

The Evolutionary Psychology FAQ

Last updated May 18, 2003.

This FAQ is written and maintained by [Edward Hagen](#), formerly of the Center for Evolutionary Psychology, University of California, Santa Barbara, and now at the Institute for Theoretical Biology in Berlin. The FAQ assumes a basic knowledge of genes and natural selection. Its purpose is to outline the foundations of evolutionary psychology. These foundations are extremely robust (though not beyond criticism). The status of specific hypotheses (e.g., mate selection preferences, cheater detection modules) is more debatable, and will not be discussed in detail here. In addition, I address many of the common misconceptions about evolutionary psychology. This FAQ draws upon the work of many individuals. Comments and criticisms regarding it are welcome: e.hagen@biologie.hu-berlin.de

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What is evolutionary psychology?

In the three and a half centuries since William Harvey proved that the purpose of the heart is to pump blood, physiologists have revealed the functional organization of the body in blinding detail. Their discoveries demonstrate beyond question that the structure of the body serves survival and reproduction. Further, there is near unanimity among biologists that this functional structure is a product of natural selection. In our century, psychologists have developed powerful techniques that conclusively demonstrate that cognition, too, has structure. Evolutionary psychologists are betting that cognitive structure, like physiological structure, has been designed by natural selection to serve survival and reproduction.

Evolutionary psychology focuses on the evolved properties of nervous systems, especially those of humans. Because virtually all tissue in living organisms is functionally organized, and because this organization is the product of evolution by

natural selection, a major presumption of evolutionary psychology is that the brain, too, is functionally organized, and best understood in evolutionary perspective. It is clear that the body is composed of a very large number of parts, and that each part is highly specialized to perform a specific function in service of the survival and reproduction of the organism. Using the body as a model for the brain, it is a fair guess that the brain, too, is composed of one or more functional parts, each of which is also specialized to facilitate the survival and reproduction of the organism (we'll get to genes in a bit). Thus, according to evolutionary psychology, neural tissue is no different from any other tissue: it is functionally organized to serve survival and reproduction. This is the foundational assumption of evolutionary psychology. Because vision, hearing, smell, pain, and motor control are indisputable functions of the nervous system that clearly have utility for survival and reproduction, this assumption has a high degree of face validity. Further, these examples suggest that the brain may best be conceived not as an organ with a single function, but rather as composed of a large, and potentially vast number of functional parts. Evolutionary biologists refer to the functional components of organisms as 'adaptations'. Evolutionary psychologists often refer to brain functions as psychological adaptations, although they are not qualitatively different from other adaptations.

The functional organization of the body has been elucidated primarily by the direct examination of morphology. A detailed analysis of the structure and composition of our organs and tissues has resulted in an excellent understanding of their purpose. Unfortunately, this has not been the case with the brain. The gross morphology of the brain appears to have little connection with its functional properties. Although we have a fair understanding of nerve cells--the primary constituents of neural tissue--the properties of the brain clearly come from higher order assemblages of such cells, not just the cells themselves. This is just as true of organs like the heart as it is of the brain. Because nerve cells can rapidly change state (e.g., their firing rate), because such state-changes involve little energy, and because they can be well insulated from their neighbors, it is possible for a nerve cell to be in one state, whereas some of its close neighbors may be in completely different states. This is in marked contrast to, say, muscle cells. If one muscle cell is involved in a contraction, then nearby cells almost certainly are as well. Neural tissue is quite different. Even the individual states of nerve cells in a network depend critically on the topology of the network itself. Further, assemblages that are actually distinct may have a complex three-dimensional distribution that can be very difficult to untangle. These properties of neural tissue make it exceedingly difficult to "see" the morphology of neural assemblages--with few exceptions, the network topology of virtually our entire brain is currently "invisible." It exists at a scale above the individual cell, but well below that which can be teased apart with any imaging technology currently available. Until recent decades, much of our immune system was similarly "invisible."

Evolutionary psychology offers one way around this technological limitation. If researchers had a sound basis for proposing brain functions a priori, they could then seek indirect evidence that brains in fact have these functional properties. Philosophers and scientists had long wondered why living things are made up of an amazing array of beautifully designed mechanisms, an organization which non-living things completely

lack. Why is it that entities that reproduce manifest overwhelming evidence of design, but entities that don't reproduce are utterly devoid of the same? As Darwin and Wallace first perceived, the association of reproduction and design is not accidental. Evolution by natural selection is currently accepted as the only process whereby entities can acquire functional properties. Functional organization is the consequence of the reproductive feedback that characterizes natural selection: if a population of reproducing entities (hereafter organisms) varies in some trait, if the variations can be passed on to offspring, and if, as a consequence of possessing a particular variant an organism produces more offspring than organisms that lack that variant, then, over time, the population will come to consist solely of organisms possessing the reproductively efficacious variant trait. In this way, populations of organisms will tend to acquire traits that facilitate reproduction and lose traits that hinder reproduction.

We now know that what is passed on to offspring is a large DNA molecule that is further partitioned into numerous sections called genes. Because the structure of this DNA is intimately bound up with the structure of the organism, variations in the DNA are strongly associated with variations in the organism. Changes in DNA are referred to as mutations, and result from environmental hazards such as radiation, toxins, etc.

Reproduction is an enormously complex process. At any given moment in the human body, there are thousands of processes that, should they fail to complete successfully, would result in death within minutes. For this reason, any given random change in the body is likely to hinder survival and reproduction, not facilitate it. There are far more ways for a mechanism to fail than there are ways to improve it. How many times has a change occurred to your car so that it got much higher than the EPA estimated miles-per-gallon rather than much lower? Thus, the vast majority of DNA mutations result in changes to the body (also called the phenotype) that hinder reproduction. Occasionally, however, a mutation occurs that results in a change to the phenotype that facilitates reproduction. Because this mutation can be passed on to offspring, and because this mutation tends to result in more offspring, the mutation becomes more frequent in the population. Over time, this process will result in organisms that have a sophisticated repertoire of mechanisms that facilitate reproduction.

