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Abstract

The theory of evolution by natural selection provides the only scientific explanation for the existence of complex adaptations. The design features of the brain, like any organ, are the result of selection pressures operating over deep time. Evolutionary psychology posits that the human brain comprises a multitude of evolved psychological mechanisms, adaptations to specific and recurrent problems of survival and reproduction faced over human evolutionary history. Although some mistakenly view evolutionary psychology as promoting genetic determinism, evolutionary psychologists appreciate and emphasize the interactions between genes and environments. This approach to psychology has led to a richer understanding of a variety of psychological phenomena, and has provided a powerful foundation for generating novel hypotheses. Critics argue that evolutionary psychologists resort to storytelling, but as with any branch of science, empirical testing is a vital component of the field, with hypotheses standing or falling with the weight of the evidence. Evolutionary psychology is uniquely suited to provide a unifying theoretical framework for the disparate subdisciplines of psychology. An evolutionary perspective has provided insights into several subdisciplines of psychology, while simultaneously demonstrating the arbitrary nature of dividing psychological science into such subdisciplines. Evolutionary psychologists have amassed a substantial empirical and theoretical literature, but as a relatively new approach to psychology, many questions remain, with several promising directions for future research.

Introduction

Darwin's theory of evolution by natural selection (Darwin, 1859)[1] revolutionized our understanding of the complexity of life, taking biological features once viewed as intelligently designed or irreducibly complex and revealing the natural, gradual, blind process behind their formation. In addition to providing a natural account of complex adaptations, evolutionary theory illustrates that the enormous biological diversity we see today, from hummingbirds and humpback whales to pine trees and *Streptococcus pneumoniae*, can all be traced to a common ancestor. Although Darwin largely avoided the topic in his *Origin of Species*,(Darwin, 1859)[1] it was clear that his theory had important implications for understanding the origin of humans. Indeed, it is now understood that humans are one branch on the tree of life, that we have existed in our anatomically modern form for roughly 200,000 years,(McDougall, Brown, & Fleagle, 2005)[2] and that our closest evolutionary relative is the chimpanzee, with whom we share a common ancestor dating back 6-7 million years.(Zimmer, 2006)[3]

Despite the acknowledgment (in the scientific community [Gallup poll, 2012][4]) of human evolution, the social, behavioral, and psychological sciences have historically ignored this reality, resulting in theoretical assumptions that have not been properly informed by an evolutionary perspective. This is particularly evident when considering what has been dubbed the *Standard Social Science Model* (SSSM),(Tooby & Cosmides, 1992)[5] a predominant view of the mind as a blank slate composed of general purpose, content-independent learning and reasoning mechanisms.(Tooby & Cosmides, 1992; Pinker, 2002; Tooby & Cosmides, 2005)[5-7] Evolutionary psychology represents a relatively new, and long overdue, paradigm shift in which the architecture of the mind is understood as a product of specific and recurrent selection pressures acting over deep evolutionary time. Here we provide a broad overview of evolutionary psychology, focusing on the core theoretical assumptions of the field, highlighting some significant empirical findings, and describing how this approach is uniquely suited to unify the currently disparate subdisciplines of psychological science within a single coherent theoretical framework.

A PRIMER ON EVOLUTION

To understand and appreciate the utility of evolutionary psychology, one must be familiar with evolutionary theory. Although there are many excellent introductions to evolutionary theory to which readers may refer,(Zimmer, 2006; Coyne, 2009; Dawkins, 2009; Dennett, 1995; Mayr, 2001)[3,8-11] we offer a brief review of several core concepts, beginning with natural selection.

Evolution is simply change over time, and natural selection is a primary driving force behind this change. The process of natural selection can be understood with reference to three components: variability, inheritance, and differential survival. If these components are present, evolution by natural selection will occur.(Darwin, 1859)[1] Variability refers to the fact that within any population of sexually reproducing organisms, individuals differ in many ways, such as color, size, shape, behavior, and other traits that may or may not be easily perceived.(Liddle, Bush, & Shackelford, 2011)[12] These variations provide the "raw materials" for evolution,(Buss, 2011)[13] as there would be nothing for natural selection to *select* if organisms did not vary.

However, variability can only play a role in evolution if the traits in question are inherited (i.e., passed on to offspring with high fidelity). Darwin (1859)[1] could only speculate about this component of natural selection, but we now know that offspring inherit their parents' genes, which provide the "recipe" for an organism's characteristics and are replicated with remarkably high fidelity. Nevertheless, genetic mutations occur and play a significant role in generating variability, along with genetic recombination through sexual reproduction and gene duplication.(Zimmer, 2006)[3] The discovery of genes and of particulate inheritance marked a pivotal advance in scientific understanding, with its incorporation into evolutionary theory described as the "Modern Synthesis."(Dobzhansky, 1937; Huxley, 1942)[14,15] The gene has taken center stage in evolutionary theory, since it is the fundamental unit of selection.(Dawkins, 2006)[16]

If natural selection operates at the level of the gene rather than the level of the individual, it is possible for traits to evolve that are beneficial to the genes that built them but costly to the individuals that house them. This possibility exists because of the existence of genetic relatives. Since relatives share genes by descent, if an organism performs a costly behavior that increases the survival chances or reproduction of a genetic relative, that trait may be selected for because the genes related to that trait are shared by the relative. The genes are reaping the rewards of an increased possibility of transmission to the next generation, and so the trait will be selected despite the costs to the organism displaying the trait. More specifically, a trait that is harmful to the individual who possesses it can be selected if the cost is outweighed by the benefits this trait bestows on a genetic relative, multiplied by the degree of relatedness. In other words, a trait that targets one's cousin would have to confer a higher fitness benefit to be selected compared to a trait that targets one's sibling. In short, traits evolve as a function of their impact on *inclusive* fitness (Hamilton, 1964)[17] (an individual's own reproductive success *plus* the effects the individual's actions have on the reproductive success of genetic relatives).(Buss, 2011)[13]

