Evolutionary Psychology: Theoretical Foundations

Introductory article

Leda Cosmides, University of California, Santa Barbara, USA
John Tooby, University of California, Santa Barbara, USA

CONTENTS

Evolutionary psychology is an approach to the cognitive sciences whose goal is to map the evolved, species-typical cognitive and neural architecture of humans (and other species). Its focus is on integrating what is known about evolution into the research process, allowing evolutionary psychologists to derive hypotheses about the design of human information-processing mechanisms from the large preexisting body of theories already developed and empirically tested within modern evolutionary biology.

INTRODUCTION

Evolutionary psychologists view the human mind as a set of computational machines that were designed by natural selection to solve adaptive problems faced by our hunter–gatherer ancestors. They argue that this basic Darwinian insight, when properly applied, can be uniquely informative for anyone who seeks to discover and understand the design of the human mind – that is for anyone who wishes to discover which programs reliably develop in the brains of all normal human beings, the conditions that activate these programs, and how each program processes information. In their view, attention to adaptive function will allow psychologists to (1) explain why the human mind contains those programs that are already known, (2) discover new programs that no one had thought to look for before, and (3) together with the analytical tools of the cognitive sciences, address previously intractable or neglected topics, such as emotion and motivation.

FOUNDATIONS

Although evolutionary psychology is an inclusive discipline that draws on many fields, its core ideas emerged from the intersection of three scientific research traditions: (1) work by David Marr, Noam Chomsky, and other cognitive scientists, that showed that the mind contains a number of different cognitive programs, many of which are specialized for performing a particular function (such as seeing or learning a language), (2) hunter–gatherer and primate studies, and (3) the revolution in evolutionary biology led by George C. Williams, W. D. Hamilton, John Maynard Smith, and Richard Dawkins, that replaced vague notions of function with a theoretically and empirically rigorous modern adaptationism, based on theories of natural selection that were formalized using game theory and replicator dynamics.

Out of replicator dynamics, evolutionary researchers derived a series of theories about how natural selection designs mechanisms that deal with parenting, mating, cooperation, kinship, communication, conflict, and dozens of other adaptive problems. These theories were then validated on thousands of animal and plant species. Evolutionary anthropologists have enriched this body of knowledge by studying primate and hunter–gatherer behavior and ecology, investigating hominid evolution and ancestral environments, and by extending evolutionary theory to cover novel features of the human species. This allows increasingly refined models of the adaptive problems our ancestors faced and how selection acted on them.

The understanding that natural selection is the only anti-entropic force known to scientists that builds functional machinery into organisms led to the third major insight: mechanisms studied by cognitive scientists necessarily had to be adaptations. This connected evolutionary research to cognitive science in the most direct possible way: cognitive science is the study of adaptations – computational adaptations. This allowed evolutionary psychologists to widen cognitive science into a comprehensive mapping of the computational mechanisms that underlie all human behavior, not just traditional cognitive topics such as attention, learning, and memory. The fact that no single information-processing design can efficiently solve a diversity of adaptive problems means that specialized cognitive mechanisms are likely to have evolved to regulate human parenting, social interaction, mating, foraging, incest avoidance, sexual jealousy, coalitions, and so on. The goal of evolutionary psychology is the construction of a high resolution map of the whole species-typical computational architecture of humans, including motivational and emotional mechanisms.

Engineering and Reverse Engineering

Evolutionary psychologists approach their field conceptually as if it were a form of reverse engineering. Engineers start with a problem, and then design machines that are capable of solving that problem in an efficient manner. As a result, the machine's structure reflects its function: it has certain properties and components rather than others because those structures solve a problem better than alternative ones.

Engineers can also work in reverse: given a strange machine, they can figure out what its design features are – i.e., which of its components are functional and how their arrangement accomplishes the machine's function. Doing this is relatively simple if one knows what problem the machine was designed to solve, because one can then look for structures capable of accomplishing that function. But, as any engineer will confirm, reverse engineering is exceedingly difficult when one has no idea what the machine was designed to do. Without a theory of function, how does one determine which parts are functional.

Cognitive psychologists are engineers working in reverse: the brain is a strange machine, and cognitive psychologists are attempting to figure out how it works, i.e. which of its components are functional and how their arrangement accomplishes various functions. Doing this is difficult, however, without knowing what problems this organic machine was designed to solve.

