Adaptations, Exaptations, and Spandrels

David M. Buss and Martie G. Haselton *University of Texas at Austin*
Todd K. Shackelford *Florida Atlantic University*
April L. Bleske *University of Texas at Austin*
Jerome C. Wakefield *Rutgers, The State University of New Jersey*

Adaptation and natural selection are central concepts in the emerging science of evolutionary psychology. Natural selection is the only known causal process capable of producing complex functional organic mechanisms. These adaptations, along with their incidental by-products and a residue of noise, comprise all forms of life. Recently, S. J. Gould (1991) proposed that exaptations and spandrels may be more important than adaptations for evolutionary psychology. These refer to features that did not originally arise for their current use but rather were co-opted for new purposes. He suggested that many important phenomena—such as art, language, commerce, and war—although evolutionary in origin, are incidental spandrels of the large human brain. The authors outline the conceptual and evidentiary standards that apply to adaptations, exaptations, and spandrels and discuss the relative utility of these concepts for psychological science.

Over the past decade, evolutionary psychology has emerged as a prominent new theoretical perspective within the field of psychology. Evolutionary psychology seeks to synthesize the guiding principles of modern evolutionary theory with current formulations of psychological phenomena (Buss, 1995; Daly & Wilson, 1988; Pinker, 1997b; Symons, 1987; Tooby & Cosmides, 1992). The concepts of adaptation and natural selection are central to evolutionary approaches and, therefore, have figured prominently in this emerging perspective. At the same time, criticisms have been leveled at the concept of adaptation and the importance of natural selection, especially as they are applied to human behavior. In particular, Gould (1991), in an influential and widely cited analysis, suggested that "exaptation," a feature not arising as an adaptation for its current function but rather co-opted for new purposes, may be a more important concept for the emerging paradigm of evolutionary psychology.

Psychologists in cognitive, developmental, social, personality, and clinical psychology are increasingly incorporating the evolutionary concepts of adaptation and exaptation in their theoretical frameworks and empirical research (e.g., Buss, 1994; Cosmides, 1989; Cosmides & Tooby, 1994; Daly & Wilson, 1988; Kenrick & Keefe, 1992; Lilienfeld & Marino, 1995; MacNeilage, 1997; Piattelli-Palmarini, 1989; Pinker & Bloom, 1992; Richters & Cicchetti, 1993; Sedikedes & Skowronski, 1997; Wakefield, 1992, in press). Much confusion exists, however, about what these central concepts mean, how they should be distinguished, and how they are to be applied to psychological phenomena.

The confusion can be traced to several factors. First, psychologists typically receive no formal training in evolutionary biology and, therefore, cannot be expected to wade through what has become a highly technical field. Second, although evolutionary theorizing about humans has a long history (e.g., Baldwin, 1894; Darwin, 1859/1958; James, 1890/1962; Jennings, 1930; Morgan, 1896; Romanes, 1889), the empirical examination within psychology of evolutionary hypotheses regarding human psychological mechanisms is much more recent, and confusion often inheres in newly emerging approaches as practitioners struggle, often with many false starts, to use an incipient set of theoretical tools.[1] Third, psychologists dating back to Darwin's time have had a history of wariness about evolutionary approaches and, therefore, often have avoided a serious consideration of their potential utility. Fourth, there are genuine differences in scientific

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Author's note. David M. Buss, Martie G. Haselton, and April L. Bleske, Department of Psychology, University of Texas at Austin; Todd K. Shackelford, Division of Science–Psychology, Florida Atlantic University; Jerome C. Wakefield, School of Social Work, Rutgers, The State University of New Jersey.

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Correspondence concerning this article should be addressed to David M. Buss, Department of Psychology, University of Texas, Austin, TX 78712. Electronic mail may be sent to dbuss@psy.utexas.edu.

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[1] The empirical application of evolutionary ideas to the study of nonhuman animal behavior, of course, has a long and rich history of success (see Alcock, 1993). Indeed, theory and research emerging from the study of animal behavior have been of great benefit to evolutionary psychology, and comparative psychology continues to inform research about humans (Tooby & Cosmides, 1992). Furthermore, over the past 40 years, ethologists have applied evolutionary functional analysis to manifest human behavior, such as in the study of fixed action patterns (e.g., Lorenz, 1952; Tinbergen, 1951) and universals of facial expression (Ekman, 1973). It was not until the late 1980s, however, that underlying psychological mechanisms, such as those postulated by cognitive psychologists subsequent to the cognitive revolution in psychology, were explored empirically from an evolutionary perspective (e.g., Buss, 1989; Cosmides, 1989).

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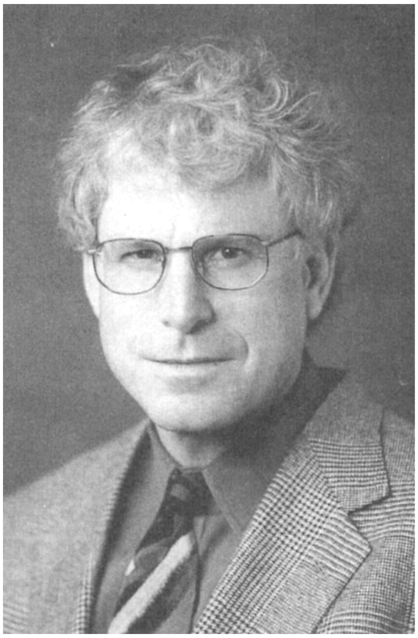

David M. Buss

opinion about which concepts should be used, what the concepts actually mean, and how they should be applied. This article seeks to provide psychologists with a guide to the basic concepts involved in the current dispute over evolutionary explanations and to clarify the role that each of these concepts plays in an evolutionary approach to human psychology.

The Evolutionary Process

The process of evolution—changes over time in organic structure—was hypothesized to occur long before Charles Darwin (1859/1958) formulated his theory of evolution. What the field of biology lacked, however, was a causal mechanism to account for these changes. Darwin supplied this causal mechanism in the form of natural selection.

Darwin's task was more difficult than it might appear at first. He wanted not only to explain why life-forms have the characteristics they do and why these characteristics change over time but also to account for the particular ways in which they change. He wanted to explain how new species emerge (hence the title of his book, *On The Origin of Species by Means of Natural Selection;* Darwin, 1859/1958) as well as how others vanish. Darwin wanted to explain why the component parts of animals—the long necks of giraffes, the wings of birds, the trunks of elephants, and the proportionately large brains of humans—exist in the particular forms they do. In addition, he wanted to explain the apparent purposive quality of these complex organic forms, or why they seem to function to help organisms to accomplish specific tasks.