Finally, for evolution by natural selection to occur, there must be a differential survival of organisms within a population. If all members of a population were equally successful at surviving and reproducing, the population would grow exponentially and quickly reach unsustainability.(Malthus, 1798)[18] Given limited resources available in the environment, the result is a struggle for existence, with some organisms thriving while others fail to survive and reproduce. To the extent that inherited variations influence one's chances of success in the struggle for existence, natural selection will take place, selecting *for* traits that increase one's chances and selecting *against* traits that decrease one's chances.

In summary, natural selection is the non-random selection of random genetic variants that impact an organism's fitness (i.e., the likelihood of passing on one's genes, determined by survival and reproductive success). There is, of course, no actual "selector" in nature pulling invisible strings. This process is blind and inevitable, as genes that provide survival benefits and improve reproductive success will necessarily become more prevalent in subsequent generations, since the organisms most likely to pass on their genes are, on average, those who possess these beneficial genes. When discussing this process, it is useful to refer to traits being selected for or against, but it is important to keep in mind that there is no conscious entity overseeing this process. Natural selection has no goals, foresight, or morality; all that matters are the effects that inherited traits have on survival and reproduction.

The Products of Evolution

Much like the imperceptible geological forces that build mountains and sink islands, natural selection operates over vast periods of time, selecting favorable variants within a population over thousands of generations. This gradual process eventually leads to the construction of an adaptation, which can be defined as "an inherited and reliably developing characteristic that came into existence through natural selection because it helped to solve a problem of survival or reproduction during the period of its evolution" (Ref 13[Buss, 2011], p. 38). These problems of survival or reproduction are *selection pressures*, meaning that any inherited trait that helps solve a particular problem is likely to become more prevalent in the population over time via natural selection. Given enough time (and the appropriate genetic variants), adaptations can become quite complex, as each random and slight improvement in design is selected. A good example is the human eye, which researchers have estimated can evolve in fewer than 400,000 generations through a series of intermediate steps beginning with a patch of light-sensitive cells.(Nilsson & Pelger, 1994)[19] The key is that for selection to occur, each step in the eye's evolution should confer some benefit over the previous design, which is a justifiable assumption given the discovery of many of these "steps" in the fossil record and in extant species.(Coyne, 2009)[8]

Adaptations are a focal point of evolutionary theory, but they are not the only products of evolution. Evolution may also result in byproducts or noise (Buss et al., 1998)[20] Byproducts are characteristics that result from the existence of adaptations. A good example is the belly button, which has no adaptive function but results from the existence of the umbilical cord, an adaptation for obtaining nutrients throughout fetal development.(Buss, 2011)[13] Another example is the whiteness of bones, which also serves no function but results from high concentrations of calcium, a likely adaptation for improved bone strength.[21] Noise refers to inherited variants that do not have any impact on survival and reproduction and, therefore, are not selected for or against.(Buss et al., 1998)[20]

Because there are several different products of evolution, it is helpful to rely on specific criteria to determine whether a trait qualifies as an adaptation. Such criteria were developed by George Williams (Williams, 1966)[22] and continue to be relied on by researchers today.(Buss, 2011)[13] In short, for a particular trait to be considered an adaptation, it should exhibit *reliability* (reliably developing in all or most members of a species when in a species-typical environment), *efficiency* (solving the adaptive problem well), and *economy* (solving the adaptive problem without imposing large costs on the organism).(Buss, 2011; Williams, 1966)[13,22] Although these criteria are not exhaustive, attention to these criteria can reduce the possibility of mistakenly categorizing byproducts or noise as adaptations.

Middle-Level Theories

The theory of evolution by natural selection is simple: organisms gradually change over many generations as a result of inherited variants impacting survival and reproduction. However, evolutionary theory becomes more complex when one considers middle-level theories, which provide key insights that are consistent with, but not directly derivable from, general evolutionary theory.(Buss, 2011; Ketelaar & Ellis, 2000)[13,23] Several of these theories have played important roles in guiding evolutionary psychological research, and we summarize these theories next.

Sexual Selection

Twelve years after *Origin of Species* was published, Darwin discussed human evolution and provided an important addendum to natural selection in *The Descent of Man, and Selection in Relation to Sex*.(Darwin, 1871)[24] The addendum was sexual selection, a process that emphasized the importance of reproductive success in determining the selection of inherited traits. Although the process is technically indistinguishable from natural selection, sexual selection highlights the unequal fitness benefits derived from survival and reproduction. Traits that increase reproductive success at a cost to the organism's long-term survival will be selected over traits that increase long-term survival at a cost to the organism's reproductive success. An organism that lives for 100 years and fails to produce offspring will have the same fitness as an organism that dies immediately after birth, and both will have a much lower fitness than an organism that lives for a week and produces several offspring.