Evolutionary biology is helpful because it provides theories about what problems the brain was designed to solve, that is, theories about the functions of its constituent programs. This is done using (1) knowledge about basic problems any organism must solve if it is to survive and reproduce (e.g., finding food efficiently, choosing a fertile mate), (2) knowledge about ancestral environments for the species in question, and (3) evolutionary game theory to model which of an array of possible solutions would have replicated fastest under ancestral conditions (and therefore have been favored by natural selection). From these elements, one can develop a task analysis for an adaptive problem, the first step in developing a design specification: an answer to the question, 'What would a machine capable of solving this problem well under ancestral conditions look like?' The answer(s) to this question then guide one's empirical investigations.

For example, certain species (including our own) trade goods and favors (cooperation for mutual benefit). But results from evolutionary game theory showed that natural selection will not favor cognitive machinery enabling this somewhat unusual form of cooperation unless the individuals involved are able to detect cheaters (those who do not reciprocate favors). This led Cosmides and Tooby to look for, and find, reasoning programs specialized for cheater detection. Baron-Cohen's research on 'mindreading' – programs that allow people to infer the intentions, beliefs, and desires of others – was guided by theories about coevolutionary arms races, as well as by knowledge about what information was available in ancestral environments for inferring mental states. In the evolutionary past (as now) eye direction provided reliable and useful information about the intentions of other people and of predators. Noting this, Baron-Cohen hypothesized that specialized eye direction detectors may have evolved as a component of social cognition and predator detection, and he designed experiments testing for their existence and design.

Despite all the obvious differences between living beings and human-made machines, reverse engineering is a successful strategy for studying organisms because the two resemble each other in one crucial respect. Like human-made machines, organisms are comprised of structures that reflect their function. This is an inevitable consequence of how natural selection works, and fundamental to the logic of evolutionary psychology (see below).

Evolutionary Restrictions on the Concept of 'Function'

George Williams's 1966 book, *Adaptation and Natural Selection*, played a key role in the development of evolutionary psychology. Williams elucidated the levels at which natural selection can operate (genes and individuals, yes; groups, species, and ecosystems, weakly or not at all); he demonstrated why it will operate most powerfully in constructing adaptations at the level of the gene and individual; he clarified the logic of adaptationism; and he established standards of evidence that must be met before any trait can be considered an adaptation.

Before Williams, vague, panglossian functionalist thinking permeated evolutionary biology (and such thinking continues, implicitly, to saturate other fields even today). Evolutionary accounts explain the existence of traits by reference to their function, but many biologists (and psychologists) were attributing functionality merely by identifying a beneficial consequence to some entity, whether this was an individual, social group, species, or ecosystem. They did not focus on establishing whether the design systematically caused the propagation of its genetic basis reliably under ancestral conditions, as the theory of natural selection requires. Williams showed why looser notions of function were deficient, demonstrated how tightly constrained any adaptationist (i.e., functionalist) or byproduct claim had to be to be consistent with neo-Darwinism, and outlined the strict criteria such claims had to meet. Evolutionary psychologists attempt to apply these stringent adaptationist constraints on functionalism to limit the looser and less formalized ideas of function commonly employed in the cognitive, neural, and social sciences. They maintain that cognitive scientists should be aware that cognitive theories typically assume complex functional organization of types that are inconsistent with what evolution is likely to have produced.

Perhaps more importantly, when cognitive scientists do not understand what legitimately counts as a function in an evolved system, they fail to look for forms of complex functional organization that natural selection is likely to have produced. For example, although cognitive neuroscientists look for brain systems designed to cause fear in response to physical threats, they do not look for systems designed to cause sexual jealousy in response to threats to a mating relationship. This failure to investigate stems from an erroneous belief that 'beneficial' refers to survival rather than gene replication. A system that causes sexual jealousy jeopardizes the individual's survival by triggering aggressive conflicts, yet it would have promoted its own reproduction in the past in relation to the design alternative: indifference to a mate's extrapair sexual behavior. Unsurprisingly, adaptations to prevent others from having sexual access to one's mate have evolved in a large variety of animal species, including humans (as Buss, Symons and Daly & Wilson have shown).

THE DESIGN OF ORGANISMS

The goal of Darwin's theory was to explain the designs of organisms. Darwin asked, for example, why the beaks of finches differ from one species to the next, and have the forms that they do. Why do animals expend energy attracting mates, energy that could be spent on survival? Why are human facial expressions of emotion similar to those found in other primates?