We now have the answer to the question posed above: what functions is the brain likely to perform? If brain tissue is organized like all other tissue, it will perform precisely those functions that facilitate reproduction. More accurately, because evolution by natural selection is an historical process, and because the future cannot be predicted, the brain and body will perform functions that *facilitated* reproduction (note the past tense). Whether they currently do so will depend on how closely the present resembles the past. If we can develop an accurate picture of a species' reproductive ecology--the set of physical transformations that had to occur over evolutionary time for individuals to reproduce--we can infer those properties the organism is likely to have in order to ensure that those transformations reliably took place. Evolutionary time, the time it takes for reproductively efficacious mutations to arise and spread in the population, is often taken to be roughly 1000-10,000 generations; for humans, that equals about 20,000-200,000 years.

Over the last 200,000 years, humans regularly encountered spiders and snakes, creatures whose toxins would have significantly impeded the reproduction of individuals unlucky enough to get injected with them. Over the last 100 years, humans have regularly encountered automobiles, encounters that also can seriously impede reproduction (e.g., by getting run over). Because 200,000 years is long enough for humans to evolve protective mechanisms, but 100 years isn't, we can predict that humans may well possess an innate aversion to spiders and snakes, but not to automobiles--even though far more people are currently killed by cars than by spiders or snakes. Once we have firmly established that avoiding spiders and snakes would have reliably facilitated the reproduction of ancestral humans, we can then design experiments to determine whether humans in fact possess an innate, cognitive ability to detect and avoid these animals (more on how to do this below). A major lesson of evolutionary psychology is that if you want to understand the brain, look deeply at the environment of our ancestors as focused through the lens of reproduction. If the presumptions of evolutionary psychology are correct, the structure of our brains should closely reflect our ancestral reproductive ecology. Thus, evolutionary psychology provides a method for perceiving the functional organization of the brain by studying the world--currently a far more tractable problem than disentangling neural assemblages.

What is the EEA and why is it important? (general answer)

The Environment of Evolutionary Adaptedness. This phrase, first coined by John Bowlby of attachment theory fame, has been the source of much confusion and controversy. First of all, the EEA is NOT a specific time or place. Roughly, it is the environment to which a species is adapted. Animals that lived in different environments or made their livings in different ways faced different reproductive problems, and that's why all animals aren't the same. Fish faced different problems than did butterflies, and as a result they have different adaptations. The EEA for any specific organism is the set of reproductive problems faced by members of that species over evolutionary time. The EEA for a particular species of fish is likely to be completely different than the EEA for a particular species of butterfly, even if those species both evolved in the same locations over the same periods of time. Each of these species faced reproductive problems that the other didn't, and thus their EEA's are different. The EEA concept is very similar to the notion of 'niche' in evolutionary biology.

I have used the past tense when referring to the solving of reproductive problems because adaptations evolved over a large number of generations and are therefore "tuned" to *reliable* aspects of past environments (see the next section). If the environment changes, then the adaptation may be "out of tune" with the present environment and fail to properly perform its reproductive function.

The EEA concept is extremely important for understanding the functional properties of organisms, including the functional organization of the human brain. As outlined in the previous section, the functional properties of organisms arise by the process of evolution by natural selection. This means that the functions that organisms have are precisely those that solved long standing, recurrent reproductive problems. Reproductive problems

are all the various things organisms had to do to survive and reproduce in a particular environment over evolutionary time--find food, find mates, avoid predators, combat pathogens, etc.

This observation is particularly important for understanding the functional organization of the human brain. Because we cannot (yet) directly study the wiring of the brain (except in a very few cases), we need another 'window' or set of tools for perceiving brain functions. Darwin's theory provides this window. If we can specify all the reproductive problems faced by our ancestors (i.e., if we can specify the human EEA), we can specify all the potential functions that our bodies and brains could have, in principle. With respect to the brain in particular, if we can specify all the reproductive problems involving information processing, we can specify all the possible psychological mechanisms that could have evolved. Whether humans possess any particular psychological mechanism (i.e., an ability to solve a particular reproductive problem involving information processing), becomes an empirical question. Fortunately, it is much easier to find something if you have some idea what you are looking for. Studying the past is, at present, easier than studying brain wiring. The EEA concept therefore provides a much needed tool for determining, a priori, what kinds of functions, or mechanisms, the human brain is likely to have: the human brain solves the reproductive problems posed by past environments; it allows us to do all the things we needed to do to survive and reproduce in ancestral environments--find food, find mates, detect and avoid predators and other dangerous animals, etc. We can understand the functional organization of human bodies and brains precisely to the extent that we can understand the human EEA.

What is the EEA? (detailed answer)

In order to understand the precise definition of the EEA, we must understand the definition of a selection pressure. Many of the misconceptions about the EEA can be avoided by adhering closely to the precise definition of the EEA derived from the theory of natural selection. As noted above, the EEA is the set of all selection pressures faced by an organism's ancestors over 'recent' evolutionary time (i.e., over approximately the last 1000-10,000 generations). To understand what a selection pressure is, we must understand how a mutation spreads in a population. It must alter the phenotype in some way that enhances reproduction (ignoring drift and other similar processes for the moment). As emphasized elsewhere in this FAQ, reproduction is an enormously complex process; that it happens at all is a near miracle. Reproduction involves a vast number of physical processes that must proceed correctly if reproduction is to be successful. Given the design of an organism, given all the physical transformations that have to take place in order to reproduce, and given ALL the environmental conditions that the organism may encounter with some non-zero probability during its life, there is a (relatively) small set of *potential* transformations of the environment--where the term environment may include aspects of the organism itself--that will enhance rather than impede reproduction. **These potential reproduction enhancing transformations are called *selection pressures*.** Stated another way, selection pressures are those aspects of the environment that can have a notable impact on the reproduction of members of a particular species

over evolutionary time. The EEA of any species is the set of *all* features of the environment that could have had some impact on the reproduction of members of this species over recent evolutionary time.

For example, let's assume that an herbivore regularly ingests a particular plant toxin, and that this toxin has a detrimental effect on sperm quality. Let's also assume that there are enzymes that can neutralize this toxin, but that the herbivore cannot produce these enzymes. The fact that the plant toxin can be neutralized by an enzyme is an example of a **potential** transformation that could facilitate the reproduction of the herbivore (because it would result in improved sperm quality). Thus, the plant toxin is a *selection pressure* and is therefore an aspect of the EEA of the herbivore. Should a mutation arise that produces a toxin neutralizing enzyme, this mutation will spread in the population. After many generations, all herbivores of this particular species will now be able to neutralize this plant toxin. If the plant goes extinct, the herbivores will still be able to produce the detoxifying enzyme (for many generations, at least), and this particular toxin is still considered an aspect of the species' EEA. Alternatively, if no mutation ever arose to produce a detoxifying enzyme, this plant toxin was still a feature of the species EEA. It was a selection pressure, even though no adaptation evolved to neutralize it.