Darwin's (1859/1958) answer to all these puzzles of life was the theory of natural selection. Darwin's theory of natural selection had three essential ingredients: variation, inheritance, and selection. Animals within a species vary in all sorts of ways, such as wing length, trunk strength, bone mass, cell structure, fighting ability, defensive maneuverability, and social cunning. This variation is essential for the process of evolution to operate. It provides the raw materials for evolution.

Only some of these variations, however, are reliably passed down from parents to offspring through successive generations. Other variations, such as a wing deformity caused by a chance environmental accident, are not inherited by offspring. Only those variations that are inherited play a role in the evolutionary process.

The third critical ingredient of Darwin's (1859/1958) theory was selection. Organisms with particular heritable attributes produce more offspring, on average, than those lacking these attributes because these attributes help to solve specific problems and thereby contribute to reproduction in a particular environment. For example, in an environment in which the primary food source is nut-bearing trees or bushes, some finches with a particular shape of beak might be better able to crack nuts and get at their meat than finches with alternative beak shapes. More finches that have the beaks better shaped for nut-cracking survive than those with beaks poorly shaped for nut-cracking. Hence, those finches with more suitably shaped beaks are more likely, on average, to live long enough to pass on their genes to the next generation.

Organisms can survive for many years, however, and still fail to contribute inherited qualities to future generations. To pass on their qualities, they must reproduce. Differential reproductive success, by virtue of the possession of heritable variants, is the causal engine of evolution by natural selection. Because survival is usually necessary for reproduction, survival took on a critical role in Darwin's (1859/1958) theory of natural selection.

Darwin (1859/1958) envisioned two classes of evolved variants—one playing a role in survival and one playing a role in reproductive competition. For example, among humans, sweat glands help to maintain a constant body temperature and thus presumably help humans to survive. Humans' tastes for sugar and fat presumably helped to guide their ancestors to eat certain foods and to avoid others and thus helped them to survive. Other inherited attributes aid more directly in reproductive competition and are said to be sexually selected (Darwin, 1871/1981). The elaborate songs and brilliant plumage of various bird species, for example, help to attract mates, and hence to reproduce, but may do nothing to enhance the individual's survival. In fact, these characteristics may be detrimental to survival by carrying large metabolic costs or by alerting predators.

In summary, although differential reproductive success of inherited variants was the crux of Darwin's (1859/1958) theory of natural selection, he conceived of two classes of variants that might evolve—those that help organisms survive (and thus indirectly help them to reproduce) and those that more directly help organisms in

Martie G. Haselton
Photo by Scott W. Jennings

reproductive competition. The theory of natural selection unified all living creatures, from single-celled amoebas to multicellular mammals, into one grand tree of descent. It also provided for the first time a scientific theory to account for the exquisite design and functional nature of the component parts of each of these species.

In its modern formulation, the evolutionary process of natural selection has been refined in the form of inclusive fitness theory (Hamilton, 1964). Hamilton reasoned that classical fitness—a measure of an individual's direct reproductive success in passing on genes through the production of offspring—was too narrow to describe the process of evolution by selection. He proposed that a characteristic will be naturally selected if it causes an organism's genes to be passed on, regardless of whether the organism directly produces offspring. If a person helps a brother, a sister, or a niece to reproduce and nurture offspring, for example, by sharing resources, offering protection, or helping in times of need, then that person contributes to the reproductive success of his or her own genes because kin tend to share genes and, moreover, contributes to the reproductive success of genes specifically for brotherly, sisterly, or niecely assistance (assuming that such helping is partly heritable and, therefore, such genes are likely to be shared by kin). The implication of this analysis is that parental care—investing in one's own children—is merely a special case of caring for kin who carry copies of one's genes in their bodies. Thus, the notion of classical fitness was expanded to inclusive fitness.

Technically, inclusive fitness is not a property of an individual organism but rather a property of its actions or effects (Hamilton, 1964; see also Dawkins, 1982). Inclusive fitness can be calculated from an individual's own reproductive success (classical fitness) plus the effects the individual's actions have on the reproductive success of his or her genetic relatives, weighted by the appropriate degree of genetic relatedness.

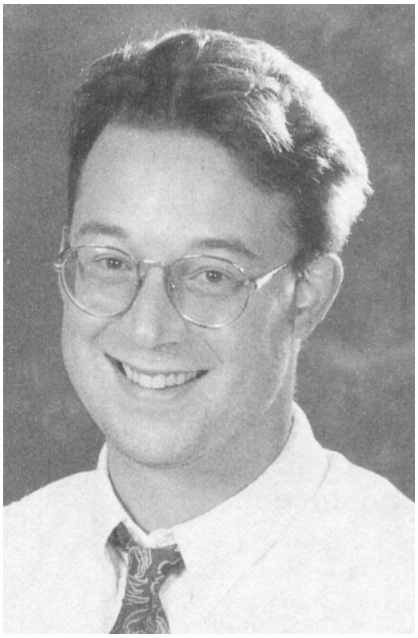
It is critical to keep in mind that evolution by natural selection is not forward looking or intentional. A giraffe does not notice juicy leaves stirring high in a tree and ''evolve'' a longer neck. Rather, those giraffes that happen to have slightly longer necks than other giraffes have a slight advantage in getting to those leaves. Hence, they survive better and are more likely to live to pass on genes for slightly longer necks to offspring. Natural selection acts only on those variants that happen to exist. Evolution is not intentional and cannot look into the future to foresee distant needs.

Products of the Evolutionary Process: Adaptations, By-products, and Random Effects

In each generation, the process of selection acts like a sieve (Dawkins, 1996). Variants that interfere with successful solutions to adaptive problems are filtered out. Variants that contribute to the successful solution of an adaptive problem pass through the selective sieve. Iterated over thousands of generations, this filtering process tends to produce and maintain characteristics that interact with the physical, social, or internal environment in ways that promote the reproduction of individuals who possess the characteristics or the reproduction of the individuals' genetic relatives (Dawkins, 1982; Hamilton, 1964; Tooby & Cosmides, 1990a; Williams, 1966). These characteristics are called adaptations.

There has been much debate about the precise meaning of adaptation, but we offer a provisional working definition. An *adaptation* may be defined as an inherited and reliably developing characteristic that came into existence as a feature of a species through natural selection because it helped to directly or indirectly facilitate reproduction during the period of its evolution (after Tooby & Cosmides, 1992). Solving an adaptive problem—that is, the manner in which a feature contributes to reproduction—is the function of the adaptation. There must be genes for an adaptation because such genes are required for the passage of the adaptation from parents to offspring. Adaptations, therefore, are by definition inherited, although environmental events may play a critical role in their ontogenetic development.