The conceptualization of sexual selection was motivated, in part, by the apparent contradiction between natural selection and the peacock's train. The large and vibrant train appears to be a characteristic that would be selected against because it is metabolically costly to produce and negatively impacts survival, both by increasing visibility to predators and decreasing ability to escape from predators. However, Darwin realized that such a characteristic could be selected *if* it had a positive impact on the reproductive success of peacocks, thus outweighing the costs to survival. Indeed, researchers have demonstrated that peahens preferentially mate with peacocks based on the quality of their trains, as artificially removing or adding eyespots to trains decreases and increases their reproductive success, respectively.(Petrie, Halliday, & Sanders, 1991; Petrie & Halliday, 1994) [25,26] One possible explanation is that peahens prefer more elaborate trains *because* they are more costly for peacocks to produce, as this would provide an honest signal of genetic quality—because only the highest quality males would be capable of producing and surviving with such a handicapping characteristic.(Zahavi & Zahavi, 1996)[27]

Sexual selection further expands upon general evolutionary theory by describing two general contexts in which selection occurs. The preference for elaborate trains by peahens is an example of *intersexual selection*, which refers to the selection of traits in one sex as a result of preferential mate choices by the other sex. The second context in which sexual selection operates is *intrasexual competition*, which refers to the selection of traits in one sex that provide a benefit in competing with same-sex rivals for access to mates. An example of intrasexual competition is two stags locking horns in combat.(Buss, 2011)[13] In competitions such as these, the victor gains increased mating access to members of the other sex. This type of sexual selection is observed among males in many species, and to appreciate why this is the case, we must refer to another middle-level theory.

Parental Investment Theory

The theory of parental investment (Trivers, 1972)[28] describes the important role that investment in offspring plays in determining sex differences in intersexual selection and intrasexual competition. This theory is based on the observation that, among sexually reproducing species, there is often a difference between the sexes in the minimum obligatory investment provided to offspring. This is particularly evident in placental mammals, in which females provide higher minimum obligatory investment via internal fertilization, gestation, and nursing, whereas the minimum obligatory

investment for males is the contribution of sperm. (Liddle, Shackelford, & Weekes-Shackelford, 2012)[29]

Parental investment theory predicts that the sex which invests more heavily in offspring will also be more discriminating when choosing mates, since the greater costs associated with producing offspring translate into greater costs associated with poor mate choice (i.e., investing limited resources into genetically inferior offspring that have a reduced likelihood of survival and reproductive success). The choosier sex thus represents a limiting factor for the reproductive success of the other sex. Therefore, the sex that invests less in offspring is predicted to be more competitive and to engage in riskier behaviors in the pursuit of mating opportunities. This explains traits such as violent competition between stags and the sexual dimorphism observed in gorillas and elephant seals,(Cartwright, 2008)[30] but the predictive power of parental investment theory is highlighted when observing species in which the typical sex difference in investment is reversed. In species such as the Mormon cricket,(Buss, 2011)[13] pipefish seahorse,(Buss, 2011)[13] and Australian cassowary,(Ghiglieri, 1999)[31] males invest more in offspring than females and are the choosier sex, whereas females typically compete for access to mates.

DEFINING EVOLUTIONARY PSYCHOLOGY

In regards to understanding humans, the social, psychological, and behavioral sciences have long been dominated by theories that fail to take human evolutionary history into account.(Tooby & Cosmides, 2005)[7] Psychologists often focus on the immediate, salient reasons for a given phenomenon; that is, they rely on *proximate* explanations.(Liddle, Bush, & Shackelford, 2011)[12] Although proximate causes are important pieces of the puzzle of human nature, it is necessary to also examine the *ultimate* causes to understand why certain psychological phenomena exist in the first place. Evolutionary psychology represents an attempt to uncover such ultimate causes by relying on evolutionary theory as a foundation for generating hypotheses about the fundamental components of human nature.(Buss, 2011)[13] Next we highlight some of the basic tenets of evolutionary psychology.

Evolved Psychological Mechanisms

Evolutionary psychology is based on the premise that the brain, like all other organs, consists of design features that are the result of natural selection operating over human evolutionary history (as well as design features that were inherited from ancestral species that existed millions of years before humans). Evolutionary psychologists argue that the brain is not a domain-general problem-solving device. When one examines any other organ, such as the heart or kidneys, it is clear that they represent evolved solutions to specific adaptive problems. Therefore, given the variety of functions accomplished by the brain, and the fact that adaptations result from recurrent and specific problems of survival and reproduction, evolutionary psychology posits that our brains consist of a multitude of domain-specific adaptations, each of which solves a unique adaptive problem. Evolutionary psychologists refer to these adaptations as evolved psychological mechanisms (EPMs),(Buss, 2011)[13] and propose that they possess the following properties:

> (1) An EPM exists in the form that it does because it solved a specific problem of survival or reproduction recurrently over evolutionary history.
>
> (2) An EPM is designed to take in only a narrow slice of information.
>
> (3) The input of an EPM tells an organism the particular adaptive problem it is facing.
>
> (4) The input of an EPM is transformed through decision rules into output.
>
> (5) The output of an EPM can be physiological activity, information to other psychological mechanisms, or manifest behaviors.
>
> (6) The output of an EPM is directed toward the solution to a specific adaptive problem. (Ref. 13 [Buss, 2011], pp. 48-50)

Liddle, Bush and Shackelford (2011)[12] illustrate how these properties can be applied to a hypothesized EPM for detecting and inducing a fear of snakes:

> First, such an adaptation would clearly solve a specific problem of survival: avoiding dangerous environmental stimuli. Second, a module for detecting dangerous organisms may indeed take in only a limited type of information – it may induce us to pay special attention to serpentine forms and to motivate a fear response only towards a specific type of phenomena: perception of snakes. The third and fourth criteria are also met, in that the input—sensory processing of a snake or something snake-like—provides the organism with the information to produce a response appropriate to that particular input based on the adaptive problem that mechanism evolved to solve, which in turn activates a particular decision rule: fear and increased attention to the stimuli. The outcome of detecting a snake meets the final criteria, as the evolved mechanism for fear of snakes induces us to take action to remove ourselves from the danger, clearly a physiological response evolved to preventing bodily harm. (p. 180)

The concept of an EPM provides a powerful framework for generating hypotheses about how the mind works by guiding researchers to identify the design features that are necessary for the mind to solve the various adaptive problems faced by our ancestors.