Two Principles: Common Descent and Adaptation

One of the most important evolutionary principles accounting for the characteristics of organisms is common descent. An increasing body of evidence indicates that all organisms alive today are the descendents of a single originating organism. Over the course of evolutionary time, new species originate because one breeding population sometimes becomes subdivided into two or more populations, and stops interbreeding. Although they start out with the same set of genes, they subsequently can evolve independently because the different populations no longer exchange genes through matings. This process of species splitting gives a hierarchical tree structure of similarity to all species on Earth. Offspring inherit their parents' genes and design features, which stay the same across the generations unless selection or chance modifies genes. So, the more recently two species were descended from the same ancestral species, the more design features they will share in common. Hence, we expect to find many similarities between humans and our closest primate relatives. For example, humans and chimpanzees both use exactly the same set of muscles in making parallel facial expressions.

This is the phylogenetic approach, and it consists of the search for features (called 'homologous features') that are similar because both species inherited them from the species that was their common ancestor. This approach has a long and productive history in psychology. But as valuable as it is for many questions, this approach cannot adequately address features that evolved uniquely in only one lineage, because there are then no similarities to compare. Because there is the widespread misimpression that evolutionary psychology consists solely or primarily of applying a phylogenetic approach, many take it as a given that evolutionary psychology cannot address the large set of properties that make us uniquely human. They think it is limited to the study of characteristics that we share with other animal species.

However, the second principle that accounts for the characteristics of organisms is that natural selection builds adaptations into their designs. Indeed, natural selection can cause the designs of different species to diverge from one another, sometimes producing characteristics that are unique to a given species, such as the elephant's trunk or the cognitive mechanisms that allow humans to learn language. *Adaptationism* is the name for the research program that gives a central role to exploring how natural selection functionally organizes the designs of organisms. It can be applied to analyze features that are unique to humans, because the theory of natural selection illuminates equally well features that are shared and features that are unique to a single species.

Although evolutionary psychologists certainly appreciate and invoke phylogenetic explanations where they are appropriate (as well as other relevant theories and analytic tools), it is the application of adaptationist logic that has provided the brightest illumination to formerly murky issues in human psychology.

Organization in Evolved Systems

Organisms, like watches or automobile engines, exhibit a multitude of parts and subassemblies that are arranged in precise and highly ordered ways so that they operate to achieve the functional ends they were designed to perform. The eyes, immune system, umbilical cord, cell nucleus, and lungs, to pick a handful of examples, all display a very advanced technology, built out of organic molecules. The more that chance events, such as accidents or violence, act to randomize this internal order, the more the watch, automobile, or organism is damaged. In a world where everything is bombarded by chance forces, where did all this functional order in animals and plants come from?

The evolutionary process has only two components, chance and natural selection, that govern how the genes in a species change over time. Chance processes act to randomize relationships within the organism, and so cannot account for the accumulation of the highly ordered arrangements of functional parts that permeate organisms. For this reason, modern researchers now understand that natural selection is the only component of the evolutionary process that can build complex functional organization into a species' structure. This means that all complex *functional* design in organisms was created by natural selection. Consequently, we know that all functional organization in humans must be built in a way that is consistent with the principles of natural selection. This recognition is what makes evolutionary biology the foundation of psychology and neuroscience, not to mention anatomy, physiology, the medical sciences, and the social sciences. Our functional order originally comes from evolution.

To be sure, there is much that is not functional in organisms as well, introduced by chance evolutionary and non-evolutionary processes. But the functional architecture of organisms is central to their organization, and they would not exist without it. Indeed, in evolved systems there is a sense in which function determines structure, and that is the key to understanding the design of the human cognitive architecture.

Natural Selection: How (and Why) Function Determines Structure

The notion that species evolve – that their design changes over time – had been proposed and hotly debated before Darwin was born. But the early evolutionists lacked a clear and convincing account of how or why this happens. That is what Darwin and Wallace provided. They discovered a materialist mechanism – natural selection – that explains how organisms acquire their design, as well as why that design changes over time. The revolution that ensued bears Darwin's name because he is the one who elaborated the theory, provided the most extensive evidence for it, and was willing to pursue its implications wherever they led – even when they led to the human mind.

Many breakthroughs in science happen not because of new data, but because of a new way of looking at things. This was true for Darwin. Everyone already knew that organisms reproduce, and that when they do, they give rise to similar organisms: rabbits give birth to rabbits, not to ducks. They also knew that, while offspring closely resemble their parents, they are not perfect replicas of them. They vary a bit, and some of these variants are able to perform certain tasks, such as producing milk, better than others. This was common knowledge based on centuries of animal husbandry in which people selectively bred individual animals with special abilities – cows that produced more milk, sheep that grew softer wool. And Darwin, like Descartes, Harvey, and many others before him, knew that an organism can be thought of as a machine: a system whose parts are designed to perform certain functions.