Ontogenetic events play a profound role in several ways. First, interactions with features of the environment during ontogeny (e.g., certain placental nutrients, aspects of parental care) are critical for the reliable development and emergence of most adaptations. Second, input during development may be required to activate existing mechanisms. There is some evidence, for example, that experience in committed sexual relationships activates sex-linked jealousy adaptations (Buss, Larsen, Westen, & Semmelroth, 1992). Third, developmental events may channel individuals into one of several alternative adaptive paths specified by evolved decision rules. Lack of an investing father during the first several years of life,



Todd K. Shackelford
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for example, may incline individuals toward a short-term mating strategy, whereas the presence of an investing father may shift individuals toward a long-term mating strategy (e.g., Belsky, Steinberg, & Draper, 1991; for alternative theories, see Buss & Schmitt, 1993; Gangestad & Simpson, 1990). Fourth, environmental events may disrupt the emergence of an adaptation in a particular individual, and thus the genes for the adaptation do not invariantly result in its intact phenotypic manifestation. Fifth, the environment during development may affect where in the selected range someone falls, such as which language a person speaks or how anxious a person tends to be. Developmental context, in short, plays a critical role in the emergence and activation of adaptations (see DeKay & Buss, 1992, for a more extended discussion of the role of context).

To qualify as an adaptation, however, the characteristic must reliably emerge in reasonably intact form at the appropriate time during an organism's life. Furthermore, adaptations tend to be typical of most or all members of a species, with some important exceptions, such as characteristics that are sex-linked, that exist only in a subset because of frequency-dependent selection, or that exist because of temporally or spatially varying selection pressures.

Adaptations need not be present at birth. Many adaptations develop long after birth. Bipedal locomotion is a reliably developing characteristic of humans, but most humans do not begin to walk until a year after birth. The breasts of women and a variety of other secondary sex characteristics reliably develop, but they do not start to develop until puberty.

The characteristics that make it through the filtering process in each generation generally do so because they contribute to the successful solution of adaptive problems—solutions that either are necessary for reproduction or enhance relative reproductive success. Solutions to adaptive problems can be direct, such as a fear of dangerous snakes that solves a survival problem or a desire to mate with particular members of one's species that helps to solve a reproductive problem. They can be indirect, as in a desire to ascend a social hierarchy, which many years later might give an individual better access to mates. Or they can be even more indirect, such as when a person helps a brother or a sister, which eventually helps that sibling to reproduce or nurture offspring. Adaptive solutions need not invariably solve adaptive problems in order to evolve. The human propensity to fear snakes, for example, does not inevitably prevent snakebites, as evidenced by the hundreds of people who die every year from snakebites (Than-Than et al., 1988). Rather, adaptive designs must provide reproductive benefits on average, relative to their costs and relative to alternative designs available to selection, during the period of their evolution.

Each adaptation has its own period of evolution. Initially, a mutation occurs in a single individual. Most mutations disrupt the existing design of the organism and hence hinder reproduction. If the mutation is helpful to reproduction, however, it will be passed down to the next generation in greater numbers. In the next generation, therefore, more individuals will possess the characteristic. Over many generations, if it continues to be successful, the characteristic will spread among the population. In sum, natural selection is the central explanatory concept of evolutionary theory, and adaptation refers to any functional characteristic whose origin or maintenance must be explained by the process of natural selection.[2]

Most adaptations, of course, are not caused by single genes. The human eye, for example, takes thousands of genes to construct. An adaptation's environment of evolutionary adaptedness (EEA) refers to the cumulative selection processes that constructed it piece by piece until it came to characterize the species. Thus, there is no single EEA that can be localized at a particular point in time and space. The EEA will differ for each adaptation and is best described as a statistical aggregate of selection pressures over a particular period of time that are responsible for the emergence of an adaptation (Tooby & Cosmides, 1992).

The hallmarks of adaptation are features that define *special design*—complexity, economy, efficiency, reliability, precision, and functionality (Williams, 1966). These qualities are conceptual criteria subject to empirical testing and potential falsification for any particular hypothesis about an adaptation. Because, in principle, many alternative hypotheses can account for any particular constellation of findings, a specific hypothesis that a feature is an adaptation is, in effect, a probability state-

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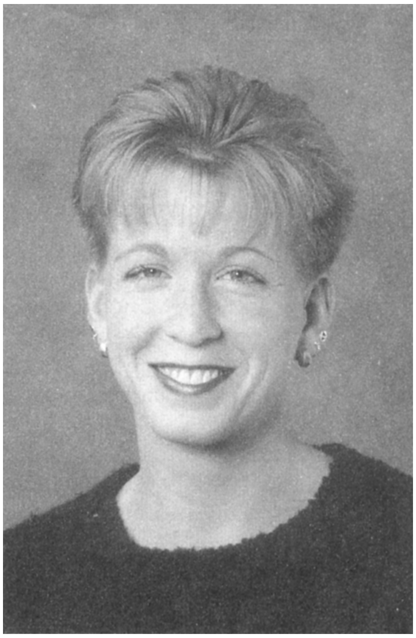
[2] Obviously, the inheritance of selected characteristics and their spread throughout a population are much more complex topics than we can do justice to here; for more extended treatments, see Dawkins (1982), Tooby and Cosmides (1992), and Williams (1966).



April L. Bleske

ment that it is highly unlikely that the complex, reliable, and functional aspects of special design characterizing the feature could have arisen as an incidental by-product of another characteristic or by chance alone (Tooby & Cosmides, 1992). As more and more functional features suggesting special design are documented for a hypothesized adaptation, each pointing to a successful solution to a specific adaptive problem, the alternative hypotheses of chance and incidental by-product become increasingly improbable.

Although adaptations are the primary products of the evolutionary process, they are not the only products. The evolutionary process also produces by-products of adaptations as well as a residue of noise. By-products are characteristics that do not solve adaptive problems and do not have to have functional design. They are carried along with characteristics that do have functional design because they happen to be coupled with those adaptations. The whiteness of bones, for example, is an incidental by-product of the fact that they contain large amounts of calcium, which was presumably selected because of properties such as strength rather than because of whiteness (see Symons, 1992).

