexistent) functional consequences that it had over many generations on the design's reproduction; as a result, chance-injected traits will not tend to be coordinated with the rest of the organism's architecture in a functional way.

Although such chance events play a restricted role in evolution and explain the existence and distribution of many simple and trivial properties, organisms are not primarily chance agglomerations of stray properties. Reproduction is a highly improbable outcome in the absence of functional machinery designed to bring it about, and only designs that retain all the necessary machinery avoid being selected out. To be invisible to selection and, therefore, not organized by it a modification must be so minor that its effects on reproduction are negligible. As a result, chance properties do indeed drift through the standard designs of species in a random way, but they are unable to account for the complex organized design in organisms and are, correspondingly,

usually peripheralized into those aspects that do not make a significant impact on the functional operation of the system (Tooby and Cosmides, 1990a, 1990b, 1992). Random walks do not systematically build intricate and improbably functional arrangements such as the visual system, the language faculty, face recognition programs, emotion recognition modules, food aversion circuits, cheater detection devices, or motor control systems, for the same reason that wind in a junkyard does not assemble airplanes and radar.

Brains are composed primarily of adaptive problem-solving devices

In fact, natural selection is the only known cause of and explanation for complex functional design in organic systems. Hence, all naturally occurring functional organization in organisms should be ascribed to its operation, and hypotheses about function are likely to be correct only if they are the kinds of functionality that natural selection produces.

This leads to the most important point for cognitive neuroscientists to abstract from modern evolutionary biology: Although not everything in the designs of organisms is the product of selection, all complex functional organization is. Indeed, selection can only account for functionality of a very narrow kind: approximately, design features organized to promote the reproduction of an individual and his or her relatives in ancestral environments (Williams, 1966; Dawkins, 1986). Fortunately for the modern theory of evolution, the only naturally occurring complex functionality that ever has been documented in undomesticated plants, animals, or other organisms is functionality of just this kind, along with its derivatives and by-products.

This has several important implications for cognitive neuroscientists:

1. *Technical definition of function.* In explaining or exploring the reliably developing organization of a cognitive device, the *function* of a design refers solely to how it systematically caused its own propagation in ancestral environments. It does not validly refer to any intuitive or folk definitions of function such as “contributing to personal goals,” “contributing to one’s well-being,” or “contributing to society.” These other kinds of usefulness may or may not exist as side effects of a given evolved design, but they can play no role in explaining how such designs came into existence or why they have the organization that they do.

It is important to bear in mind that the evolutionary standard of functionality is entirely independent of any ordinary human standard of desirability, social value, morality, or health (Cosmides and Tooby, in press).

2. *Adapted to the past.* The human brain, to the extent that it is organized to do anything functional at all, is organized to construct information, make decisions, and generate behavior that would have tended to promote inclusive fitness in the ancestral environments and behavioral contexts of Pleistocene hunter-gatherers and before. (The preagricultural world of hunter-gatherers is the appropriate ancestral context because natural selection operates far too slowly to have built complex information-processing adaptations to the post-hunter-gatherer world of the last few thousand years.)

3. *No evolved “reading modules.”* The problems that our cognitive devices are designed to solve do not reflect the problems that our modern life experiences lead us to see as normal, such as reading, driving cars, working for large organizations, reading insurance forms, learning the oboe, or playing Go. Instead, they are the odd and seemingly esoteric problems that our hunter-gatherer ancestors encountered generation after generation over hominid evolution. These include such problems as foraging, kin recognition, “mind reading” (i.e., inferring beliefs, desires, and intentions from behavior), engaging in social exchange, avoiding incest, choosing mates, interpreting threats, recognizing emotions, caring for children, regulating immune function, and so on, as well as the already well-known problems involved in perception, language acquisition, and motor control.

4. *Side effects are personally important but scientifically misleading.* Although our architectures may be capable of performing tasks that are “functional” in the (nonbiological) sense that we may value them (e.g., weaving, playing piano), these are incidental side effects of selection for our Pleistocene competencies—just as a machine built to be a hair-dryer can, incidentally, dehydrate fruit or electrocute. But it will be difficult to make sense of our cognitive mechanisms if one attempts to interpret them as devices designed to perform functions that were not selectively important for our hunter-gatherer ancestors, or if one fails to consider the adaptive functions these abilities are side effects of.