All of these facts fall into place, Darwin realized, if you think of an organism as a self-reproducing machine. What distinguishes living from nonliving machines is reproduction: the presence in a machine of devices (organized components) that cause it to produce new and similarly reproducing machines. Given a population of living machines, this property – self-reproduction – will drive a system of positive and negative feedback that can explain the remarkable fit between organisms and their environment.

In contrast to human-made machines, which are designed by inventors, living machines acquire their intricate functional design over deep time, as a downstream consequence of the fact that they reproduce themselves. Indeed, modern Darwinism has an elegant deductive structure that logically follows from Darwin's initial insight that reproduction is the defining property of life, the driving force that causes species to change over time. That logic is as follows. When an organism reproduces, replicas of its design features are introduced into its offspring. But the replication of the design of the parental machine is not always error-free. As a result, randomly modified designs (mutants) are introduced into populations of reproducers. Because living machines are already exactingly organized so that they cause the otherwise improbable outcome of constructing offspring machines, random modifications will usually introduce disruptions into the complex sequence of actions necessary for self-reproduction. Consequently, most newly modified but now defective designs will remove themselves from the population – a case of negative feedback.

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

This increase continues until (usually) such modified designs outreproduce and thereby replace 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. Over the long run, down chains of descent, this feedback cycle pushes designs through state–space towards increasingly well-engineered – and otherwise improbable – functional arrangements. These arrangements are functional in a specific sense: the elements are well-organized to cause their own reproduction in the environment in which the species evolved.

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

Genes are simply the means by which design features replicate themselves from parent to offspring. They can be thought of as particles of design: elements that can be transmitted from parent to offspring, and that, together with stable features of an environment, cause the organism to develop some design features and not others. Genes have two primary ways they can propagate themselves: by increasing the probability that offspring will be produced by the organism in which they are situated, or by that organism's kin.

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

How well a design feature systematically promotes direct and kin reproduction is the bizarre but real engineering criterion determining whether a specific design feature will be added to or discarded from a species' design. Therefore, we can understand why our brains are constructed in the way they are, rather than in other perfectly possible ways, when we see how its circuits were designed to cause behavior that, in the world of our ancestors, led to direct reproduction or kin reproduction.

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

So, evolutionists analyze how design features are organized to contribute to lifetime reproduction not because of a warped and biasing obsession with sexuality, but because reproduction was the final causal pathway through which a functionally improved design feature caused itself to become more numerous with each passing generation, until it became standard equipment in all ordinary members of the species.

Adaptive problems create adaptations

Enduring conditions in the world that create reproductive opportunities or obstacles, such as the presence of predators, the ability to pool risk through food sharing, or the vulnerability of infants, constitute adaptive problems. Adaptive problems have two defining characteristics. First, they are conditions or cause-and-effect relationships that many or most individual ancestors encountered, reappearing again and again during the evolutionary history of the species. Second, they are that subset of enduring relationships that could, in principle, be exploited by some property of an organism to increase its reproduction or the reproduction of its relatives. Enduring relationships of this kind constitute reproductive opportunities or obstacles in the following sense: if the organism had a property that interacted with these conditions in just the right way, then this property would cause an increase in its own reproductive rate.

One can think of these reproductive opportunities and obstacles as problems. A property is a solution to such a problem when it allows organisms with this property to take advantage of prevailing conditions, where 'advantage' means a reproductive advantage. If a bird would realize a reproductive advantage by being able to travel at night, and stars are prevailing conditions that – given the right brain mechanism – would make this possible, then a brain mechanism that uses stars for navigation would be a solution to the problem of traveling at night. Egg-eating predators pose an obstacle to a bird's reproduction. A property that circumvents this obstacle – such as a program that causes the bird to remove from its nest broken eggshells whose bright white interiors are easily spotted by predators – would be a partial solution to this problem. A property is a solution to an adaptive problem if it had the systematic effect, over generations, of increasing the reproduction of individual organisms or their relatives. The causal chain linking that property to reproduction may be indirect, and the effect on the organism's own offspring or the offspring of kin may be relatively small. As long as its consequences on relative reproduction are the cause of its spreading through the population, that property is a solution to an adaptive problem. All solutions are, of course, temporary and subject to improvement over time. But each modification that spread because it improved reproduction – however stop-gap or impermanent it may turn out to have been – counts as a solution to an adaptive problem.