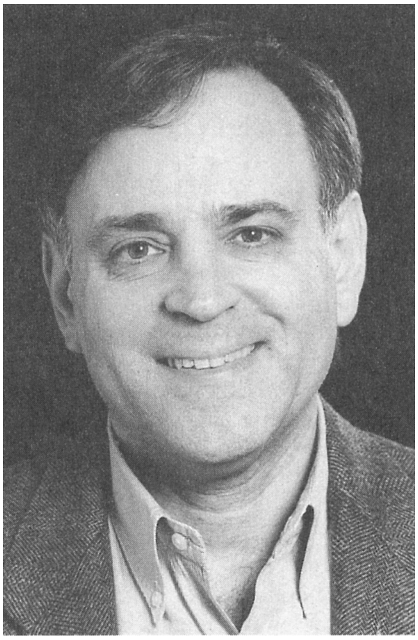
An example from the domain of humanly designed artifacts illustrates the concept of a by-product. Consider a particular lightbulb designed for a reading lamp; this lightbulb is designed to produce light. Light production is its function. The design features of a lightbulb—the conducting filament, the vacuum surrounding the filament, and the glass encasement—all contribute to the production of light and are part of its functional design. Lightbulbs also produce heat, however. Heat is a by-product of light production. It is carried along not because the bulb was designed to produce heat but rather because heat tends to be a common incidental consequence of light production.

A naturally occurring example of a by-product of adaptation is the human belly button. There is no evidence that the belly button, per se, helped human ancestors to survive or reproduce. A belly button is not good for catching food, detecting predators, avoiding snakes, locating good habitats, or choosing mates. It does not seem to be involved directly or indirectly in the solution to an adaptive problem. Rather, the belly button is a by-product of something that is an adaptation, namely, the umbilical cord that formerly provided the food supply to the growing fetus. As this example illustrates, establishing the hypothesis that something is a by-product of an adaptation generally requires the identification of the adaptation of which it is a by-product and the reason it is coupled with that adaptation (Tooby & Cosmides, 1992). In other words, the hypothesis that something is a by-product, just like the hypothesis that something is an adaptation, must be subjected to rigorous standards of scientific confirmation and potential falsification. As we discuss below, incidental by-products may come to have their own functions or may continue to have no evolved function at all, and they may be ignored or valued and exploited by people in various cultures.

The third and final product of the evolutionary process is noise, or random effects. Noise can be produced by mutations that neither contribute to nor detract from the functional design of the organism. The glass encasement of a lightbulb, for example, often contains perturbations from smoothness due to imperfections in the materials and the process of manufacturing that do not affect the functioning of the bulb; a bulb can function equally well with or without such perturbations. In self-reproducing systems, these neutral effects can be carried along and passed down to succeeding generations, as long as they do not impair the functioning of the mechanisms that are adaptations. Noise is distinguished from incidental by-products in that it is not linked to the adaptive aspects of design features but rather is independent of such features.

In summary, the evolutionary process produces three products: naturally selected features (adaptations), by-products of naturally selected features, and a residue of noise. In principle, the component parts of a species can be analyzed, and empirical studies can be conducted to determine which of these parts are adaptations, which are by-products, and which represent noise. Evolutionary scientists differ in their estimates of the relative sizes of these three categories of products. Some argue that many obviously important human qualities, such as language, are merely incidental by-products of large brains (e.g., Gould, 1991). Others argue that qualities such as language show evidence of special design that render it highly improbable that it is anything other than a well-designed adaptation for communication and conspecific manipulation (Pinker, 1994). Despite these differences among competing scientific views about the importance and prevalence of adaptations and by-products, all evolu-

Jerome C. Wakefield



tionary scientists agree that there are many constraints on optimal design.

Constraints on Optimal Design

Adaptationists are sometimes accused of being *panglossian,* a term named after Voltaire's (1759/1939) Pangloss, who proposed that everything was for the best (Gould & Lewontin, 1979). According to this criticism, adaptationists are presumed to believe that selection creates optimal design, and practitioners are presumed to liberally spin adaptationist stories. Humans have noses designed to hold up eyeglasses and laps designed to hold computers, and they grow bald so that they can be more easily spotted when lost! This sort of fanciful storytelling, lacking rigorous standards for hypothesis formulation and evidentiary evaluation, would be poor science indeed. Although some no doubt succumb to this sort of cocktail banter, evolutionists going back to Darwin have long recognized important forces that prevent selection from creating optimally designed adaptations (see Dawkins, 1982, for an extensive summary of these constraints).

First, evolution by selection is a slow process, so there will often be a lag in time between a new adaptive problem and the evolution of a mechanism designed to solve it. The hedgehog's antipredator strategy of rolling into a ball is inadequate to deal with the novel impediment to survival created by automobiles. The moth's mechanism for flying toward light is inadequate for dealing with the novel challenge to survival of candle flames. The existence in humans of a preparedness mechanism for developing a fear of snakes may be a relic not well designed to deal with urban living, which currently contains hostile forces far more dangerous to human survival (e.g., cars, electrical outlets) but for which humans lack evolved mechanisms of fear preparedness (Mineka, 1992). Because of these evolutionary time lags, humans can be said to live in a modern world, but they are burdened with a Stone Age brain designed to deal with ancient adaptive problems, some of which are long forgotten (Allman, 1994).

A second constraint on adaptation occurs because of local optima. A better design may be available, in principle, atop a ''neighboring mountain,'' but selection cannot reach it if it has to go through a deep fitness valley to get there. Selection requires that each step and each intermediate form in the construction of an adaptation be superior to its predecessor form in the currency of fitness. An evolutionary step toward a better solution would be stopped in its tracks if that step caused too steep a decrement in fitness. Selection is not like an engineer who can start from scratch and build toward a goal. Selection works only with the available materials and has no foresight. Local optima can prevent the evolution of better adaptive solutions that might, in principle, exist in potential design space (Dennett, 1995; Williams, 1992).

Lack of available genetic variation imposes a third constraint on optimal design. In the context of artificial selection, for example, it would be tremendously advantageous for dairy breeders to bias the sex ratio of offspring toward milk-producing females rather than nonlactating males. But all selective-breeding attempts to do this have failed, presumably because cattle lack the requisite genetic variation to bias the sex ratio (Dawkins, 1982). Similarly, it might, in principle, be advantageous for humans to evolve X-ray vision to see what is on the other side of obstacles or telescopic vision to spot danger from miles away. But the lack of available genetic variation, along with other constraints, has apparently precluded such adaptations.