On the other hand, if a different toxic plant also grew in the same area as the first toxic plant, but the herbivores never ate that plant, then the second plant and its toxin are not considered part of the species' EEA. The second plant and its toxin were never a selection pressure--they had no impact on the herbivores' reproduction, and no transformation of the second toxin would facilitate herbivore reproduction. So, in use, the EEA refers not only to transformations of the environment that were necessary for reproduction, but also transformations that could have **potentially** facilitated reproduction. It does **not** refer to aspects of the past that could not impact reproduction in any way.

Notice that for a mutation to spread to fixation (i.e., to the entire population), it must transform the environment in a reproduction facilitating way for many generations (1000, say). This means that the mutation must interact, via the phenotype, with a recurrent aspect of the environment--an aspect that the organism and its descendants are likely to encounter with some significant probability over each of their lifetimes. For example, in the case of the plant toxin, it is not necessary that *every* individual herbivore regularly ingested the toxin; it is only necessary that, over evolutionary time, members of this species encountered the toxin frequently enough that those who could neutralize it would have had, *on average*, a reproductive advantage over those who couldn't.

Once a mutation has reached fixation, it must continue to experience a selection pressure (stabilizing selection) in order to remain in the genome; otherwise it will tend to be eliminated by subsequent mutations. Eyes evolved long before humans appeared, but if sunlight was not a part of the human EEA, we would have lost our visual capabilities, as have certain species of cave-dwelling fish. In the case of the plant toxin, if that particular plant went extinct, the ability to produce the neutralizing enzyme would degrade over time due to random mutations of the gene that produced the enzyme--there would be no selection pressure against organisms that could no longer neutralize the toxin, because the

toxin is no longer part of the environment. Thus, even if an adaptation evolved in an ancestor species (as eyes did in an ancient ancestor of humans), the selection pressures that maintained eyes over recent evolutionary time are considered part of the human EEA. Stabilizing selection pressures are part of the EEA.

It is worth noting that the organism is part of its own EEA. For example, the heart creates a pressure differential in the circulatory system; this pressure differential then results in a nutrient rich liquid (blood) being circulated to other tissues. Thus blood, arteries, and veins were essential features of the EEA of the heart (and thus of all organisms with hearts, including humans).

The definition of the EEA as the set of all selection pressures acting over recent evolutionary time has some notable implications. First of all, selection pressures are adaptation specific. The selection pressures acting on visual abilities are (in general) not the same as those acting on toxin neutralizing abilities. Thus, the evolutionary history of vision will (again, in general) not be the same as the evolutionary history of toxin neutralization. For example, one adaptation (like vision) may have a much longer evolutionary history than another (like the ability to neutralize a specific toxin). Another implication is that species can be adapted to a variety of mutually exclusive environmental conditions e.g., day and night, hot and cold, feast and famine, high population densities, low population densities, male biased sex ratios, female biased sex ratios, lots of predators, few predators, etc., so the EEA definitely does not refer to a fixed or static time or place.

Perhaps the most important implication is the following: organisms possess functional traits because those traits were selected for over evolutionary time. This means that those traits reliably performed their functions in past environments, and may or may not properly perform them in current environments. Thus, the EEA refers to those aspects of *past* environments to which an organism is adapted. Any organism can possess adaptations which no longer serve any reproductive function, and may even impede reproduction.

A couple of quick examples will illustrate many of the foregoing points. We have lungs because oxygen existed in our atmosphere **in the past,** not because oxygen exists in the immediate present. Should oxygen somehow disappear from the atmosphere, we would still have lungs, they just wouldn't work (and we would quickly go extinct). Fortunately, the current environment strongly resembles the EEA in this regard. As another example, Richard Coss has done work on physiological and psychological ground squirrel adaptations to rattlesnake predation. He shows quite convincingly that these ground squirrels retain protective adaptations even when they haven't faced rattlesnake predation pressure for very long periods, but that these adaptations are increasingly degraded the longer the squirrels have been in rattlesnake free environments.

Some aspects of the modern environment do diverge quite radically from the human EEA. Two examples: 1) automobiles kill far more people today than do spiders or snakes, but people seem to be far more averse to spiders and snakes than they are to automobiles.

Why? Because in the EEA, spiders and snakes were a serious threat, whereas automobiles didn't exist. Thus, it was possible for us to evolve an innate aversion to spiders and snakes, but not to automobiles. 2) Safe and highly effective birth control is a modern invention. For most of human history, women were pregnant or lactating for much of their adult lives. Interestingly, women in natural fertility populations (modern populations that don't have access to modern methods of birth control) appear to have a much lower rate of reproductive cancers than do women in populations with easy access to modern birth control. It has been argued that early and frequent pregnancies may prevent reproductive cancers. Because modern forms of birth control did not exist in the EEA, there was no selection pressure against the reproductive cancers that may accompany their use.

If the current environment of a particular species fails to resemble the species' EEA in too many ways, then the species will go extinct. Since the human species is clearly not going extinct, the common complaint that evolutionary psychology views humans as currently living in an entirely novel environment is clearly false. Most aspects of the modern environment closely resemble the human EEA. Hearts, lungs, eyes, language, pain, locomotion, memory, the immune system, pregnancy, etc., all work as advertised--excellent evidence that the modern environment does not radically diverge from the EEA.

Much research in evolutionary psychology proceeds as follows. First, identify a plausible selection pressure (often called a reproductive problem), like predation, for example. Second, hypothesize a cognitive solution to this problem, e.g., the ability to detect and avoid predators. Finally, devise and conduct experiments to see if humans in all populations have a specialized ability to detect predators and then avoid them. If they do, this implies that the human species has evolved psychological mechanisms for detecting and avoiding predators. [Click here for more on this particular example.](#)

Isn't it true that we can't know what happened in the distant past, so the EEA concept is useless?