Most adaptive problems have to do with relatively mundane aspects of how an organism lives from day to day: what it eats, what eats it, who it mates with, who it socializes with, how it communicates, and so on. Adaptive problems for our hunter–gatherer ancestors included such recurrent tasks as giving birth, winning social support from band members, remembering the locations of edible plants, hitting game animals with projectiles, breast-feeding, breathing, identifying objects, recognizing emotional expressions, protecting family members, maintaining mating relationships, self-defense, heart regulation, assessing the character of self and others, causing impregnation, acquiring language, maintaining friendships, thwarting antagonists, and so on.

An enduring adaptive problem constantly selects for design features that promote the solution to the problem. Over evolutionary time, more and more design features accumulate that fit together to form an integrated structure or device that is well engineered to solve its particular adaptive problem. Such a structure or device is called an 'adaptation'. Indeed, an organism can be thought of as largely a collection of adaptations, such as the functional subcomponents of the eye, liver, hand, uterus, or circulatory system. Each of these adaptations exists in the human design now because it contributed to the process of self and kin reproduction in the past.

Recognizing adaptations

Natural selection is a hill-climbing feedback process that chooses among alternative designs on the basis of how well they function. It has produced exquisitely engineered biological machines – the vertebrate eye, photosynthetic pigments, efficient foraging algorithms, color constancy systems – whose performance is unrivaled by any machine yet designed by humans.

Because adaptations are problem-solving machines, they can be identified using the same standards of evidence that one would use to recognize human-made machines (e.g., TV versus stove): design evidence. One can identify an aspect of the phenotype as an adaptation by showing that (1) it has many design features that are complexly specialized for solving an adaptive problem, (2) these phenotypic properties are unlikely to have arisen by chance alone, and (3) they are not better explained as the byproduct of mechanisms designed to solve some alternative adaptive problem.

Adaptations, byproducts, and noise

The features of a species' cognitive or neural architecture can be partitioned into: adaptations, which are present because they were selected for (e.g., the enhanced recognition system for snakes coupled with a decision-rule to acquire a motivation to avoid them); byproducts, which are present because they are causally coupled to traits that were selected for (e.g., the avoidance of harmless snakes); and noise, which was injected by the stochastic components of evolution (e.g., the fact that a small percentage of humans sneeze when exposed to sunlight). The standards for recognizing adaptations also allow one to recognize byproducts and noise.

One payoff of integrating adaptationist analysis with cognitive science was the realization that, in long-lived, sexually recombining species (like humans), complex functional structures will be overwhelmingly species-typical. That is, the complex adaptations that compose the human cognitive architecture must be human universals (at least at the genetic level), whereas variation caused by genetic differences is predominantly noise: minor random perturbations around the species-typical design. This principle allows cross-cultural triangulation of the species-typical design, which is why many evolutionary psychologists include cross-cultural components in their research.

WHAT IS A COMPUTATIONAL ADAPTATION?

Organisms are composed of many parts, but only some of these parts are computational. By *computational* we mean that they are designed to (1) monitor the environment for specific changes, and (2) regulate the operation of other parts of the system functionally on the basis of the changes detected. For example, the diaphragm muscle, which causes the lungs to contract and expand, is not computational. But the system that measures carbon dioxide in the blood and regulates the contraction and extension of the diaphragm muscle is. The plastic cover on a thermostat is not computational, nor are the parts of a furnace that generate heat. But the thermocouple that responds to ambient temperature by toggling the switch on the furnace, and the connections between them, form a computational system. Muscles are not computational, but the visual system that detects the presence of a hungry-looking lion, the inference mechanisms that judge whether that lion has seen you or not, and the circuits that cause your muscles either to run to a nearby tree (if the lion has seen you) or freeze (if it hasn't seen you) do compose a computational system. The language of information-processing can be used to express the same distinction: one can identify the computational components of a system by isolating those aspects that were designed to regulate the operation of other parts of the system on the basis of information from the internal and external environment.

By 'monitoring the environment for specific changes', we mean the system is designed to detect a change in the world. That change can be internal to the organism (such as fluctuations in carbon dioxide levels in the blood or the activation of a memory trace) or external to the organism (such as the onset of a rainstorm or the arrival of a potential mate). Changes in the world become *information* when (1) they interact with a physical device that is designed to change its state in response to variations in the world (i.e., a transducer), and (2) the changes that are registered then participate in a causal chain that was designed to regulate the operation of other parts of the system. A photon, for example, does not become information until it causes a chemical reaction in a retinal cell, which was designed for this purpose and is part of a causal system that was itself designed to regulate an organism's behavior on the basis of inferences about what objects exist in the world and where they are.