The Environment of Evolutionary Adaptedness

Another important concept within evolutionary psychology is the environment of evolutionary adaptedness (EEA), which "refers to the statistical composite of selection pressures that occurred during an adaptation's period of evolution responsible for producing the adaptation" (Ref. 13 [Buss, 2011], p. 39). For every adaptation, there is a unique EEA, a unique set of selection pressures that played a role in the process of selecting for inherited variants that led to the construction of the adaptation in question. Importantly, the EEA should not be misconstrued as referring to a single environment or time period. In fact, the concept of an EEA serves as a reminder that one should not think of a single "ancestral environment" as providing an accurate summary of the selection pressures influencing the evolution of the mind. Throughout our evolutionary history, humans have experienced and adapted to a variety of environments and selection pressures. By focusing on the specific selection pressures faced by our ancestors, based on defensible assumptions and informed

by sources of data such as archaeological records and observations of hunter-gatherer societies, (Buss, 2011)[13] evolutionary psychologists develop testable hypotheses about the existence and function of specific EPMs.

Misconceptions of Evolutionary Psychology

One useful way to illustrate the basic tenets of evolutionary psychology is to explain what evolutionary psychology *isn't*. Evolutionary psychology has been met with a variety of criticisms, most of which stem from misconceptions or misunderstandings. Although a number of excellent rebuttals to such criticisms already exist,(Liddle, Bush, & Shackelford, 2011; Bryant, 2006; Confer et al., 2010; Geher, 2006; Hagen, 2005; Kurzban, 2002; Liddle & Shackelford, 2009; Sell, Hagen, Cosmides, & Tooby, 2003)[12,32-38] we highlight a few misconceptions of the field to illustrate additional core ideas underlying evolutionary psychology.

Genetic Determinism

One common criticism of evolutionary psychology is that it implies genetic determinism,(Nelkin, 2000; Rose, 2000; Shakespeare & Erikson, 2000)[39-41] which suggests that behavior is exclusively controlled by genes without environmental influence.(Buss, 2011)[13] In reality, evolutionary psychology highlights the importance of both genes and the environment, arguing that the two interact in important ways. Duntley and Buss argue that "environmental interactions are essential at every step of the causal chain—from the origins of adaptations, to their development during ontogeny, to their expression in manifest behavior" (Ref. 42[Duntley & Buss, 2008], p. 31). EPMs operate by processing specific types of environmental input. Without the necessary input, an EPM will not be activated and will not generate output.

Furthermore, evolutionary psychologists posit that novel environmental inputs can have significant effects on psychological mechanisms that evolved under different conditions. For example, humans have an evolved preference for sweet and fatty foods,(Birch, 1999; Krebs, 2009)[43,44] which would have been adaptive for our ancestors who often faced food scarcity. Those who had a preference for calorically-dense foods would have been more likely to survive and reproduce compared to those who lacked the EPM that generated such a preference. However, in societies in which sweet and fatty foods are cheap and plentiful, such a mechanism can result in obesity, diabetes, coronary disease, and other medical problems. This mismatch between adaptations and the environment exists because the novel environmental stimulus has not existed for enough time to select against the evolved mechanism. Another example of the mismatch between an EEA and the current environment is the fear of snakes, an adaptive response to stimuli that posed a threat recurrently over human evolutionary history. People reliably develop such fears, even in contemporary environments in which the associated adaptive problems (i.e., likelihood of receiving a poisonous bite) no longer exist.(Buss, 2011; Ohman & Mineka, 2001)[13,45] Conversely, people do not reliably develop fears of stimuli that *are* threatening in contemporary environments (e.g., automobiles, electrical outlets), because these threats have not persisted long enough for the selection of specialized adaptive solutions (e.g., fear, avoidance). In summary, evolutionary psychologists not only acknowledge the importance of environmental stimuli in determining behavior, but illustrate specific ways in which novel stimuli are predicted to interact with evolved psychological mechanisms.

Just-So Stories

Another criticism of evolutionary psychology is the assertion that researchers in the field resort to *ad hoc* storytelling to explain psychological phenomena (i.e., "just-so stories") (Coyne, 2009)[8] and that evolutionary psychological hypotheses are untestable and unfalsifiable.(Gould, 2000)[46] First, it is simply not the case that evolutionary psychological hypotheses are unfalsifiable.(Williams, 1966)[22] As in any other scientific field, hypothesis testing is a vital component of evolutionary psychology, with hypotheses standing or falling with the weight of the evidence. Not only do evolutionary psychologists empirically test hypotheses, but they do so using a wide variety of methods,(Buss, 2011)[13] including comparisons between different species,(Vonk & Shackelford, 2012)[47] cross-cultural studies,(Gangestad, Haselton, & Buss, 2006; Lippa, Collaer, & Peters, 2010)[48,49] physiological measurements,(Buss, Larsen, Westen, & Semmelroth, 1992)[50] brain imaging,(Platek, Keenan, & Shackelford, 2007)[51] and behavioral (Segal, 2011)[52] and molecular genetic (Ebstein, 2006)[53] methods, along with experimental methods traditionally used in psychological science.