No! It is a common misconception that the EEA refers to aspects of the past that *differ* from the present. In fact, the EEA refers the aspects of the past *whether or not* they correspond to aspects of the present. For any living species, most aspects of its EEA will correspond closely to aspects of its present environment, otherwise it would go extinct; if the present environment of any organism differs too much from its EEA, its functions will most probably fail to ensure survival and reproduction.

There are many mundane facts about the past that we know to be true (which also happen to be true of the present): there was gravity, sunlight, oxygen, plants, animals, parasites, cliffs, rivers, lakes, predators, toxins, men, women, children, old people, parents, brothers and sisters, mates, rocks, sticks, trees, faces, etc., etc. We also know that women got pregnant and men didn't. This single fact about the EEA is the foundation for much research on mating strategies in both humans and other animals. Pregnancy involves numerous costs, and we therefore expect that females in many species will be more picky

about mating than will males. This prediction has strong empirical support for both humans and other animals.

There are also several aspects of the human EEA that differ from most present human environments. We also know that population densities were much lower than today, that most societies were very probably kin-based, that child mortality rates were very probably much higher than today. However, humans still took more than a dozen years to reach sexual maturity, and fathers were less certain of paternity than mothers were of maternity (as they are today, absent a genetic test). These latter facts form the foundation for considerable research into differential parental investment. Human offspring require enormous investment to reach sexual maturity. If half of one's children were likely to die, parents needed to be able to target their investment towards the healthiest, most viable offspring. Similarly, males should have targeted their investment at offspring that were likely to be their own. Both of these hypotheses have found considerable support among both humans and other animals.

The EEA concept is an essential and logically necessary aspect of the theory of natural selection. We have lungs because there was an oxygen atmosphere in the *past.* Should our atmosphere suddenly disappear we would still have lungs, but they would be useless. If we could truly say *nothing* about the past, we would have to abandon the concept of adaptation. Fortunately, archaeologists, paleontologists, paleoanthropologists, historians, detectives, and cosmologists all make a living studying the past, so the problem obviously isn't insurmountable.

Why is the EEA equated with the Pleistocene?

The EEA is the set of selection pressures faced by a population over evolutionary time. The Pleistocene is a specific period of time beginning about 1.8 million years ago, and ending about 11,000 years ago. So, the two are not equal. However, the set of selection pressures that resulted in the evolution of the human body, including the brain, are almost certainly the selection pressures that acted on humans during the Pleistocene. As noted above, 'evolutionary time' for any species is roughly 1000-10,000 generations. Assuming a human generation to be about 20 years, that translates to 20,000 to 200,000 years. The period of time called the Pleistocene includes this, but is about 10 times longer, so that is a comfortable amount of time for *complex* adaptations to have evolved. Also, our genus, *Homo*, emerged in Africa around 2 million years ago, and by 1.8 million years, *Homo* had spread to Asia--the first hominid to leave Africa. At the end of the Pleistocene, humans invented agriculture, which resulted in a rapid abandonment of hunting and gathering, the means by which humans had survived for the preceding 2 million years. Within a few thousand years after the end of the Pleistocene, some humans were living in cities, a novel form of settlement. In short, the amount of cultural change experienced by humans over the last 10,000 years has been tremendous, possibly exposing humans to novel selection pressures, or eliminating previously important selection pressures. So, the Pleistocene--which (almost) encompasses the origins of our genus, but excludes the recent period of dramatic change--is conveniently identified as the epoch which shaped human physiology and psychology. It is important to note that many of our adaptations--

perhaps most--evolved before the Pleistocene. Human anatomy is almost identical to primate anatomy, and, indeed, mammalian anatomy, all of which took their present form well before the onset of the Pleistocene. The reason we can still roughly equate the Pleistocene with the period of time which shaped human adaptations is that, if an adaptation which evolved prior to the Pleistocene, like vision, were not under stabilizing selection during the Pleistocene, that adaptation would have been lost during the 2 million years of the Pleistocene. Stabilizing selection maintains adaptations that have already evolved. For example, assume that the sun blinked out 2 million years ago (but, implausibly, that there were no other changes to the environment and most species did not go extinct). Humans and all other animals with vision would have lost their visual capabilities. Mutations would inevitably have occurred in the genes underlying our visual system, degrading our visual abilities. Since there wasn't any light, however, this degradation would have been inconsequential, and these mutations would not have been selected out of the population. After 2 million years, the visual system would be completely gone (this has actually happened for some species of cave-dwelling fish). Consequently, we can include sunlight as part of our EEA, and our visual system as a product of stabilizing selection for vision during the Pleistocene.

Why couldn't humans have evolved during the last 10,000 years?

They could, but not much. Evolutionary psychologists downplay the possibility of significant cognitive evolution in the 10,000 or so years since the advent of agriculture (a period of time known as the Holocene) for reasons of both science and political correctness. Scientifically, 10,000 years (500 generations) is not much time for natural selection to act, and it certainly is not enough time to evolve new, complex adaptations—sophisticated mechanisms coded for by numerous genes.

It is possible, however, that humans could have evolved minor cognitive adaptations during the Holocene. Just as some populations whose subsistence relied on herds of domesticated animals evolved to digest lactose as adults, populations could have evolved simple cognitive adaptations that their hunter-gatherer ancestors did not possess. For this to occur, there would have had to have been environmental conditions that were (1) new, (2) constant over most of the Holocene, (3) relevant to reproduction, and (4) required novel cognitive abilities. Many of the changes experienced by humans over the Holocene, however, have been so rapid that natural selection just couldn't keep up. Further, we know that very little has changed physiologically in the last 10,000 years—Australian aborigines were more or less isolated from other populations for perhaps 40,000 years, yet are essentially identical physiologically to other human populations—so probably very little has changed psychologically.

Politically, EPs are understandably desperate to avoid any association with past racist attempts to essentialize population differences that are best explained by culture. If it were possible that human cognition had undergone significant evolution during the Holocene, then it would be theoretically possible to ascribe significant differences in behavior between different populations to genes, and that would be EP's worst nightmare.

If we had as thorough an understanding of our psychological adaptations as we do our physiological adaptations, then perhaps we might be able to identify some simple psychological adaptations based on one or two genes that evolved during the Holocene; these adaptations might be population specific, or they might be pan-human. But we understand almost nothing about our evolved cognitive abilities. Imagine studying skin color without knowing what skin is. That would be a complete waste of time! EP rightly emphasizes a current focus on pan-human, complex cognitive adaptations that, like the rest of the body's adaptations, were selected for during the two million years of the Pleistocene.