A set of features is not computational unless it was *designed* to exhibit these properties. For example, the outer cells of a dead tree stump expand in the rain, and as this happens, the inner portions of the stump might become compressed. But these dead cells were not designed for detecting changes in weather. More importantly, although their swelling does cause a change in the inner part of the stump, it is not *regulating* the operation of the stump. Regulation means more than merely influencing or changing something. It means systematically modifying the operation of a system so that a *functional* outcome is achieved. In the case of a thermostat, that function was determined by the intentions of the engineer who designed it. In the case of an organism, that function was determined by natural selection, which acted to organize the properties of the organism.

The Relationship between Brains, Computation, and Selection

Neurons do not perform any significant metabolic function for an organism. They exist because of the computational relationships they create. Natural selection retains neural mechanisms on the basis of their ability to create functionally 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). Each neural program was selected for because it created the correct information–behavior or information–physiology relationship, and, so long as a physical implementation produces this relationship, its particular form is free to vary according to other factors. (Indeed, when people recover function after brain damage, repair processes often restore the original information-processing relationship – but using a different set of physical connections.)

In other words, the brain was designed by natural selection to be an information-processing device. The brain has the physical structure that it does *because* this structure embodies a particular set of programs, and each program has the computational structure that it does *because* that structure solved a particular problem in the past. This is the causal chain that licenses inferences from function to program structure to physical structure. If one knows what problems our ancestors faced, then one can make educated guesses about what programs evolved to solve them, including what computational procedures they would have required. Once the existence of these programs has been experimentally confirmed, one can search for their neural basis. Having a theory of adaptive function is useful to psychologists and neuroscientists because it allows one to look for programs and neural systems that otherwise one would not look for. It also allows one to understand why programs already known have the computational design that they do.

Function Determines Computational Structure

In principle, a computer or neural circuit could be designed so that any given stimulus in the environment (e.g., feces) could cause any kind of resulting behavior (avoid it, eat it, dance around it, meditate, declaim, sculpt, etc.). Which behavior a stimulus gives rise to is a function of the neural circuitry of the organism. This means that if you were a superhuman designer of brains, you could have engineered the human brain to respond in any way that you wanted, to link any environmental input to any behavioral output. You could have made a human being who frowns when pleased, is erotically transported by tree bark, or howls and devotedly incubates chicken eggs with her body heat whenever the days grow short enough. To explain behavior, therefore, we need a theory of brain organization that describes how circuits are designed to respond to environmental inputs throughout the lifecycle, and why they have the form they do. We will call this organization 'the design of the mind'. Because how the brain is organized to respond to the environment, prior to experience, cannot itself be supplied by the environment, it is easy to see that the design of the mind – including its learning circuits – must be built in to the developing brain. This means that the design was created by evolution.

Adaptive problems that required information-processing for their solutions selected for neural adaptations organized to compute these solutions: function determined computational structure. Over evolutionary time, neural circuits were cumulatively added to the design of the human brain because they reasoned or processed information in a way that enhanced the adaptive regulation of behavior and physiology for these enduring adaptive problems. Such cognitive adaptations include emotion programs, such as fear of falling, fear of snakes, or parental love; motivational programs, such as sexual attraction or revenge; reasoning instincts such as cheater detection algorithms; and learning programs such as the language acquisition device or the food aversion system.

Even 'learned' behaviors, such as speaking English, are the product of evolved learning programs. Evolutionarily novel skills, such as reading and writing, are learned via programs that evolved for learning other, evolutionarily important skills, such as language acquisition – reading and writing are byproducts of adaptations designed for learning other things. Consequently, the mental and neural organization that results from learning is simply another example of the operation of our evolved adaptations, not an exception.

NATURE AND NURTURE

At a certain level of abstraction, every species has a universal, species-typical evolved architecture. For example, we all have a heart, two lungs, a stomach, and so on. This is not to say there is no biochemical individuality, especially in quantitative features. Stomachs vary in size, shape, amount of HCl produced, but all stomachs have the same basic functional design. They are attached at one end to an esophagus and at the other to the small intestine, secrete the same chemicals necessary for digestion, etc. Presumably, the same is true of the brain and, hence, of the evolved architecture of our cognitive programs – of the information-processing mechanisms that generate behavior. Evolutionary psychology seeks to characterize the universal, species-typical architecture of these mechanisms.