As for the charge of generating just-so stories, it is the case that one strategy evolutionary psychologists use to generate hypotheses is observation-driven. However, researchers do not consider their job complete after generating such *ad hoc* explanations, but rather empirically test their hypotheses using the methods described earlier. Furthermore, a large proportion of research in evolutionary psychology is theory-driven rather than observation-driven,(Buss, 2011)[13] with researchers generating hypotheses to discover new facts rather than explain previously acknowledged facts. (Liddle, Bush, & Shackelford, 2011)[12] For example, on the basis of inclusive fitness theory, Daly and Wilson (1985)[54] hypothesized and subsequently confirmed that children living with one genetic parent and one stepparent face a significantly higher risk of being abused. In fact, such children are 40 times more likely to be physically abused than children living with both genetic parents,(Daly & Wilson, 1985)[54] making step-parenthood "the single most powerful risk factor for child abuse that has yet been identified" (Ref. 55[Daly & Wilson, 1988], pp. 87-88). Such findings powerfully illustrate the importance of generating and testing evolutionarily-informed hypotheses.

Critiques of Massive Modularity

Evolutionary psychologists argue that the human brain is massively modular, consisting of a large number of domain-specific EPMs, or modules. The nature and degree of modularity in the brain is a topic of considerable debate (for an in-depth discussion of the modern evolutionary psychological view of modularity, see Barrett and Kurzban[2006][56]), although a significant proportion of opposition to the view of massive modularity stems from the outdated and unnecessarily narrow Fodorian conception of modularity.(Fodor, 1983)[57] Fodor's concept of modularity includes a list of likely features of modules, such as automaticity and encapsulation. Although Fodor himself argued against such features being necessary or defining, the modern view of modularity promoted by evolutionary psychologists argues that it is premature to speculate about the design features of a module without first considering the function of that module. Barrett and Kurzban emphasize that:

> ...the concept of modularity should be grounded in the notion of *functional specialization* rather than any specific Fodorian criteria. Biologists have long held that structure reflects function, but that function comes first. That is, determining what structure one expects to

see without first considering its function is an approach inconsistent with modern biological theory. (Ref. 56[Barrett & Kurzban, 2006], p. 629)

Opposition to modularity also stems from the Fodorian concept of spatial localization. Although the idea of a module may seem to imply localization in a particular part of the brain, the modern view of modularity avoids this assumption. Modules consist of a collection of neurons, and there is no reason to suspect that these neurons must be restricted to a particular section of brain tissue. As with other design features of modules, the degree of spatial localization likely varies with respect to the function of the module in question. Until technological advances in neuroscience, particularly brain imaging, provide us with a more detailed view of the brain in action, the physical instantiation of hypothesized modules will remain nebulous, and as such the modern view of modularity remains largely agnostic on such issues.

EMPIRICAL FINDINGS

Although evolutionary psychology represents a relatively new approach to psychology, researchers in the field have amassed an impressive theoretical and empirical literature. (Buss, 2011; Buss, 2005)[13,58] Although it is beyond the scope of this article to provide an in-depth summary of this literature, we next highlight representative empirical findings in evolutionary psychology, organized in terms of the broad adaptive problems of survival and reproduction.(Buss, 2011)[13]

Survival

One of the fundamental suites of adaptive problems faced by humans throughout their evolutionary history has been the problems of survival. Survival is a necessary precondition of reproductive success, and so to the extent that increased survival benefits one's chances of reproducing, adaptations for solving the problems of survival have been selected. Although organs like the heart and lungs are clear examples of adaptations related to survival, evolutionary psychologists argue that a host of psychological mechanisms have also evolved in response to selection pressures related to the adaptive problems of survival. For example, food preferences represent an evolved solution to a particular problem of survival: the problem of acquiring nutrients.(Buss, 2011)[13] In addition to preferences for foods that are calorically dense, humans have aversions to certain foods. Foods that contain toxins taste bitter or sour.(Krebs, 2009)[44] These preferences and aversions can be found as early as infancy (Buss, 2011)[13] and have been observed in the Hadza hunter-gatherers of Tanzania.(Berbesque, 2009)[59] Qualities such as sweetness and bitterness are not intrinsic to the food in question, but rather represent output produced by psychological mechanisms designed to influence eating behavior in adaptive ways. There is nothing intrinsically "sweet" about sugar molecules, but our ancestors are those with mechanisms that rewarded the consumption of such calorie-rich molecules by generating the pleasurable experience of "sweetness."(website, 2012)[60]

Pregnancy sickness, or morning sickness, provides a compelling example of the degree of specificity that can be found in regard to adaptations. Pregnancy sickness is hypothesized to serve the adaptive function of reducing exposure to toxins that are particular harmful to a developing fetus.(Profet, 1992)[61] In support of this hypothesis, the foods that trigger pregnancy sickness are correlated with toxicity, pregnancy sickness occurs between the second and eighth weeks of pregnancy when the fetus is most vulnerable to toxins, and women who do not experience

pregnancy sickness during the first trimester are three times more likely to spontaneously abort.(Buss, 2011; Profet, 1992)[13,61]

Another important adaptation related to problems of survival is fear. Humans appear to have evolved predispositions for developing particular fears, namely fears of stimuli that posed a threat to our ancestors.(Buss, 2011)[13] The ontogenetic development of particular fears also points to functional specialization. Specific fears develop in relation to when the relevant stimuli would have been most likely encountered by our ancestors. For example, the fear of heights and strangers emerges at six months of age, which coincides with the age that infants begin to crawl away from their mothers, thus increasing the likelihood of encountering such threats to survival.(Scarr & Salapatek, 1970)[62] Similarly, animal fears emerge at two years of age, as children begin more expansive explorations of the environment.(Buss, 2011)[13] These results indicate that fears are not arbitrary,(Buss, 2011; Barrett, 2005)[13,63] but rather correspond to stimuli that were recurrent threats throughout our evolutionary history.