What is an adaptation?

Adaptations solve reproductive problems, that is, adaptations have functions. The lungs are an adaptation, and their function is to transfer gases to and from blood. Muscles are an adaptation, and their function is to apply force to various parts of the body. The function of intestines is (in part) to extract nutrients from food. In general, all members of a species of the same sex and developmental stage share the same functional organization (i.e., have the same adaptations). All humans have bones, muscles, hearts, eyes, etc. While some problem solving abilities (functions) of the nervous system are obvious (e.g., vision), many are not; the goal of evolutionary psychology is to identify *all* functions of the nervous system.

Functional organization implies specialization. Oxygenating blood is a different problem than circulating blood, and it would be difficult if not impossible for a single functional unit to effectively solve both problems. Efficiently transferring oxygen to blood requires very high surface areas of gas permeable tissue that would be quite unsuitable for pumping fluids. The nervous system is clearly specialized as well. Generating the relatively low bit rate serial streams that characterize speech is a very different problem from parallel processing the vast amount of data generated by the retinas. The nervous system appears to be composed of multiple, specialized, functional units. This begs the question, how many specialized functional units are there? A few moments of reflection reveals that there are least several: vision, hearing, speech, motor control, sensation, smell, memory. Are there only a few more than these, or many more?

Finally, functional organization appears in the world only as a product of natural selection. Thus, the domains about which functions are organized are the domains that are relevant to fitness. Organisms possess precisely those functions that facilitated survival and reproduction in past environments. Any distinction in the world that could be exploited by an organism to increase its fitness represents a selection pressure. The set of such selection pressures that has acted on the human lineage is often referred to as the Environment of Evolutionary Adaptedness (EEA). Such selection pressures may or may not have resulted in the evolution of adaptations that exploit these distinctions to the benefit of the organism (and thus the genes that code for such adaptations). A complete specification of all selection pressures that have acted on a population over evolutionary time places an upper bound on the number of adaptations that can evolve. In the absence of constraints, one adaptation would evolve for each distinct selection pressure. The view

outlined here implies that any organism can be partitioned into a finite number of functional components, and that such a partition in some sense constitutes a complete specification of the organism. This model of life is quite tractable, and has resulted in tremendous advances in biology.

What is a psychological adaptation?

A psychological adaptation is a functional component of the nervous system that solves a particular reproductive problem. Information processing is the highly abstract domain upon which psychological adaptations are thought to operate. That is, the reproductive problems solved by the nervous system are thought to be best characterized as information processing problems. Computer algorithms, broadly construed, are usually thought to provide the best model currently available for the information processing abilities of psychological adaptations. This model of animal psychology derives, in part, from the following observations:

The information content of a physical system is the number of distinct and detectable states that that system can assume. Thus, a light switch can be either off or on--two distinct states that can be abstractly represented by 0 and 1. Since two is the minimum number of discrete states possible for any system, the minimum unit of information--the bit--represents two states (e.g., 0 or 1). Notice that flipping a light switch on or off is a physical transformation of the switch that requires *energy.* This is true of any change in the information state of any system. All 'information processing' involves energy dissipating transformations of physical systems. Because all adaptations (e.g., hearts, lungs, etc.) effect transformations of physical systems that involve a change in the informational state of that system, all adaptations can be thought of as 'processing information'. **THERE IS NO FUNDAMENTAL OR QUALITATIVE DIFFERENCE BETWEEN INFORMATION PROCESSING ADAPTATIONS (i.e. psychological adaptations) AND ANY OTHER TYPE OF ADAPTATION!**

All adaptations effect physical transformations of target systems (e.g., the lens focuses light, muscles move bones) that can be construed as changing the informational state of the target system. So, in principle, the information processing model could be applied to all adaptations. However, there are quantitative differences that usefully distinguish information processing adaptations from other adaptations:

1. High information content--the system can assume a large number of distinct and detectable states. For example, hearts can assume only a limited number of different states (e.g., beating fast, beating slow), whereas the retina can assume an astronomically large number of different states (e.g., all the possible combinations of activation levels of the 125 million rods and 6.5 million cones in each eye)
2. State transformations only require small amounts of energy. Again, heart muscle requires a significant amount of energy to contract compared to the amount of energy necessary to activate a cone on the retina.

3. State transformations can occur very rapidly. The frequency of contractions of heart muscle is slow compared to the potential frequency of state changes in the cones of the retina.

The structure of animal senses suggest that the information processing model is apt. Animals devote a considerable fraction of tissue to sensors. Skin contains an extremely high density of tactile receptor cells that can individually change state in response to touch, temperature, and tissue damage. For example, the human hand has 17,000 such cells per square inch. Further, the energy required to register a sensation is relatively low. Finally, in addition to their high spatial density, receptor cells also possess the ability to represent changes with a high degree of temporal resolution. These cells are connected to the brain by nerve fibers that can communicate state changes in about 1/50 of a second. Thus, the properties of tactile sensors matches our definition of information processing adaptations quite well. If we then consider that animals also possess other high bandwidth sensors like eyes, ears, taste, and smell, and that each of these can assume a *vast* number of possible states in response to environmental conditions, we are forced to conclude that animals are organized to collect astronomical quantities of information, information which must then undergo further processing in order result in reproduction facilitating actions on the part of the animal. These, then, are the functions of psychological adaptations: collect information on the environment (including the organism itself), process this information to extract reproductively salient conclusions about the environment (e.g., there is a predator staring at me), and initiate reproduction facilitating transformations of appropriate target systems (e.g., turn around and run).

What about spandrels?

Evolutionary adaptation is a special and onerous concept that should not be used unnecessarily, and an effect should not be called a function unless it is clearly produced by design and not by chance. When recognized, adaptation should be attributed to no higher a level of organization than is demanded by the evidence. George C. Williams, opening words of *Adaptation and Natural Selection*, 1966.