Our evolved cognitive architecture, like all aspects of the phenotype from molars to memory circuits, is the joint product of genes and environment. But the development of architecture is buffered against both genetic and environmental insults, such that it reliably develops across the (ancestrally) normal range of human environments. Adaptations are not impervious to environmental conditions: a certain envelope of environmental conditions must be present for any adaptation to develop properly. Moreover, the evolutionary function of computational adaptations is to make behavior (and physiology) sensitively contingent upon information from the environment.

A mechanism – computational or otherwise – need not be present at birth to be considered an adaptation or part of the human evolved architecture (consider teeth and breasts). The development of an adaptation may be triggered at any point in life-history; the trigger can be an internal, physiological event or a set of external conditions (including social conditions).

Evolutionary psychology is not behavior genetics. Behavior geneticists are interested in the extent to which *differences* between people can be accounted for by *differences* in their genes. Evolutionary psychologists are interested in individual differences primarily insofar as these are the manifestation of an underlying architecture shared by all human beings. Because their genetic basis is universal and species-typical, the heritability of complex adaptations (e.g., the eye) is usually low, not high. Moreover, sexual recombination constrains the design of genetic systems, such that the genetic basis of any complex adaptation (such as a cognitive mechanism) *must* be universal and species-typical. This means the genetic basis for the human cognitive architecture is universal, creating what is sometimes called the 'psychic unity of humankind'.

Evolutionary psychologists do not assume that genes play a more important role in development than the environment does, or that 'innate factors' are more important than 'learning'. Instead, they reject the traditional nature/nurture dichotomies as ill-conceived. In their view, there is not a zero-sum relationship between 'nature' and 'nurture'. For them, 'learning' is not an explanation; it is a phenomenon that requires explanation. Learning is caused by cognitive mechanisms, and to understand how it occurs one needs to know the computational structure of the mechanisms that cause it. The richer the architecture of these mechanisms, the more an organism will be capable of learning: toddlers can learn English while the family dog cannot because the cognitive architecture of humans contains mechanisms that are not present in that of dogs.

DOMAIN-SPECIFICITY AND FUNCTIONAL SPECIALIZATION

Evolutionary psychologists do not assume that 'learning', reasoning, or memory are unitary phenomena. The learning mechanisms that cause the acquisition of grammar, for example, are different from those that cause the acquisition of snake phobias. Corkscrews and cups have different properties because they are solutions to different problems; similarly, machinery that causes predator fears to be reliably and efficiently acquired lacks properties that cause the reliable and efficient acquisition of grammar, and vice versa. This applies to choice as well as learning: in many cases, the computational requirements for producing adaptive behavior in one domain are incompatible with those for another. Consider, for example, the domains of food and sex. The computational structure of programs designed for choosing nutritious foods will fail to produce adaptive behavior unless they generate different preferences and trade-offs than programs designed for choosing fertile sexual partners.

Because natural selection tends to produce mechanisms that are well designed for solving adaptive problems, evolutionary psychologists expect the human mind will be found to contain a large number of information- processing devices that are functionally specialized and therefore domain-specific. Most think the multipurpose flexibility of human thought and action is possible precisely because our cognitive architecture contains a large number of these expert systems.

The proposed domain-specificity of many of these computational devices separates evolutionary psychology from those approaches to the cognitive sciences that assume the mind to be composed of a small number of domain-general, content-independent, general-purpose mechanisms.

Relevance to Modularity Debate in Cognitive Science

In cognitive science, computational systems that are functionally specialized and domain-specific are sometimes called 'modules'. The criteria for calling a device a module are inconsistent and vague (some view information encapsulation as criterial; others emphasize specialization, etc.), especially when compared to the crisp criteria for calling a device an 'adaptation'. As a result, evolutionary psychologists are more comfortable discussing functional specialization rather than modularity. That said, it is fair to say that most take a more modular view of cognition than do many cognitive scientists. (*See* **Modularity)**

Examples of evolved computational devices that show evidence of being specialized in function include: face recognition systems, a language acquisition device, mindreading systems, navigation specializations, animate motion recognition, cheater detection mechanisms, and mechanisms that govern sexual attraction. Most evolutionary psychologists are skeptical that an architecture consisting predominantly of content-independent cognitive processes, such as general-purpose pattern associators, could solve the diverse array of adaptive problems efficiently enough to reproduce themselves reliably in complex, unforgiving natural environments that include, for example, antagonistically coevolving biotic adversaries, such as parasites, prey, predators, competitors, and incompletely harmonious social partners. Such systems may be able to detect some patterns in the environment, but they are value-free: that is, they contain no criteria for deciding between alternative courses of action in a way that would have tracked fitness in ancestral environments. Indeed, evolutionary psychologists have argued that there is no single criterion for adaptive behavior that could be applied across domains yet still track fitness and, for this reason, evolution could not have produced a completely domain-general cognitive architecture.