Mating

Finding and securing a mate are crucial adaptive problems, as one's fitness is determined by reproductive success (inclusive fitness notwithstanding). As such, we can assume that there have been strong selection pressures throughout human evolutionary history for the construction of EPMs that increase one's chances of successfully mating. Evolutionary psychologists have generated a large body of theoretical and empirical work on human mating psychology.(Buss, 2011; Buss, 2005; Buss, 2003)[13,58,64] The theories of sexual selection and parental investment have proved valuable in generating hypotheses regarding sex differences in mating psychology. More specifically, the concept of intersexual selection, along with assumptions of the different adaptive problems faced by men and women as a result of different levels of minimum obligatory parental investment, has guided the generation and testing of hypotheses regarding mate preferences.

Due to a greater minimum obligatory of investment in offspring and a lower capacity for the number of offspring that can be produced (due to periods of gestation and nursing), women are the choosier sex, preferring to engage in a long-term mating strategy, and exhibiting preferences for a man's ability and willingness to invest resources in a woman and any offspring produced with her.(Buss, 2011; Buss, 2003)[13,64] Women across cultures view traits such as good financial prospects,[65] high social status (which is correlated with access to resources) (Buss, 2011)[13], slightly older age (which is correlated with increased status) (Buss, 2011)[13], and ambition (Buss & Schmitt, 1993)[66] as more desirable in a long-term mate than do men. (Buss, 2003)[64] Signals of good health are also important to women,(Buss, 2011)[13] particularly masculine features that appear to signal high levels of testosterone. Because a high level of testosterone is known to compromise the immune system in humans, the preference for such traits may be analogous to the peahen preference for elaborate trains: masculine features may provide honest signals of a man's genetic quality.(Johnston et al., 2001)[67]

Men, on the other hand, do not have their reproductive potential restricted in the same way as do women, and therefore are more likely to pursue short-term mating strategies. (Buss, 2011)[13] Also, men across cultures exhibit a s higher sex drive than women, (Buss, 2011)[13] even in societies with high levels of gender equality.(Kennair et al., 2009)[68] Furthermore, as the reproductive value (the number of children one is likely to have in the future) of women declines much more sharply

than that of men, men across cultures place a greater emphasis on youth and physical features that serve as signals of youth and fertility.(Buss, 2011; Buss, 2003)[13,64] Finally, men who pursue a short-term mating strategy exhibit a preference for sexual experience in a mate.(Buss, 2011)[13] However, when men pursue a long-term mating strategy, this preference reverses. Long-term mating for men typically consists of investing significant resources in offspring, and so men are predicted to be particularly sensitive to the adaptive problem of paternity uncertainty: the possibility that the offspring they are raising are not genetically related to them, an adaptive problem absent among women. As such, men looking for a long-term mate value chastity and sexual inexperience, as these traits signal a reduced likelihood of partner infidelity. (Buss, 2011)[13] In summary, by focusing on the adaptive problems unique to our male and female ancestors, evolutionary psychologists have advanced our understanding of mating psychology.

UNIFYING THE PSYCHOLOGICAL SCIENCES

Evolutionary psychology is best viewed as an approach to psychology rather than a subdiscipline of psychology. Evolutionary psychologists are not limited to studying particular topics such as social behavior, cognitive development, or personality; an evolutionary perspective can be applied to any area of psychological research. Evolutionary psychology is uniquely suited to provide a unifying theoretical framework for the currently disparate subdisciplines of psychology. Indeed, the current division of areas of psychological study is shown to be unnatural and arbitrary when one adopts an evolutionary perspective. Buss illustrates this well by discussing stranger anxiety, a proposed behavioral adaptation that emerges reliably in infants around six months of age and functions to reduce the likelihood of infants being harmed by dangerous humans, particularly male strangers:

> In which subdiscipline of psychology does stranger anxiety belong? It obviously involves information processing and this could be claimed by cognitive psychology. It shows a predictable ontogenetic unfolding, so it could be claimed by developmental psychology. It is activated by interactions with others, so it belongs to social psychology. Individual infants differ in the intensity of stranger anxiety, so it falls within the province of personality psychology. The mechanism can malfunction in a minority of infants, so it's relevant to clinical psychology. And its biological substrate must include the brain, so neuroscience can also lay claim. Obviously, stranger anxiety belongs simultaneously to all or to none. (Ref 69 (Buss, 2005), pp. xxiv-xxv)

An evolutionary perspective provides a non-arbitrary method for dividing up psychological science by emphasizing the different categories of adaptive problems faced by humans.(Buss, 2003)[64] In addition to the particular problems of survival and reproduction highlighted earlier, evolutionary psychologists have generated and tested hypotheses related to a wide variety of specific adaptive problems, such as problems associated with parenting (e.g., the problems of paternity uncertainty, determining how much to invest in offspring, mother-offspring conflict *in utero*,(Haig, 1993)[70] and parent-offspring conflict over mating [Apostolou, 2007][71]), kinship (e.g., the problems of kin recognition,[Weisfeld et al., 2003; Lieberman, Tooby, & Cosmides, 2007)[72,73] incest avoidance, [Weisfeld et al., 2003; Lieberman, Tooby, & Cosmides, 2007][72,73] and grandparental investment in offspring [Euler & Weitzel, 1996][74]), and group living (e.g., the problems of promoting cooperation and avoiding free-riding [Trivers, 1971; Cosmides & Tooby, 1992][75,76]). Nevertheless, the existing subdisciplines of psychology are unlikely to be dismantled any time soon, even as evolutionary

psychology becomes increasingly incorporated into mainstream psychology,(Cornwell et al., 2005)[77] and so it is useful to illustrate how an evolutionary perspective can be applied to some of these areas of research.