5. *Adaptationism provides new techniques and principles.* Whenever one finds better-than-chance functional organization built into our cognitive or neural architecture, one is looking at adaptations—devices that acquired their distinctive organization from natural selection acting on our hunter-gatherer or more distant primate ancestors. Reciprocally, when one is searching for intelligible functional organization underlying a set of cognitive or neural phenomena, one is far more likely to discover it by using an adaptationist framework for organizing observations because adaptive organization is the only kind of functional organization that is there to be found.

Because the reliably developing mechanisms (i.e., circuits, modules, functionally isolable units, mental organs, or computational devices) that cognitive neuroscientists study are evolved adaptations, all the biological principles that apply to adaptations apply to cognitive devices. This connects cognitive neuroscience and evolutionary biology in the most direct possible way. This conclusion should be a welcome one because it is the logical doorway through which a very extensive body of new expertise and principles can be made to apply to cognitive neuroscience, stringently constraining the range of valid hypotheses about the functions and structures of cognitive mechanisms. Because cognitive neuroscientists are usually studying adaptations and their effects, they can supplement their present research methods with carefully derived adaptationist analytic tools.

6. *Ruling out and ruling in.* Evolutionary biology gives specific and rigorous content to the concept of function, imposing strict rules on its use (Williams, 1966; Dawkins, 1982, 1986). This allows one to rule out certain hypotheses about the proposed function of a given cognitive mechanism. But the problem is not just that cognitive neuroscientists sometimes impute functions that they ought not to. An even larger problem is that many fail to impute functions that they ought to. For example, an otherwise excellent recent talk by a prominent cognitive neuroscientist began with the claim that one would not expect jealousy to be a “primary” emotion—that is, a universal, reliably developing part of the human neural architecture (in contrast to others, such as disgust or fear). Yet there is a large body of theory in evolutionary biology—sexual selection theory—that predicts that sexual jealousy will be widespread in species with substantial parental investment in offspring (particularly in males); behavioral ecologists have documented mate-guarding behavior (behavior designed to keep sexual competitors away from one’s mate) in a wide variety of species, including various birds, fish, insects, and mammals (Krebs and Davies, 1997; Wilson and Daly, 1992); male sexual jealousy exists in every documented human culture (Daly et al., 1982; Wilson and Daly, 1992); it is the major cause of spousal homicides (Daly and Wilson, 1988), and in experimental settings, the design features of sexual jealousy have been shown to differ between the sexes in ways that reflect the different adaptive problems faced by ancestral men and women (Buss, 1994). From the standpoint of evolutionary biology and behavioral ecology, the hypothesis that sexual jealousy is a primary emotion—more specifically, the hypothesis that the human brain includes neurocognitive mechanisms whose function is to regulate the conditions under which sexual jealousy is expressed and what its cognitive and behav-

ioral manifestations will be like—is virtually inescapable (for an evolutionary/cognitive approach to emotions, see Tooby and Cosmides, 1990a, 1990b). But if cognitive neuroscientists are not aware of this body of theory and evidence, they will not design experiments capable of revealing such mechanisms.

7. *Biological parsimony, not physics parsimony.* The standard of parsimony imported from physics, the traditional philosophy of science, or from habits of economical programming is inappropriate and misleading in biology, and hence, in neuroscience and cognitive science, which study biological systems. The evolutionary process never starts with a clean work board, has no foresight, and incorporates new features solely on the basis of whether they lead to systematically enhanced propagation. Indeed, when one examines the brain, one sees an amazingly heterogeneous physical structure. A correct theory of evolved cognitive functions should be no less complex and heterogeneous than the evolved physical structure itself and should map on to the heterogeneous set of recurring adaptive tasks faced by hominid foragers over evolutionary time. Theories of engineered machinery involve theories of the subcomponents. One would not expect that a general, unified theory of robot or automotive mechanism could be accurate.