A fourth constraint centers on the costs involved in the construction of adaptations. At puberty, male adolescents experience a sharply elevated production of circulating plasma testosterone. Elevated testosterone is linked to onset of puberty, an increase in body size, the production of masculine facial features, and the commencement of sexual interest and activity. But elevated testosterone also has an unfortunate cost—it compromises the immune system, rendering men more susceptible than women to a variety of diseases (Folstad & Karter, 1992; Wedekind, 1992). Presumably, averaged over all men through many generations, the benefits of elevated testosterone outweighed its costs in the currency of fitness. It evolved despite these costs. The key point is that all adaptations carry costs—sometimes minimal metabolic costs and at other times large survival costs—and these costs impose constraints on the optimal design of adaptations.

A fifth class of constraints involves the necessity of coordination with other mechanisms. Adaptations do not exist in a vacuum, isolated from other evolved mechanisms. Selection favors mechanisms that coordinate well with, and facilitate the functioning of, other evolved mechanisms. This process of coordination, however, often entails compromises in the evolution of an adaptation that render it less efficient than might be optimal in the absence of these constraints. Women, for example, have been selected both for bipedal locomotion and for the capacity for childbirth. The widened hips and birth canal that facilitate childbirth, however, compromise the ability to locomote with great speed. Without the need to coordinate design for running with design for childbirth, selection may have favored slimmer hips like those found on men, which facilitate running speed. The departure from optimal design for running speed in women, therefore, presumably occurs because of compromises required by the need to coordinate adaptive mechanisms with each other.[3] Thus, constraints imposed by the coordination of evolved mechanisms with each other produce design that is less than might be optimal if the mechanisms were not required to coexist.

Time lags, local optima, lack of available genetic variation, costs, and limits imposed by adaptive coordination with other mechanisms all constitute some of the major constraints on the design of adaptations, but there are others (Dawkins, 1982; Williams, 1992). Adaptations are not optimally designed mechanisms. They are better described as jerry-rigged, meliorative solutions to adaptive problems constructed out of the available materials at hand, constrained in their quality and design by a variety of historical and current forces.

Exaptations and Spandrels

Recently, Stephen J. Gould (1991, 1997b; see also Gould & Lewontin, 1979; Gould & Vrba, 1982) proposed that the concept of exaptation is a crucial tool for evolutionary psychology, providing a critical supplement to the concept of adaptation. According to this argument, some evolutionary biologists and psychologists have conflated the historical origins of a mechanism or structure with its current utility. For example, the feathers of birds may have originated as evolved mechanisms for thermal regulation. Over evolutionary time, however, the feathers appear to have been co-opted for a different function—flight. According to this distinction, the term *adaptation* would be properly applied to the original thermal regulation structure and function, but the term *exaptation* would be more appropriate for describing the current flight-producing structure and function.

Gould (1991) provided two related definitions of exaptations. First, an exaptation is "a feature, now useful to an organism, that did not arise as an adaptation for its present role, but was subsequently co-opted for its current function" (p. 43). Second, exaptations are "features that now enhance fitness, but were not built by natural selection for their current role" (p. 47). On the basis of these related definitions, a mechanism must have a function and must enhance the fitness of its bearer to qualify as an exaptation.

It should be noted that Gould was inconsistent in his usage of the concept of exaptation, even within a single article (e.g., Gould, 1991). Although the definitions of exaptation quoted verbatim here appear to reflect his most common usage (indeed, the quoted 1991 definition was first introduced by Gould and Vrba in 1982), at other times, he seemed to use the term to cover novel but functionless uses or consequences of existing characteristics. For conceptual clarity, it is critical to distinguish between exaptation, as Gould (1991) defined it in the quoted passages, and by-products that are unrelated to function in the biological sense. In the next section, we examine Gould's various usages of the term *exaptation.* However, in this article, we use *exaptation,* consistent with the above quoted definitions, to refer only to mechanisms that have new biological functions that are not the ones that caused the original selection of the mechanisms. Biologically functionless uses are referred to as "effects," "consequences," or "by-products." These two easily confused strands of Gould's discussion of exaptation are thus disentangled here and treated separately.

According to Gould (1991), exaptations come in two types. In the first type, features that evolved by selection for one function are co-opted for another function. We use the term *co-opted adaptation* to describe this first category. The feathers of birds first having evolved for thermal regulation but then later co-opted for flight is an example of a co-opted adaptation. In the second type, "presently useful characteristics did not arise as adaptations . . . but owe their origin to side consequences of other features" (Gould, 1991, p. 53). Gould called such side effects of the organism's architecture "spandrels." The term *spandrels* is an architectural term that refers to the spaces left over between structural features of a building. The spaces between the pillars of a bridge, for example, can subsequently be used by homeless persons for sleeping, even though such spaces were not designed for providing such shelter.

In sum, Gould (1991) proposed two types of functional exaptations—adaptations that initially arose through natural selection and were subsequently co-opted for another function (co-opted adaptations) and features that did not arise as adaptations through natural selection but rather as side effects of adaptive processes and that have been co-opted for a biological function (co-opted spandrels). In both cases, according to Gould's primary definition, a mechanism must possess a biological function that contributes to fitness to qualify as an exaptation.

As an example of an exaptation, Gould (1991) used the large size of the human brain and its function of enabling humans to produce speech. The large brain size, according to his argument, originally arose as an adaptation for some (unspecified) functions in humans' ancestral past (Gould, 1991). But the complexity of the human brain produces many by-products that are not properly considered to be functions of the brain: "The human brain, as nature's most complex and flexible organ,

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[3] These and other examples throughout this article are used to illustrate the conceptual points being made and should be regarded at this early stage in the development of evolutionary psychology as hypotheses to be subjected to empirical verification.

throws up spandrels by the thousands for each conceivable adaptation in its initial evolutionary restructuring'' (Gould, 1991, p. 58). Among the spandrels he cited as being by-products of large brains are religion, reading, writing, fine arts, the norms of commerce, and the practices of war. These seem to be intended as functionless uses or by-products rather than true fitness-enhancing, co-opted spandrels. Gould (1991) concluded that among features of interest to psychologists, such by-products are ''a mountain to the adaptive molehill'' (p. 59).

From these arguments, Gould (1991) concluded that the concepts of exaptations and spandrels provide a ''one-line refutation of . . . an ultra-Darwinian theory based on adaptation'' (p. 58). The two standard pillars of evolutionary biology—natural selection and adaptation—cannot, in principle, account for human behavior ''without fatal revisions in its basic intent'' (p. 58). Note that Gould was not challenging the importance of evolutionary biology for understanding human behavior. Indeed, as we show later in this article, understanding the nature of the adaptation responsible for producing spandrels (in this case, the nature of the large human brain) is critical to the analysis. Rather, he argued that there has been an overreliance on explanation in terms of adaptation, and to this important explanatory concept must be added the concept of exaptation, which is ''a crucial tool for evolutionary psychology'' (Gould, 1991, p. 43).