Evolutionary Cognitive Psychology

Cognitive psychology has traditionally focused on the study of the information-processing mechanisms of the mind. However, cognitive psychologists have also traditionally viewed cognitive architecture as general-purpose and content-free. (Buss, 2011)[13] Evolutionary psychology presents a stark contrast to this view, resulting in hypotheses that can uncover previously unnoticed features of mechanisms that have been extensively studied by cognitive psychologists.(Todd, Hertwig, & Hoffrage, 2005)[78] For example, applying an evolutionary perspective to mechanisms underlying attention and memory can highlight the evolved functions of these systems. One general prediction regarding these systems is that they should be sensitive to the types of information that have historically been related to adaptive problems. (Klein, Cosmides, Tooby, & Chance, 2002)[79] In terms of attention, an analysis of 736 front-page newspaper stories spanning eight countries and 300 years revealed a large degree of content uniformity, with a focus on the following themes: death, murder or physical assault, robbery, reputation, heroism or altruism, suicide, marital problems, harm or injury to offspring, abandoned or destitute family, taking a stand or fighting back, and rape or sexual assault. (Davis & McLeod, 2003)[80] As Buss explains, these results "provide naturalistic evidence that human attention is specially targeted toward information content of maximal relevance for solving adaptive problems that have recurred for humans over deep time" (Ref. 13 [Buss, 2011], p. 394).

An evolutionary perspective can also lead to unique predictions about memory performance. For example, regarding jealousy, men place greater emphasis on are more distressed by cues to a partner's sexual infidelity (an evolved solution to the problem of paternity uncertainty), whereas the same effects in women are triggered more by a partner's emotional infidelity (an evolved solution to the problem of long-term diversion of investment by a mate). (Buss et al., 1992)[50] Based on these findings, Schützwohl and Koch (2004)[81] predicted and found that men and women exhibit greater memory recall for cues to sexual and emotional infidelity, respectively. Findings such as these suggest that mechanisms often viewed as domain-general problem-solvers include design features built to aid in solving domain-specific adaptive problems.

Evolutionary Social Psychology

Humans are an intensely social species, a fact that some argue was the primary selection driving the rapid increase in brain size throughout hominid evolution.(Zimmer, 2006)[3] Given the important influence of social behavior on survival and reproduction throughout human evolutionary history, one can reasonably posit that the mind includes many EPMs devoted to solving adaptive problems related to social life. (Buss, 2011)[13] Traditional social psychology has generated a large number of descriptions of psychological phenomena, such as the fundamental attribution error, (Jones & Harris, 1967)[82] self-handicapping, (Leary & Shepperd, 1986)[83] and the confirmation bias, (Hansen, 1980)[84] but the field lacks an overarching, ultimate explanation for such phenomena.(Kenrick, Maner, & Li, 2005)[85]

Several theories that inform evolutionary psychological thinking are directly related to social behavior. For example, cooperative and altruistic behavior can be partially explained by referring to

inclusive fitness theory and the benefits that such behavior can confer to genetic relatives. However, humans often cooperate with individuals to whom they are not genetically related. Evolutionary theory has provided insights about this type of behavior as well, particularly with the theories of reciprocal altruism[75] and indirect reciprocity. (Alexander, 1987)[86] Reciprocal altruism posits that altruistic behavior between genetically unrelated individuals can be selected if altruistic acts are reciprocated in the future by the beneficiaries of such acts, whereas indirect reciprocity posits that altruistic behavior can be selected without direct reciprocity if such acts positively impact the altruist's reputation and status in the community. Empirical studies suggest that all three theories provide a partial explanation for the variety of cooperative and altruistic acts exhibited by humans (Liddle & Shackelford, 2011)[87] and other animals. (Buss, 2011)[13] These and other insights from evolutionary theory offer a framework within which currently disjointed social psychological explanations of phenomena can be understood and unified.

Evolutionary Developmental Psychology

Humans face different sets of adaptive problems throughout their development, or ontogeny. (Buss, 2011)[13] This implies the existence of ontogenetic adaptations, or adaptations limited to a particular period of development. (Bjorklund & Pellegrini, 2002)[88] This is the focus of evolutionary developmental psychology, a perspective that guides researchers to consider, for example, particular characteristics of childhood not as incomplete versions of adult characteristics, but as adaptations that solve adaptive problems related to that period of development. (Bjorklund & Pellegrini, 2002; Ellis & Bjorklund, 2005)[88,89] For example, boys more than girls engage in rough-and-tumble play. Although the common view of such behavior is that it represents an incomplete version of adult fighting, evolutionary developmental psychologists have emphasized the apparent functions of this behavior, such as constituting a way for boys to establish hierarchies and leadership within the peer group by assessing each other's strengths.(Bjorklund & Pellegrini, 2002; Pellegrini & Smith, 1998)[88,90] Another example is children's overestimation of their own abilities. This could be viewed as an example of immature cognition, but an evolutionary developmental perspective led to the proposal that there may be a functional explanation for this phenomenon. Indeed, overestimation appears to be beneficial in certain contexts and at specific ages. As Bjorklund and Pellegrini explain, "As a result [of overestimation], bright young children continue to experiment with new behaviors and practice old ones, improving their skills at a time when trial-and-error learning is so important" (Ref. 88 [Ellis & Bjorklund, 2005], p. 203).