8. *Many cognitive adaptations.* Indeed, analyses of the adaptive problems humans and other animals must have regularly solved over evolutionary time suggest that the mind contains a far greater number of functional specializations than is traditionally supposed, even by cognitive scientists sympathetic to “modular” approaches. From an evolutionary perspective, the human cognitive architecture is far more likely to resemble a confederation of hundreds or thousands of functionally dedicated computers, designed to solve problems endemic to the Pleistocene, than it is to resemble a single general purpose computer equipped with a small number of domain-general procedures, such as association formation, categorization, or production rule formation (for discussion, see Cosmides and Tooby, 1987, 1994; Gallistel, 1990; Pinker, 1997; Sperber, 1994; Symons, 1987; Tooby and Cosmides, 1992; see also chapter 81 of this volume).

9. *Cognitive descriptions are necessary.* Understanding the neural organization of the brain depends on understanding the functional organization of its computational relationships or cognitive devices. The brain originally came into existence and accumulated its particular set of design features only because these features functionally contributed to the organism’s propagation. This contribution—that is, the evolutionary function of the brain—is obviously the adaptive regulation of behavior and physiology *on the basis of information* derived

from the body and from the environment. The brain performs no significant mechanical, metabolic, or chemical service for the organism—its function is purely informational, computational, and regulatory in nature. Because the function of the brain is informational in nature, its precise functional organization can only be accurately described in a language that is capable of expressing its informational functions—that is, in cognitive terms, rather than in cellular, anatomical, or chemical terms. Cognitive investigations are not some soft, optional activity that goes on only until the “real” neural analysis can be performed. Instead, the mapping of the computational adaptations of the brain is an unavoidable and indispensable step in the neuroscience research enterprise. It must proceed in tandem with neural investigations and provides one of the primary frameworks necessary for organizing the body of neuroscience results.

The reason is straightforward. Natural selection retained neural structures on the basis of their ability to create adaptively organized relationships between information and behavior (e.g., the sight of a predator activates inference procedures that cause the organism to hide or flee) or between information and physiology (e.g., the sight of a predator increases the organism’s heart rate, in preparation for flight). Thus, it is the information-processing structure of the human psychological architecture that has been functionally organized by natural selection, and the neural structures and processes have been organized insofar as they physically realize this cognitive organization. Brains exist and have the structure that they do because of the computational requirements imposed by selection on our ancestors. The adaptive structure of our computational devices provides a skeleton around which a modern understanding of our neural architecture should be constructed.

Brain architectures consist of adaptations, by-products, and random effects

To understand the human (or any living species’) computational or neural architecture is a problem in reverse engineering: We have working exemplars of the design in front of us, but we need to organize our observations of these exemplars into a systematic functional and causal description of the design. One can describe and decompose brains into properties according to any of an infinite set of alternative systems, and hence there are an indefinitely large number of cognitive and neural phenomena that could be defined and measured. However, describing and investigating the architecture in terms of its adaptations is a useful place

to begin, because (1) the adaptations are the cause of the system’s organization (the reason for the system’s existence), (2) organisms, properly described, consist largely of collections of adaptations (evolved problem-solvers), (3) an adaptationist frame of reference allows cognitive neuroscientists to apply to their research problems the formidable array of knowledge that evolutionary biologists have accumulated about adaptations, (4) all of the complex functionally organized subsystems in the architecture are adaptations, and (5) such a frame of reference permits the construction of economical and principled models of the important features of the system, in which the wealth of varied phenomena fall into intelligible, functional, and predictable patterns. As Ernst Mayr put it, summarizing the historical record, “the adaptationist question, ‘What is the function of a given structure or organ?’ has been for centuries the basis for every advance in physiology” (Mayr, 1983, p. 32). It should prove no less productive for cognitive neuroscientists. Indeed, all of the inherited design features of organisms can be partitioned into three categories: (1) adaptations (often, although not always, complex); (2) the by-products or concomitants of adaptations; and (3) random effects. Chance and selection, the two components of the evolutionary process, explain different types of design properties in organisms, and all aspects of design must be attributed to one of these two forces. The conspicuously distinctive cumulative impacts of chance and selection allow the development of rigorous standards of evidence for recognizing and establishing the existence of adaptations and distinguishing them from the nonadaptive aspects of organisms caused by the nonselectionist mechanisms of evolutionary change (Williams, 1966, 1985; Pinker and Bloom, 1992; Symons, 1992; Thornhill, 1991; Tooby and Cosmides, 1990a, 1990b, 1992; Dawkins, 1986).