Repeating an argument made earlier by George Williams (1966), a couple of Harvard guys (Gould and Lewontin 1979) got a lot of mileage out of the observation that many organism 'traits' are not adaptations, but simply incidental byproducts. This is obviously true because the vague term 'trait' can refer to any conceivable aspect of an organism, like the grumbling of its stomach or snoring. Unlike the Harvard guys, Williams offered a way to separate the wheat from the chaff: adaptations must exhibit evidence of design.

Williams' criterion is critical. Without it, it is possible to assign every molecule, cell, and tissue in the body to a spandrel. Consider this thought experiment. A CAT scan produces a detailed 2D image of a cross-section of the body, like slicing open an orange and photographing the freshly revealed surface. By taking a large number of 2D scans perpendicularly along the length of the body and inputting the stack of images into a computer, one can build up an amazing 3D view of the body's internal anatomy, just as one could build up a 3D view of the internal structure of an entire orange by slicing it into

a large number of thin sections, photographing each one, and scanning the stack of 2D photographs into 3D software.

Imagine that a team of scientists who know nothing of anatomy gets hold of a large stack of CAT scans of an entire human body, revealing all its tissues in detailed cross-sectional images. The scientists begin analyzing the body using the 2D images, not realizing that the individual scans can be composited into a single, 3D model. Instead, each scientist gets her own 2D image to analyze independently from the others. Each scientist develops sophisticated statistical models of the patterns of light and dark on her image, scribbling down elegant equations describing the image's shapes and curves. The statistics and equations developed by the team are a rigorous, factual description of the entire body, but it is a description that is empty. The patterns of tissues revealed by the CAT scans are, if considered alone, spandrels of the true, underlying functional organization that the team has failed to recognize. Ask the wrong questions, and virtually all normal body tissues will be part of a spandrel. Ask the right questions, and most normal body tissues will be recognized as playing a vital, functional role in the survival and reproduction of the organism.

But wait! Isn't it somehow scientifically dangerous (e.g., Gould 1997), or at least embarrassing, to over hypothesize adaptive functions for traits that might not be adaptations? Nope. Such mistakes are no more scientifically dangerous than the opposite—under attributing function. Consider this example. Lumps of tissue at the back of the throat often become infected and therefore are (or were) frequently removed by surgery. Which scientific response do you prefer?: (1) Mock any suggestion that the lumps (tonsils) might serve an important function by loudly insisting that not all traits have adaptive functions; or (2) generate and test as many functional hypotheses as you can think of to make sure that by removing the tonsils no lasting harm is done to the patient?

Just as anatomists have made mistakes, EPs will sometimes over attribute function to psychological phenomena that aren't really adaptations (my work, Hagen 1999, 2003, could be a prime example) and sometimes they will fail to recognize genuine functions. On one level I find it bizarre that Gould, Lewontin, or anyone else could possibly fear the "dangers and fallacies" (Gould 1997) of what is in fact routine science with an outstanding record—proposing and testing functional hypotheses for organism structure. On another level, however, I understand Gould and Lewontin's distress. EP has rudely broken into the cathedral of the mind, spray-painting 'sex', 'violence', and 'competition' across their beloved spandrels.

Make no mistake, many spandrels, which EP terms byproducts, are enormously important in their own right. Symons (1979), a founder of EP, argued, for example, that the capacity of women to orgasm is a byproduct of a male adaptation for orgasm. It is an unstated premise of EP, however, that, by failing to recognize the evolved functional organization of the brain, psychology and the rest of the human behavioral sciences, like our team of misguided scientists, are condemned to study nothing but spandrels.

Refs:

Gould SJ (1997) The exaptive excellence of spandrels as a term and prototype. *Proceedings of the National Academy of Sciences* 94:10750-10755.

What is domain specificity and why is it necessary?

Domain specificity is an important property of physiological adaptations, and is presumed to be an important property of psychological adaptations as well. Domain specificity means that adaptations evolve to solve problems in particular domains, and therefore are less well suited to solve problems in other domains. A domain is a selection pressure or (equivalently) a reproductive problem. It is a physical transformation that, completed successfully, would facilitate the reproduction of the organism (or, more properly, genes coding for phenotypic traits that effect the transformation). Examples of domains include oxygenating blood, killing harmful bacteria, focusing light, extracting nutrients from food, filtering or neutralizing toxins, regenerating damaged tissue, etc. In other words, any of the myriad physical processes necessary for reproduction. In order to be successful, reproduction requires that a vast number of physical transformations complete efficiently and effectively. Adaptations are the structures that effect or evoke the necessary transformations. Lungs oxygenate blood, the immune system kills bacteria, the lens focuses light, the intestines extract nutrients from food, etc.

Reliably and efficiently evoking a specific transformation requires a highly specialized structure. For example, extracting large quantities of oxygen from the atmosphere is a difficult task. Compared to solids and liquids, gases are quite dilute. Further, oxygen comprises only 20% of our atmosphere, and the earth's atmospheric pressure is relatively low. In order to transfer substantial quantities of oxygen into our (liquid) blood stream, it is necessary to efficiently expose blood to large quantities of air. In addition, it is important to keep blood inside the body while keeping air on the outside of the body. One solution would be to have a thin, very high surface area membrane that is continually 'washed' with air on one side, while a thin layer of blood circulates on the other side. This is exactly the type of structure that has evolved to solve this problem. The surface area of our lungs is about equal to that of a tennis court, and blood flows across one side in a single-celled layer--i.e., in the thinnest layer that is theoretically possible. Although lungs are ideal for oxygenating blood, they would be completely ineffective for circulating blood. Delicate lung tissue possesses none of the properties necessary to pump large quantities of liquids. The dense muscles of the heart are far more effective for this task. Thus, lung tissue has evolved to be highly specific to the domain of gas transfer, whereas heart tissue has evolved to be highly specific to the domain of pumping liquids. Specializing to solve a reproductive problem in one domain generally precludes an ability to solve reproductive problems in other domains. This appears to be a general property of mechanisms: mechanisms that do one thing well will not do other things well. Because reproduction involves a large number of distinct transformations of the world, organisms will be comprised of a large number of domain specific adaptations to effect these transformations.

Evolutionary psychology is betting that psychological adaptations have to be just as domain specific as physiological adaptations. Information processing appears to be an excellent model for the general class of problems solved by psychological mechanisms. In the field of information processing, no one has invented a computer program that solves all problems. Each information processing problem requires specialized software to solve that problem. Spreadsheets are different from word processors are different from video games. Similarly, vision is different from hearing is different from pain is different from smell is different from sexual desire is different from navigation. In short, transformations of information are just as specialized as any other physical transformation and require equally specialized mechanisms to complete the task. Thus, psychological adaptations are as likely to be as domain specific as any other adaptation.