Terminological and Conceptual Confusions in the Invocation of Exaptation and Adaptation

To apply evolutionary concepts to psychology and to properly evaluate and contrast the concepts of exaptation and adaptation as potentially critical tools for evolutionary psychology, several distinctions need to be made, and some common terminological confusions should be clarified.

Confusion 1: Adaptation Versus Intuitions About Psychological Adjustment

Psychologists often use the term *adaptive* or *maladaptive* in a colloquial nonevolutionary sense. Often, these usages refer to notions such as personal happiness, social appropriateness, the ability to adjust to changing conditions, or other intuitive notions of well-being. It is important to distinguish these colloquial uses from the technical evolutionary uses, although evolved mechanisms may eventually turn out to be important in explaining personal happiness, well-being, or the ability to adjust to changing conditions (see, e.g., Nesse, 1990).

Confusion 2: Current Utility Versus Explanation in Terms of Past Functionality

Taken literally, Gould's (1991) cited definition of exaptation requires that a feature be co-opted for its current function and that it now enhances fitness. It may seem from these phrases that exaptations concern only functions operating at the present moment, whether or not they operated in the past. However, evolutionary psychologists and biologists are generally interested in explaining existing features of organisms. Obviously, a characteristic cannot be explained by current fitness-enhancing properties that came about after the characteristic already existed. When evolutionists attempt to explain the existence of a feature, they must do so by reference to its evolutionary history. All evolutionary explanations of the existence of species-wide mechanisms are to this extent explanations in terms of the past fitness effects of that kind of mechanism that led to the current existence of the mechanism in the species. The fact that a mechanism currently enhances fitness, by itself, cannot explain why the mechanism exists or how it is structured (Tooby & Cosmides, 1990b).

There are good reasons to think that it is not scientifically illuminating to demonstrate a feature's current correlation with fitness (Symons, 1992; Tooby & Cosmides, 1990b), unless such correlations reveal longer term, past selective pressures. It is not clear that such correlations shed any light on the mechanism's design or status as an adaptation. Such correlations may reveal the current direction of selection, although even this assumes that such correlations will continue to be obtained in future generations—a questionable assumption given the rapidly changing biotic and abiotic environments. Evolutionary explanation focuses on explaining why a feature exists, not what incidental interactions the feature may be having with the current environment.

Confusion 3: Current Functions Versus Past Functions That Are No Longer Active

Another confusion lurking in Gould's (1991) language is that it seems to imply that the past functions that explain the existence of a mechanism must still be operating now and literally be a current function to be an adaptation or exaptation. The concepts of adaptation and exaptation are intended as explanatory concepts, and they may be explanatorily useful even when the cited functions are no longer operative. Selected features often cease having the fitness-enhancing effects that got them selected in the first place; for example, it is possible that a selected taste for fatty foods to ensure adequate caloric intake is no longer fitness-enhancing in industrial societies where excessive fat is harmfully common and available for consumption. When evolutionists attempt to explain why humans have a taste for fatty foods, however, they generally say that this taste likely is (or was) an adaptation to ensure adequate caloric intake. Current fitness enhancement is not at issue; at issue is the past function explaining the existence of the mechanisms behind the taste for fatty foods.

A similar point holds for an exaptation. For example, if birds that fly subsequently were to become nonflying, so their feathers would no longer have the exapted function of supporting flight, the existence of feathers at that future time would still need to be explained in terms of (a) an original adaptation for heat insulation and (b) a later exaptation for flying, followed by (c) a functionless period too short for feathers to be selected out. So, the use of exaptation as an evolutionary explanatory concept does not require that there be a current function, any more than the use of adaptation requires such a current function. However, the use of exaptation requires, as Gould (1991) was trying to convey, that there be an original function and a distinct later function (he appeared to use ''current'' to conveniently distinguish the later function from the original function). What is required for exaptational explanation is not that there be an active current function but that there was an active function at the time that the feature is claimed to have served as an exaptation.

Confusion 4: Function Versus Functionless By-product

The most central confusion in applying Gould's (1991) ideas pertains to distinguishing between exaptations, as Gould defined them, and the novel use of existing features that are currently unrelated to function and fitness. Although Gould (1991) defined an exaptation as a feature ''coopted for its current function'' (p. 43) and features that ''now enhance fitness, but were not built by natural selection for their current role'' (p. 46), he sometimes argued that ''function'' does not describe the utility of exaptations; instead, he suggested that the utility of an exaptation is better described as ''effect'' (p. 48). Even more confusing, he referred to ''culturally useful features'' (p. 58) of the brain as exaptations. Gould's stated definitions seem to require that these effects and culturally useful features must contribute to fitness and have specifiable biological functions to qualify as exaptations, but it seems implausible that Gould intended to claim that such cultural practices as reading and writing are explainable by biological functions. Accordingly, exaptations must be distinguished from novel uses of existing mechanisms, where the novel uses are not explained by a biological function.

Consider the human hand as an adaptation. Clearly, the human hand is now used for many activities that were not part of its original set of functions—playing handball or disc golf, manipulating a joystick on a Super Nintendo game, or writing a computer program by pecking on a keyboard. But it seems unlikely that Gould (1991) meant to claim that these activities serve any functions in the formal sense, as solutions to adaptive problems that contribute to reproduction, although they certainly serve *functions* in the colloquial meaning of the term—helping to achieve some goal (e.g., staying in shape, engaging in a stimulating and distracting activity). The same problem arises for many of the activities enumerated by Gould as hypothesized exaptations of the large human brain. Indeed, many of the features Gould claimed to be exaptations or spandrels in human behavior do not seem to fall under his own definitions of exaptation or spandrel and seem instead to be functionless by-products. The key point is that novel uses of existing mechanisms that are not explained by biological function or fitness (i.e., functionless by-products) must be distinguished from true functional exaptations, such as the feathers of birds coopted for flight.

Confusion 5: What Causal Process or Mechanism Is Doing the Co-opting?

Intimately related to the confusion between exaptations and functionless by-products is a confusion pertaining to the causal process responsible for co-opting an existing structure (see Pinker, 1997a). In the example of birds' feathers, which were originally evolved for thermal regulation but subsequently co-opted for flight, it is clearly natural selection that is responsible for transforming an existing structure into a new, modified structure with a different function. In other cases, however, Gould (1991) appeared to imply that human psychological capacities, such as cognitive capacities, human instrumental actions, or motivational mechanisms, are responsible for the co-opting.