DESIGN EVIDENCE Adaptations are systems of properties (“mechanisms”) crafted by natural selection to solve the specific problems posed by the regularities of the physical, chemical, developmental, ecological, demographic, social, and informational environments encountered by ancestral populations during the course of a species’ or population’s evolution (table 80.1). Adaptations are recognizable by “evidence of special design” (Williams, 1966)—that is, by recognizing certain features of the evolved species-typical design of an organism “as components of some special problem-solving machinery” (Williams, 1985, p. 1). Moreover, they are so well organized and such good engineering solutions to adaptive problems that a chance coordination between problem and solution is effectively ruled out

TABLE 80.1
The formal properties of an adaptation

An adaptation is:

1. A cross-generationally recurring set of characteristics of the phenotype
2. that is reliably manufactured over the developmental life history of the organism,
3. according to instructions contained in its genetic specification,
4. in interaction with stable and recurring features of the environment (i.e., it reliably develops normally when exposed to normal ontogenetic environments),
5. whose genetic basis became established and organized in the species (or population) over evolutionary time, because
6. the set of characteristics systematically interacted with stable and recurring features of the ancestral environment (the "adaptive problem"),
7. in a way that systematically promoted the propagation of the genetic basis of the set of characteristics better than the alternative designs existing in the population during the period of selection. This promotion virtually always takes place through enhancing the reproduction of the individual bearing the set of characteristics, or the reproduction of the relatives of that individual.

Adaptations. The most fundamental analytic tool for organizing observations about a species' functional architecture is the definition of an adaptation. To function, adaptations must evolve such that their causal properties rely on and exploit these stable and enduring statistical structural regularities in the world, and in other parts of the organism. Things worth noticing include the fact that an adaptation (such as teeth or breasts) can develop at any time during the life cycle, and need not be present at birth; an adaptation can express itself differently in different environments (e.g., speaks English, speaks Tagalog); an adaptation is not just any individually beneficial trait, but one built over evolutionary time and expressed in many individuals; an adaptation may not be producing functional outcomes currently (e.g., agoraphobia), but only needed to function well in ancestral environments; finally, an adaptation (like every other aspect of the phenotype) is the product of gene-environment interaction. Unlike many other phenotypic properties, however, it is the result of the interaction of the species-standard set of genes with those aspects of the environment that were present and relevant during the species' evolution. For a more extensive definition of the concept of adaptation, see Tooby and Cosmides, 1990b, 1992.

as a counter-hypothesis. Standards for recognizing special design include whether the problem solved by the structure is an evolutionarily long-standing adaptive problem, and such factors as economy, efficiency, complexity, precision, specialization, and reliability, which, like a key fitting a lock, render the design too good a solution to a defined adaptive problem to be coinci-

dence (Williams, 1966). Like most other methods of empirical hypothesis testing, the demonstration that something is an adaptation is always, at core, a probability assessment concerning how likely a set of events is to have arisen by chance alone. Such assessments are made by investigating whether there is a highly non-random coordination between the recurring properties of the phenotype and the structured properties of the adaptive problem, in a way that meshed to promote fitness (genetic propagation) in ancestral environments (Tooby and Cosmides, 1990b, 1992). For example, the lens, pupil, iris, retina, visual cortex, and other parts of the eye are too well coordinated, both with each other and with features of the world, such as the properties of light, optics, geometry, and the reflectant properties of surfaces, to have co-occurred by chance. In short, like the functional aspects of any other engineered system, they are recognizable as adaptations for analyzing scenes from reflected light by their organized and functional relationships to the rest of the design and to the structure of the world.