What is a module?

A module is a psychological adaptation (see above). Note that this usage of the term 'module' differs from several of the definitions of 'module' used by cognitive psychologists. For those familiar with the 'modularity' debate, I will make one brief comment: psychological adaptations (and thus 'modules', as they are defined here) are not necessarily informationally encapsulated, contrary to assertions by Fodor and others. Psychological adaptations are perfectly capable of using information that is also used by other psychological adaptations, and they are perfectly capable of providing information to other adaptations. Psychological adaptations are informationally encapsulated only in the following very restricted sense. Psychological adaptations are algorithms which transform information. The structure of the algorithm (including, e.g., any 'scratchpad' memory used by the algorithm) is itself information that is generally not available to other adaptations--the visual system almost certainly does not have detailed information on how the auditory system works, even if both systems make use of information provided by the other. Here is a computer analogy: Microsoft Word can exchange information with Adobe Photoshop. Neither of these programs is informationally encapsulated. But, Word has little-to-no information on the structure of the Photoshop code, nor does it need to have any such information. That would be redundant. Adaptations don't need to have detailed information on how other adaptations work, they just need to be able to share information with them.

How can we identify psychological adaptations?

We can identify psychological adaptations using the same criteria we use to identify any other adaptation: EVIDENCE OF DESIGN. We know the lung is an adaptation because 1) the many features of the lung--numerous chambers of gas-permeable tissue each surrounded by a network of blood vessels and each connected to the windpipe--correspond precisely to the nature of the problem: transferring oxygen to the blood, 2) solving this problem (oxygenating blood) would have greatly facilitated reproduction in ancestral environments (as it does in modern environments), and 3) natural selection is the only source of functional organization. QED, the lung is, without doubt, an adaptation. We can use these same criteria to identify psychological adaptations.

In order to effectively solve reproductive problems, mechanisms (a.k.a. adaptations, functions, modules, organs) must possess a suite of specific structural features that effect the required transformations of the world. These features are called 'design features.' The gas-permeable chambers, surrounding blood vessels, and connections to the windpipe constitute some of the design features of the lung. By precisely specifying the nature of a particular reproductive problem (a process sometimes referred to as a task analysis), we can, *a priori*, describe the design features that a putative adaptation must possess if it is to effectively solve the problem. This is as true of information processing problems as it is of any other type of reproductive problem. For the case of psychological adaptations, we must first identify an information processing problem faced by humans in the EEA. We must then determine the features that any psychological adaptation designed to solve this problem must possess. Finally, we seek both direct and indirect evidence that the nervous system possesses the required design features--that is, that it can solve the reproductive problem. The more design features that are necessary to solve the problem, and the more such features that the nervous system appears to possess, the higher the probability that a psychological adaptation to solve the reproductive problem in fact exists. Thus, the determination that a psychological adaptation exists is an inherently probabilistic enterprise.

A hypothetical example: suppose we can make the case that navigating in unfamiliar terrain would have been a reproductively important ability for ancestral humans. We would then specify all the information processing features relevant to solving this problem: measuring the angle of the sun, keeping accurate track of time, integrating velocity vectors, etc. We could then conduct numerous experiments to determine whether humans in fact possess each of these abilities, and, if so, whether they are properly integrated so that humans can effectively navigate in unfamiliar terrain. The more such abilities we can identify in humans, the greater the probability that humans possess a psychological adaptation for navigating in unfamiliar terrain.

Why are adaptations *not* for the good of the species?

Adaptations evolve through the differential reproduction of alternative alleles within a population or species. Thus, organisms acquire properties which allow them to out-reproduce members of their own species, not members of other species. It is theoretically possible for the differential survival of gene pools (species) to result in the evolution of organism features which would promote species survival at a personal reproductive cost to individual members of the species; it is extremely unlikely, however, that this process is responsible for the incredible array of complex functionality evinced by sexually reproducing, diploid species (Williams 1966). The length of time between speciation or extinction events is vastly longer than the length of time between generations.

Consequently, differential reproduction of alleles within species can produce complex functionality much faster than can differential reproduction between species. An allele that provided a benefit to the species at an expense to the individual would be driven to extinction long before it could have a measurably positive impact on the survival of the species. (There are other forms of group selection, however, that are worth considering; see, e.g., Sober and Wilson *Unto Others*).

Why are genes selfish?

Richard Dawkins wrote a very popular book called the *Selfish Gene* that explained, for a popular audience, many of the exciting new theories and discoveries being made in evolutionary biology in the 1960's and 70's. The metaphor Dawkins chose, the selfish gene, was an extremely powerful metaphor, so powerful that it has often overshadowed the science itself! The controversies that swirl around EP are often tightly bound up with Dawkins' metaphor. If our genes are selfish, are we all, deep down, unalterably selfish ourselves? Why did Dawkins chose this metaphor, what does it really mean, and what are its implications for EP and human nature?

Simplifying greatly for the sake of the argument, there is a molecule, called a nucleotide, that comes in four different types, A, C, G, & T. Large numbers of these nucleotides can be linked together in a linear strand to make a much bigger molecule called DNA. Schematically, DNA looks like this: ACGTGCCT...etc. Human DNA consists of about 3 billion nucleotides chained together. Simplifying greatly again, small sections of the DNA strand called 'genes', which are usually several hundred to several thousand nucleotides long, are able to create a different type of long, linear molecule called a protein. Proteins are a kind of plastic—technically, a polymer—that, like the DNA chain, are made up of a small number of different molecular building blocks called amino acids (there are 20 different amino acid building blocks). Just as the different chemical structure of the plastic in a plastic bag versus the chemical structure of the plastic in dental floss versus the chemical structure of the plastic in bullet-proof vests gives these different materials very different properties, the exact sequence of the different amino acids in a particular protein determines its biological properties. Different amino acid sequences give different proteins very different properties.