The distinction that evolutionary psychologists make between underlying mechanisms and manifest behavior is helpful in clarifying this confusion. Both adaptations and exaptations, as underlying mechanisms, may be subsequently used for novel behaviors that may have no functional relevance whatsoever. When people use their hands to grip a tennis racquet, for example, this evolutionarily recent manifest behavior is clearly not the function for which the hands evolved. A full understanding of this novel behavior, however, requires an understanding of the underlying mechanism that is used (the hand) and is aided by insight into the functions for which it was designed (e.g., the power grip). The activity (e.g., tennis) may be partially understood by invoking evolved motivational mechanisms (e.g, social networking, hierarchy negotiation, enhancement of appearance) that are responsible for humans co-opting or exploiting existing mechanisms to pursue this novel activity.

In this example, human motivational mechanisms conjoined with current cognitive and physical capacities, not natural selection, are responsible for co-opting the existing mechanism of the hand. The same logic applies to many of Gould's (1991) other examples of exaptations, such as reading and writing—these are evolutionarily novel activities that are presumably too recent to have been co-opted by natural selection and so apparently must have been invented and co-opted by existing human psychological mechanisms. Such human co-optation must be distinguished from biological exaptations that natural selection has transformed from one function to another.

In summary, evolutionary functional analysis is useful regardless of whether natural selection or some other causal process, such as an existing human motivation, is responsible for the co-opting. Even in cases where a feature has no biological function and is proposed to be a functionless by-product, an understanding of novel behaviors must involve (a) an understanding of the evolved mechanisms that make humans capable of performing the behavior and (b) an understanding of the evolved cognitive and motivational mechanisms that led humans to exploit such capabilities. It is not sufficient from a scientific point of view to merely present a long speculative list of purported exaptations, however interesting or intuitively compelling they might be.

The hypothesis that something is an exaptation or even a functionless effect should be subjected to reasonable standards of hypothesis formulation and empirical verification, just as hypotheses about adaptation must meet these standards. The hypothesis that religion, to use one of Gould's (1991) examples, is an exaptation would seem to require a specification of (a) the original adaptations or by-products that were co-opted to produce religion; (b) the causal mechanism responsible for the coopting (e.g., natural selection or an existing motivational mechanism); and (c) the exapted biological function of religion, if any; that is, the manner in which it contributes to the solution to an adaptive problem of survival or reproduction. These predictions can then be subjected to evidentiary standards of empirical testing and potential falsification.

Hypotheses about functionless by-products must meet rigorous scientific standards that include a functional analysis of the original adaptations responsible for producing the functionless by-products and the existing human cognitive and motivational mechanisms responsible for the co-opting. Without this specification, the mere assertion that this or that characteristic is an exaptation encounters the same problem that Gould (1991) leveled against adaptationists—the telling of "just-so stories."

Confusion 6: Are Exaptations Merely Adaptations?

A final conceptual issue pertains to whether the concept of exaptation is usefully distinct from the concept of adaptation. Dennett (1995) argued that it is not:

> According to orthodox Darwinism, every adaptation is one sort of exaptation or the other—this is trivial, since no function is eternal; if you go back far enough, you will find that every adaptation has developed out of predecessor structures each of which either had some other use or no use at all. (p. 281)

If all adaptations are exaptations, and all exaptations are adaptations, then having two terms to describe one thing would certainly be superfluous.

Although Dennett's (1995) argument has some merit in pointing to the limits of the distinction between adaptation and exaptation, we think he is wrong in suggesting that there is no difference, and we believe that there is utility in differentiating between the two concepts. Granted, the distinction may end up being more a matter of degree than an absolute distinction because exaptations themselves often involve further adaptations; nonetheless, understanding the degree to which a new function is superimposed on a predecessor structure that already existed as an adaptation or as a by-product may indeed shed light on its nature. The notion that a bird's feathers originally were designed for thermal regulation rather than for flying, for example, may help to explain some of its current features that do not seem to contribute to flight (e.g., insulating, heat-retention features).

In sum, Gould's (1991) concept of exaptation can be meaningfully distinguished from adaptation. Both concepts invoke function; therefore, both must meet the conceptual and evidentiary standards for invoking function. The concepts differ, however, in that adaptations are characteristics that spread through the population because they were selected for some functional effect, whereas exaptations are structures that already exist in the population and continue to exist, albeit sometimes in modified form, for functional reasons different from the ones for which they were originally selected.

The Role of Natural Selection in Adaptations and Exaptations

Some readers of Gould (1997a) come away believing that the role of natural selection is somehow diminished to the degree that exaptations are important. This is a mistake, as Gould himself took pains to point out: "I accept natural selection as the only known cause of 'eminently workable design' and . . . 'adaptive design must be the product of natural selection' " (p. 57). Natural selection plays a key role in both adaptations and exaptations.

When exaptations are co-opted adaptations, where the mechanism being co-opted for a new function was an adaptation, selection is required to explain the original adaptation being co-opted. Fishes' fins designed for swimming may have been co-opted to produce mammalian legs for walking. Birds' feathers, perhaps originally designed for thermal regulation, may have been co-opted for flying. In all these cases, however, natural selection is required to explain the origins and nature of the adaptations that provided the existing structures capable of being co-opted.

When exaptations are co-opted spandrels, where the mechanism being co-opted for a new function was not an adaptation but rather an incidental by-product of an adaptation, then selection is required to explain the adaptation that produced the incidental by-product. Recall that the hypothesis that a mechanism with a function is a spandrel implies that the mechanism was a by-product, and supporting a by-product hypothesis generally requires specifying the adaptation responsible for producing the by-product (Tooby & Cosmides, 1992). Natural selection is required to explain the origin and design of the adaptation—it is the only known causal process capable of producing adaptation. Without specifying the origin of the adaptation that produced the by-product that was co-opted to become a spandrel, the hypothesis that something is a spandrel generally cannot be tested.