In contrast, concomitants or by-products of adaptations are those properties of the phenotype that do not contribute to functional design per se, but that happen to be coupled to properties that are. Consequently, they were dragged along into the species-typical architecture because of selection for the functional design features to which they are linked. For example, bones are adaptations, but the fact that they are white is an incidental by-product. Bones were selected to include calcium because it conferred hardness and rigidity to the structure (and was dietarily available), and it simply happens that alkaline earth metals appear white in many compounds, including the insoluble calcium salts that are a constituent of bone. From the point of view of functional design, by-products are the result of "chance," in the sense that the process that led to their incorporation into the design was blind to their consequences (assuming that they were not negative). Accordingly, such by-products are distinguishable from adaptations by the fact that they are not complexly arranged to have improbably functional consequences (e.g., the whiteness of bone does nothing for the vertebrae).

In general, by-products will be far less informative as a focus of study than adaptations because they are consequences and not causes of the organization of the system (and hence are functionally arbitrary, unregulated, and may, for example, vary capriciously between individuals). Unfortunately, unless researchers actively seek to study organisms in terms of their adaptations, they usually end up measuring and investigating arbitrary and random admixtures of functional and functionless aspects of organisms, a situation that hampers the discovery of

the underlying organization of the biological system. We do not yet, for example, even know which exact aspects of the neuron are relevant to its function and which are by-products, so many computational neuroscientists may be using a model of the neuron that is wildly inaccurate.

Finally, entropic effects of many types are always acting to introduce disorder into the design of organisms. Traits introduced by accident or by evolutionary random walks are recognizable by the lack of coordination that they produce within the architecture or between the architecture and the environment, as well as by the fact that they frequently cause uncalibrated variation between individuals. Examples of such entropic processes include genetic mutation, recent change in ancestrally stable environmental features, and developmentally anomalous circumstances.

How well-engineered are adaptations?

The design of our cognitive and neural mechanisms should only reflect the structure of the adaptive problems that our ancestors faced to the extent that natural selection is an effective process. Is it one? How well or poorly engineered are adaptations? Some researchers have argued that evolution primarily produces inept designs, because selection does not produce perfect optimality (Gould and Lewontin, 1979). In fact, evolutionary biologists since Darwin have been well aware that selection does not produce perfect designs (Darwin, 1859; Williams, 1966; Dawkins, 1976, 1982, 1986; for a recent convert from the position that organisms are optimally designed to the more traditional adaptationist position, see Lewontin, 1967, 1979; see Dawkins, 1982, for an extensive discussion of the many processes that prevent selection from reaching perfect optimality). Still, because natural selection is a hill-climbing process that tends to choose the best of the variant designs that actually appear, and because of the immense numbers of alternatives that appear over the vast expanse of evolutionary time, natural selection tends to cause the accumulation of very well-engineered functional designs.

Empirical confirmation can be gained by comparing how well evolved devices and human engineered devices perform on evolutionarily recurrent adaptive problems (as opposed to arbitrary, artificial modern tasks, such as chess). For example, the claim that language competence is a simple and poorly engineered adaptation cannot be taken seriously, given the total amount of time, engineering, and genius that has gone into the still unsuccessful effort to produce artificial systems that can remotely approach—let alone equal—human speech per-

ception, comprehension, acquisition, and production (Pinker and Bloom, 1992).

Even more strikingly, the visual system is composed of collections of cognitive adaptations that are well-engineered products of the evolutionary process, and although they may not be “perfect” or “optimal”—however these somewhat vague concepts may be interpreted—they are far better at vision than any human-engineered system yet developed.

Wherever the standard of biological functionality can be clearly defined—semantic induction, object recognition, color constancy, echolocation, relevant problem-solving generalization, chemical recognition (olfaction), mimicry, scene analysis, chemical synthesis—evolved adaptations are at least as good as and usually strikingly better than human engineered systems, in those rare situations in which humans can build systems that can accomplish them at all. It seems reasonable to insist that before a system is criticized as being poorly designed, the critic ought to be able to construct a better alternative—a requirement, it need hardly be pointed out, that has never been met by anyone who has argued that adaptations are poorly designed. Thus, although adaptations are certainly suboptimal in some ultimate sense, it is an empirically demonstrable fact that the short-run constraints on selective optimization do not prevent the emergence of superlatively organized computational adaptations in brains. Indeed, aside from the exotic nature of the problems that the brain was designed to solve, it is exactly this sheer functional intricacy that makes our architecture so difficult to reverse-engineer and to understand.