Some cognitive scientists have argued in favor of domain-general computational processes (usually of an unspecified nature) on the grounds that they can solve a wider array of problems, including evolutionarily novel ones (such as learning to read or write). Even if this were true (and there are strong reasons to believe it is false, having to do with combinatorial explosion and the greater inferential power of a knowledge-rich over a knowledge-poor reasoning system), it would provide no basis for assuming that the human cognitive architecture is composed primarily of domain-general, knowledge-free (i.e., content-independent) computational systems.

This is because selection drives design features to become incorporated into architectures in proportion to the actual distribution of adaptive problems encountered by a species over evolutionary time. There is no selection to generalize the scope of problem-solving to include never or rarely encountered problems at the cost of efficiency in solving frequently encountered problems. To the extent that problems cluster into types (domains) with statistically recurrent properties and structures (e.g., facial expression statistically cues emotional state), it will often be more efficient to include computational specializations tailored to inferentially exploit the recurrent features of the domain (objects always have locations, are bounded by surfaces, cannot pass through each other without deformation, can be used to move each other, etc.). Because the effects of selection depend on iteration over evolutionary time, evolutionary psychologists expect the detailed design features of domain-specific inference engines to intricately reflect the enduring features of domains. Consequently, they are very interested in careful studies of enduring environmental and task regularities, because these predict details of functional design. Adaptationist predictions of domain-specificity have gained support from many sources (e.g., from cognitive neuroscience), demonstrating that many dissociable cognitive deficits show surprising content-specificity, and from developmental research indicating that infants come equipped with evolved domain-specific inference engines (an intuitive physics, a mindreading system, a folk biology, etc.).

The Environment of Evolutionary Adaptedness (EEA)

Evolutionary psychologists do not study behavior *per se*; they study the cognitive machinery that generates behavior, using the theory of evolution by natural selection to develop hypotheses about its design and function. According to this view, behavior in the present is generated by information-processing mechanisms that exist because they solved adaptive problems in the past – in the ancestral environments in which the human line evolved.

As a result, evolutionary psychology is relentlessly past-oriented. Cognitive mechanisms that exist because they solved problems efficiently in the past will not necessarily generate adaptive behavior in the present (e.g., a taste for fat, adaptive in fat-poor ancestral environments, can generate maladaptive behavior in a modern environment flush with fast-food restaurants). Indeed, evolutionary psychologists reject the notion that one has 'explained' a behavior pattern by showing that it promotes fitness under modern conditions.

Although the hominid line is thought to have evolved on the African savannas, the environment of evolutionary adaptedness, or EEA, is not a place or time. It is the statistical composite of selection pressures that caused the design of an adaptation.

Further Reading

Baron-Cohen S (1995) *Mindblindness: An essay on Autism and Theory of Mind*. Cambridge, MA: MIT Press.

Barkow J, Cosmides L and Tooby J (1992) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. New York, NY: Oxford University Press.

Buss DM (1994) *The Evolution of Desire*. New York, NY: Basic Books.

Cosmides L and Tooby J (2002) *Universal Minds: Explaining the New Science of the Mind*. London, UK: Weidenfeld & Nicolson.

Daly M and Wilson M (1988) *Homicide*. New York, NY: Aldine.

Dawkins R (1976) *The Selfish Gene*. New York, NY: Oxford University Press.

Dawkins R (1982) *The Extended Phenotype*. San Francisco, CA: W.H. Freeman.

Dawkins R (1986) *The Blind Watchmaker*. New York, NY: Norton.

Gallistel CR (1990) *The Organization of Learning*. Cambridge, MA: MIT Press.

Kelly R (1995) *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington, DC: Smithsonian Institution Press.

Pinker S (1997) *How the Mind Works*. New York, NY: Norton.

Symons D (1979) *The Evolution of Human Sexuality*. New York, NY: Oxford University Press.

Tooby J and DeVore I (1987) The reconstruction of hominid behavioral evolution through strategic modeling. In: Kinzey W (ed.) *Primate Models of Hominid Behavior*, pp. 183–237. New York, NY: SUNY Press.

Wakefield J (1999) Evolutionary versus prototype analyses of the concept of disorder. *Journal of Abnormal Psychology* **108**: 374–399.

Williams GC (1966) *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton, NJ: Princeton University Press.