To summarize, the sequence of nucleotides in small sections of our DNA (called genes) determines the sequence of amino acids of proteins created by the genes, and these amino acid sequences determine the proteins' biological properties. Although scientists are still debating the exact number, DNA contains somewhere between 30,000 and 60,000 different genes, and can therefore create between 30,000 and 60,000 different proteins, each with unique properties. As I mentioned, proteins are a kind of plastic, so our DNA functions, in part, to create a large number of different plastics with different properties. These highly specialized plastics with very special biological properties are what our bodies are made of. DNA is a kind of lumber yard that provides, among other things, a large number of plastic building materials for making organisms.

Simplifying once more (this time by ignoring sex), individuals pass on an exact copy of their DNA chain to their offspring: if my body is made up of a particular set of plastics, because my offspring has an exact copy of my DNA, my offspring's body will be made up of exactly the same set of plastics, and so it will be exactly like me. Occasionally, however, one of the molecules in the DNA chain (i.e., one of the A, C, G, or T nucleotides), can become mutated (altered) by cosmic radiation, environmental toxins, etc.; these mutagens turn one type of nucleotide into another type of nucleotide (e.g., an A turns into G). If I pass on this mutated DNA, where only one of the 3 billion

nucleotides is different from my own, then my offspring will be made of proteins that are almost exactly like mine, except for the protein which was made by the mutated section of DNA (the mutated gene), which will be a different protein with different properties. My offspring will not be exactly like me—he will be said to have a different phenotype (body type).

Imagine that the gene that was mutated was the gene that made the plastic forming the lens of the eye. This plastic has a very special property: it is almost completely transparent. Most proteins, like those forming your skin, muscles, hair, etc., are not transparent. Because my offspring has a mutated form of the lens gene, there are now two types of genes in the population that make the lens protein: the normal version, possessed by most individuals (which I will call T_{normal} , for normal transparency) and the mutated version possessed by my offspring. Different forms of the same gene are called alleles. Because it is far easier to make something worse than it is to make it better, most of the time when the gene producing the lens protein is mutated (and this happens very rarely), the altered lens protein produced by the mutated gene will not be as transparent as the original version (so I will label this allele T_{low} , for low transparency). My offspring will therefore not be able to see as well as other members of his species who have the T_{normal} allele, and thus normal versions of the lens protein.

Let's assume that my offspring's lens protein is only slightly less transparent than the normal version. He will be able to live his life and have offspring. The population will therefore contain a mix of lens alleles; most of the population will have T_{normal} , but some will have T_{low} . Because those with the T_{low} allele will not be able to see quite as well as other members of their species possessing T_{normal} , on average they will not have as many offspring. Perhaps they notice prey slightly less often, and thus not have quite as much food, or perhaps they fail to notice predators slightly more often, and will therefore be killed and eaten at a slightly higher frequency. Over many, many generations, the fraction of individuals with the T_{low} allele will decrease relative to those with the T_{normal} allele simply because individuals possessing the T_{low} allele produce, on average, fewer offspring. We say that the T_{low} allele producing the less transparent lens protein is selected against, and that the frequency of this allele decreases with time. Notice that, if the total population size remains constant, that the decrease in frequency of the T_{low} allele results in an increase in the frequency of the T_{normal} allele.

Imagine another mutation of the normal lens allele, creating a third allele (T_{super}) that produces a super transparent lens protein. The population now contains three alleles, T_{low} , T_{normal} , and T_{super} . Individuals possessing the T_{super} allele detect prey, on average, at slightly higher frequencies, and thus have more food, and they more frequently detect predators and therefore are eaten slightly less frequently. As a consequence, on average, they have more offspring than individuals possessing T_{normal} . Over many, many generations, the frequency of the T_{super} allele will increase in the population, whereas the frequencies of the T_{normal} and T_{low} alleles will decrease, and perhaps disappear altogether. This is called evolution by natural selection: the frequencies of the three alleles have changed as a consequence of their reproductive effects. Over time, a population will acquire alleles that produce proteins that better solve critical reproductive problems, and

lose alleles that produce proteins that less effectively solve these problems. There is widespread agreement that evolution by natural selection is responsible for the origins of the sophisticated organs and tissues like hearts, lung, livers, etc., that enable organisms to reproduce.

Because, in a population of a given size, the increase in the frequency of T_{super} must decrease the frequencies of the other alleles, biologists began saying that different alleles were 'competing'. (Usually, but not always, alleles increase their frequency by causing individuals possessing them to produce, on average, more offspring.) Dawkins, highlighting the iron-clad logic that alleles increase their frequency in the population if they cause more copies of themselves to be made relative to other alleles, and that by increasing their own frequency, they decrease the frequency of the alternative (competing) alleles, termed genes 'selfish'. Alleles increase their frequency at the expense of other alleles.

Do selfish genes mean selfish people?

Not necessarily. Describing genes as selfish is an analogy that has nothing to do with our folk notion of selfishness. Adaptations evolve via the differential reproduction of alleles (different versions of the same gene). This means that one version of a gene (allele A) at a particular locus causes organisms bearing that version to have a different phenotype (body structure) than organisms bearing a different version of the gene (allele B) at the same locus. If organisms with phenotype A produce more offspring than those with phenotype B, allele A will increase in frequency in the population. Allele A is said to have 'out-competed' allele B. Thus, allele A is a 'selfish gene'--it increased its frequency at the expense of allele B. But, *every* adaptation in the body evolved in this manner! That means that the genes coding for your hair are just as 'selfish' as the genes coding for your fingernails, which are just as 'selfish' as the genes coding for your kneecaps! The same goes for psychological adaptations: the genes coding for vision are just as 'selfish' as the genes coding for memory, which are just as 'selfish' as the genes coding for muscle control.

There is a narrow range of psychological adaptations whose properties do correspond to our folk notion of selfishness. When critical resources are limited, organisms which are able to obtain adequate supplies of these resources will out-reproduce those that don't. Obtaining such resources will often involve direct conflict between organisms, such as fighting for food or mates. Genes that code for fighting abilities that would allow organisms possessing those genes to out-compete other organisms for scarce resources will increase in frequency. So, the fact that some resources are limited means that strategies like aggression are likely to evolve in many species. Psychological adaptations for aggression correspond to our folk notions of 'selfishness', but it should be noted that these adaptations evolved by the same process as every other adaptation. The genes underlying these adaptations are no more 'selfish' than are the genes underlying any other adaptation.