Cognitive adaptations reflect the structure of the adaptive problem and the ancestral world

Four lessons emerge from the study of natural competences, such as vision and language: (1) most adaptive information-processing problems are complex; (2) the evolved solution to these problems is usually machinery that is well engineered for the task; (3) this machinery is usually specialized to fit the particular nature of the problem; and (4) its evolved design often embodies substantial and contentful “innate knowledge” about problem-relevant aspects of the world.

Well-studied adaptations overwhelmingly achieve their functional outcomes because they display an intricately engineered coordination between their specialized design features and the detailed structure of the task and task environment. Like a code that has been torn in two and given to separate couriers, the two halves (the structure of the mechanism and the structure of the task) must be put together to be understood. To function,

adaptations evolve such that their causal properties rely on and exploit these stable and enduring statistical and structural regularities in the world. Thus, to map the structures of our cognitive devices, we need to understand the structures of the problems that they solve and the problem-relevant parts of the hunter-gatherer world. If studying face recognition mechanisms, one must study the recurrent structure of faces. If studying social cognition, one must study the recurrent structure of hunter-gatherer social life. For vision, the problems are not so very different for a modern scientist and a Pleistocene hunter-gatherer, so the folk notions of function that perception researchers use are not a problem. But the more one strays from low-level perception, the more one needs to know about human behavioral ecology and the structure of the ancestral world.

Experimenting with ancestrally valid tasks and stimuli

Although bringing cognitive neuroscience current with modern evolutionary biology offers many new research tools (Preuss, 1995; see also chapter 84), we have out of necessity limited discussion to only one: an evolutionary functionalist research strategy (see chapter 87 and Tooby and Cosmides, 1992, for a description; for examples, see chapters in Barkow et al., 1992; Daly and Wilson, 1995; Gaulin, 1995; and chapter 81). The adoption of such an approach will modify research practice in many ways. Perhaps most significantly, researchers will no longer have to operate purely by intuition or guesswork to know which kinds of tasks and stimuli to expose subjects to. Using knowledge from evolutionary biology, behavioral ecology, animal behavior, and hunter-gatherer studies, they can construct ancestrally or adaptively valid stimuli and tasks. These are stimuli that would have had adaptive significance in ancestral environments, and tasks that resemble (at least in some ways) the adaptive problems that our ancestors would have been selected to be able to solve.

The present widespread practice of using arbitrary stimuli of no adaptive significance (e.g., lists of random words, colored geometric shapes) or abstract experimental tasks of unknown relevance to Pleistocene life has sharply limited what researchers have observed and can observe about our evolved computational devices. This is because the adaptive specializations that are expected to constitute the majority of our neural architecture are designed to remain dormant until triggered by cues of the adaptively significant situations that they were designed to handle. The Wundtian and British Empiricist methodological assumption that complex stimuli, behaviors, representations, and compe-

tences are compounded out of simple ones has been empirically falsified in scores of cases (see, e.g., Gallistel, 1990), and so, restricting experimentation to such stimuli and tasks simply restricts what researchers can find to a highly impoverished and unrepresentative set of phenomena. In contrast, experimenters who use more biologically meaningful stimuli have had far better luck, as the collapse of behaviorism and its replacement by modern behavioral ecology have shown in the study of animal behavior. To take one example of its applicability to humans, effective mechanisms for Bayesian inference—undetected by 20 years of previous research using “modern” tasks and data formats—were activated by exposing subjects to information formatted in a way that hunter-gatherers would have encountered it (Brase et al., 1998; Cosmides and Tooby, 1996; Gigerenzer and Hoffrage, 1995). Equally, when subjects were given ancestrally valid social inference tasks (cheater detection, threat interpretation), previously unobserved adaptive reasoning specializations were activated, guiding subjects to act in accordance with evolutionarily predicted but otherwise odd patterns (Cosmides, 1989; Cosmides and Tooby, 1992; see also chapter 87).