These examples only scratch the surface, because like evolutionary psychology, evolutionary developmental psychology is not a particular subdiscipline, but instead represents an approach that can be applied to any psychological phenomena. (Buss, 2011)[13] Indeed, as Buss describes, "Because few psychological mechanisms emerge at birth fully developed, a developmental perspective will necessarily be an essential part of the proper description and understanding of nearly every psychological mechanism" (Ref. 13 [Buss, 2011], p. 410).

Evolutionary Clinical Psychology

Traditional clinical psychology consists of defining, categorizing, and providing proximate explanations for mental "disorders," along with developing interventions for treatment. However, the determination of what constitutes a mental disorder has historically lacked a theoretical foundation, evidenced by the extensive revisions that have led to the fifth and current version of the

Diagnostic and Statistical Manual of Mental Disorders. (APA, 2013)[91] An evolutionary perspective can provide such a foundation. For example, by viewing the mind as a collection of EPMs, one can interpret mental disorders as "harmful dysfunctions" of particular mechanisms. More specifically, a dysfunction results from "the failure of an internal mechanism to perform a natural function for which it was designed" (Ref. 92 [Wakefield, 1992], p. 374). EPMs can dysfunction in several ways, such as failing to become activated when confronted by the relevant stimuli, becoming activated by the wrong stimuli, or failing to properly coordinate with other mechanisms.(Buss, 2011)[13] If the dysfunction in question is shown to "cause significant harm to the person under present environmental circumstances and according to present cultural standards" (Ref. 92 [Wakefield, 1992], p. 383), then it qualifies as a mental disorder. Focusing on the function of EPMs, these criteria, along with other insights from evolutionary psychology, can alter our understanding of what constitutes a mental disorder.

Evolutionary clinical psychology can provide a fresh perspective for understanding phenomena that are thought to result from mental disorders. One example is suicide, which may seem, even from an evolutionary perspective, to serve no adaptive function. However, some cases of suicide may be best understood in terms of inclusive fitness. Suicide may serve an adaptive function under specific circumstances, namely: when one's reproductive potential is very low, and one is a burden to genetic relatives. From a gene's-eye view, the possibility of being passed on to future generations may increase if someone meeting these criteria were to take their own life. The fitness impact of no longer being able to reproduce would be negligible if one's reproductive potential is already low, and reducing the burdensomeness to genetic relatives may increase their fitness, resulting in a higher inclusive fitness when compared to not committing suicide. Consistent with this hypothesis, variables related to reproductive success (e.g., sex in the last month, sex in the last year, success in heterosexual relationships, number of children) and perceived burdensomeness to family members are correlated with the likelihood and strength of suicidal ideation. [de Catanzaro, 1995][93] This analysis is not meant to suggest that suicide under these or any conditions is desirable, but an evolutionary perspective can highlight contexts that may trigger an historically adaptive suicidal response, thereby facilitating the prevention of such behavior.

Conclusion

Evolutionary psychology emphasizes the fact that the design features of the brain, like all other organs, have been built as a result of evolution by natural selection. General evolutionary theory, along with several middle-level theories, provides a powerful framework within which specific hypotheses regarding the evolved psychological mechanisms of the mind can be produced. Although evolutionary psychology has been met with many criticisms, these largely stem from misconceptions of the field, and the gradual but steady integration of evolutionary psychology into mainstream psychology suggests that these misconceptions are fading. This integration includes the incorporation of an evolutionary perspective into many of the traditional subdisciplines of psychology, although there is still much work to be done before evolutionary psychology is accepted as the unifying framework of psychological science. A necessary component of this transition is the acknowledgment of the currently arbitrary division of subdisciplines within psychology. Evolutionary psychology provides a non-arbitrary method of creating subdisciplines by focusing on the categories of adaptive problems over evolutionary history and the psychological mechanisms relevant to these

problems, but it remains to be seen whether mainstream psychology will adopt this system of classification.

Despite the large theoretical and empirical literature that has been generated by evolutionary psychologists in recent years, evolutionary psychology is still a relatively young field, and as such there remain many exciting areas for future research. For example, evolutionary psychologists have historically avoided theorizing about individual differences, focusing instead on species- or sex-typical adaptations. This trend has begun to change over recent years, particularly with the advancement of evolutionary personality psychology, [Figueredo et al., 2005][94] but researchers are still in the early stages of testing hypotheses that have been generated within this subdiscipline. Related topics that will benefit from increased empirical attention are culture and cultural differences. (Buss, 2011)[13] For example, although the literature on the evolution of religious beliefs and behaviors has expanded rapidly in recent years, (Atran, 2002; Boyer, 2001; Wright, 2009; Kirkpatrick, 2008)[95-98] there is still considerable debate as to whether religion is best viewed as an adaptation, a byproduct, or a combination of the two. In addition to these topics, areas that have received considerably more attention, such as mating psychology, still harbor many unanswered questions and debated issues. Some examples include whether female orgasm is an adaptation or byproduct,(Kaighobadi, Shackelford, & Weekes-Shackelford, 2012)[99] the evolution of concealed ovulation[13] and whether men have adaptations for detecting ovulation, (Symons, 1995)[100] and the evolution of homosexuality. (Buss, 2011)[13] In short, the rich behavioral repertoire and complex cognitive architecture of humans ensures that an evolutionary psychological perspective still has much to tell us about human nature.

Sidebar title

[Please include sidebars in the body of the text where appropriate]

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