Everyone accepts that one cannot study human language specializations by exposing subjects to meaningless sounds: the acoustic stimuli must contain the subtle, precise, high level relationships that make sound language. Similarly, to move on to the study of other complex cognitive devices, subjects should be exposed to stimuli that contain the subtle, ancestrally valid relationships relevant to the diverse functions of these devices. In such an expanded research program, experimental stimuli and tasks would involve constituents such as faces, smiles, disgust expressions, foods, the depiction of socially significant situations, sexual attractiveness, habitat quality cues, animals, navigational problems, cues of kinship, rage displays, cues of contagion, motivational cues, distressed children, species-typical “body language,” rigid object mechanics, plants, predators, and other functional elements that would have been part of ancestral hunter-gatherer life. Investigations would look for functional subsystems that not only deal with such low-level and broadly functional competences as perception, attention, memory, and motor control, but also with higher-level ancestrally valid competences as well—mechanisms such as eye direction detectors (Baron-Cohen, 1994), face recognizers (e.g. Johnson and Morton, 1991), food memory subsystems (e.g., Hart et al., 1985; Caramazza and Shelton, 1998), person-specific memory, child care motivators (Daly and Wilson, 1995), and sexual jealousy modules.

Although these proposals to look for scores of content-sensitive circuits and domain-specific specializations will strike many as bizarre and even preposterous, they are well grounded in modern biology. We believe that in a decade or so they will look tame. If cognitive neuroscience is anything like investigations in domain-specific cognitive psychology (Hirschfeld and Gelman, 1994) and in modern animal behavior, researchers will be rewarded with the materialization of a rich array of functionally patterned phenomena that have not been observed so far because the mechanisms were never activated in the laboratory by exposure to ecologically appropriate stimuli. Although presently, the functions of most brain structures are largely unknown, pursuing such research directions may begin to populate the empty regions of our maps of the brain with circuit diagrams of discrete, functionally intelligible computational devices.

In short, because theories and principled systems of knowledge can function as organs of perception, the incorporation of a modern evolutionary framework into cognitive neuroscience may allow the community to detect ordered relationships in phenomena that otherwise seem too complex to be understood.

Conclusion

The aforementioned points indicate why cognitive neuroscience is pivotal to the progress of the brain sciences. There are an astronomical number of physical interactions and relationships in the brain, and blind empiricism rapidly drowns itself among the deluge of manic and enigmatic measurements. Through blind empiricism, one can equally drown at the cognitive level in a sea of irrelevant things that our computational devices can generate, from writing theology or dancing the mazurka to calling for the restoration of the Plantagenets to the throne of France. However, evolutionary biology, behavioral ecology, and hunter-gatherer studies can be used to identify and supply descriptions of the recurrent adaptive problems humans faced during their evolution. Supplemented with this knowledge, cognitive research techniques can abstract out of the welter of human cognitive performance a series of maps of the functional information-processing relationships that constitute our computational devices and that evolved to solve this particular set of problems: our cognitive architecture. These computational maps can then help us abstract out of the ocean of physical relationships in the brain that exact and minute subset that implements those information-processing relationships because it is only these relationships that explain the existence and functional organization of the system. The immense number of

other physical relationships in the brain are incidental by-products of those narrow aspects that implement the functional computational architecture. Consequently, an adaptationist inventory and functional mapping of our cognitive devices can provide the essential theoretical guidance for neuroscientists that will allow them to home in on these narrow but meaningful aspects of neural organization and to distinguish them from the sea of irrelevant neural phenomena.

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NOTE

1. The genes underlying complex adaptations cannot vary substantially between individuals because if they did, the obligatory genetic shuffling that takes place during sexual reproduction would break apart the complex adaptations that had existed in the parents when these are recombined in the offspring generation. All the genetic subcomponents necessary to build the complex adaptation rarely would reappear together in the same individual if they were not being supplied reliably by both parents in all matings (for a discussion of the genetics of sexual recombination, species-typical adaptive design, and individual differences, see Tooby, 1982; Tooby and Cosmides, 1990b).

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