Selection is necessary not only to explain the adaptations and by-products that are available for co-optation but also to explain the process of exaptation itself. Selection is required to explain the structural changes in an existing mechanism that enable it to perform the new exapted function: "Exaptations almost always involve structural changes that enable the preexisting mechanism, designed for another function, to perform the new function; these changes require explanation by natural selection'' (Wakefield, in press). When feathers for thermal regulation become wings capable of flight, it is highly unlikely that the new function can occur without any modification of the original mechanism. Selection would have to act on the existing feathers, favoring those individuals that possess more aerodynamic features over those possessing less aerodynamic features. Furthermore, these changes would have to be coordinated with other changes, such as a musculature capable of generating sufficient flapping, alterations in the visual system to accommodate the new demands of aerial mobility, and perhaps modifications of the feet to facilitate landing without damage (e.g., a redesigned shape of the feet). All these changes require the invocation of natural selection to explain the transformation of the original adaptation to an exaptation (e.g., an adaptation with a new function). Similar explanations would generally be necessary for explaining how functionless by-products are transformed into co-opted spandrels that perform specific functions.

Selection is also required to explain the maintenance of an exaptation over evolutionary time, even if no changes in structure occur: ''Even in rare cases where exaptations involve no structural changes whatsoever, selective pressures must be invoked to fully explain why the mechanism is maintained in the population'' (Wakefield, in press). The forces of selection, of course, are never static. The fact that more than 99% of all species that have ever existed are now extinct is harsh testimony to the changes in selection over time (Thiessen, 1996). If the selection pressure responsible for the original adaptation becomes neutral or reversed, then the adaptation will eventually degrade over time because of forces such as the cumulative influx of new mutations and competing metabolic demands of other mechanisms. Selection is not only the force responsible for the origins of complex mechanisms but also the force responsible for their maintenance. Thus, even in the odd event that an existing mechanism is co-opted for a new function with no change whatsoever, selection is required to explain why this mechanism and its new function are maintained in the population over time.

In summary, adding exaptation to the conceptual toolbox of evolutionary psychology does not diminish the importance of natural selection as the primary process responsible for creating complex organic design—a point apparently endorsed by all sides involved in these conceptual debates. Selection is responsible for producing the original adaptations that are then available for co-optation. It is responsible for producing the adaptations, of which spandrels are incidental by-products. It is responsible for producing structural changes in exaptations in order to fulfill their new functions. And it is responsible for maintaining exaptations in the population over evolutionary time, even in the rare cases where no structural changes occurred. The distinctions between exaptation and adaptation are important, and Gould (1991) deserves credit for highlighting them. However, the distinctions should not be taken to mean that natural selection is not the basic explanatory principle in biology and evolutionary psychology.

Testing Hypotheses About Adaptations, Exaptations, and Spandrels

Evolutionary psychological hypotheses about adaptations are sometimes derided as mere storytelling, but the same accusation can be leveled at hypotheses about exaptations and spandrels, and even at more standard social science notions such as socialization, learning, and culture as causal explanations (Tooby & Cosmides, 1992). In all these approaches, as in the case of evolutionary hypotheses about adaptation, it is easy to concoct hypotheses about how a feature might be explained. The key issue is not whether a hypothesis is a story or not—at some level, all scientific hypotheses can be viewed as stories. Rather, the key questions are (a) Is the evolutionary psychological hypothesis formulated in a precise and internally consistent manner? (b) Does the hypothesis coordinate with known causal processes in evolutionary biology, much like hypotheses in cosmology must coordinate with known laws of physics? (Tooby and Cosmides [1992] called this ''conceptual integration'') (c) Can new specific empirical predictions about behavior or psychology be derived from the hypothesis for which data are currently lacking? (d) Can the hypothesis more parsimoniously account for known empirical findings, and overall, is it more evidentially compelling than competing hypotheses? and (e) Is the proposed psychological mechanism computationally capable of solving the hypothesized problem (Cosmides & Tooby, 1994; Marr, 1982)? These are scientific criteria that can be applied whether the hypothesis is or is not explicitly evolutionary and whether the hypothesis invokes an adaptation, exaptation, spandrel, or functionless by-product.

There is nothing about the fact that a hypothesis is explicitly evolutionary that makes it virtuous or more likely to be correct. Many evolutionarily inspired hypotheses turn out to be wrong, however reasonable they may seem. The hypothesis that the female orgasm functions to facilitate sperm transport, for example, is eminently reasonable on evolutionary grounds and leads to specific testable predictions. At present, however, the evidence for this hypothesis is weak (Baker & Bellis, 1995). In contrast, the hypothesis that male sexual jealousy has evolved to serve the function of combating paternity uncertainty has accrued a reasonable volume of empirical support across diverse methods, samples, and cultures (Baker & Bellis, 1995; Buss, 1988; Buss et al., 1992; Buss & Shackelford, 1997; Buunk, Angleitner, Oubaid, & Buss, 1996; Daly & Wilson, 1988; Daly, Wilson, & Weghorst, 1982; Shackelford & Buss, 1996; Symons, 1979; Wiederman & Allgeier, 1993; Wilson & Daly, 1992).

When a particular hypothesis about an evolved mechanism fails to be supported empirically, then a number of options are available to researchers. First, the hypothesis may be right but may have been tested incorrectly. Second, the hypothesis may be wrong, but an alternative functional hypothesis could be formulated and tested. Third, the phenomenon under examination might not represent an adaptation or exaptation at all but might instead be an incidental by-product of some other evolved mechanism, and this hypothesis could be tested.

Researchers then can empirically test these alternatives. Suppose, for example, that the sperm transport hypothesis of the female orgasm turned out to be wrong, with the results showing that women who had orgasms were no more likely to conceive than were women who did not have orgasms. The researchers could first scrutinize the methodology to see whether some flaw in the research design may have gone undetected (e.g., had the researchers controlled for the ages of the women in the two groups, because inadvertent age differences may have concealed the effect?). Second, the researchers could formulate an alternative hypothesis—perhaps the female orgasm functions as a mate selection device, providing a cue to the woman about the quality of the man or his investment in her (see Rancour-Laferriere, 1985, for a discussion of this and other hypotheses about the female orgasm)—and this alternative could be tested. Third, the researchers could hypothesize that the female orgasm is not an adaptation at all but rather an incidental by-product of some other mechanism, such as a common design shared with men, who do possess the capacity for orgasm for functional reasons (see Symons, 1979, for the original proposal of this functionless by-product hypothesis, and Gould's, 1987, subsequent endorsement of this hypothesis). In this case, researchers could try to disconfirm all existing functional explanations and could try to identify how the known mechanisms for development of naturally selected male orgasmic capacities led to the female orgasmic capacities as a side effect. Different researchers undoubtedly will have different proclivities about which of these options they pursue. The key point is that all evolutionary hypotheses—whether about adaptations, exaptations, spandrels, or functionless by-prod-

Table 1
Thirty Recent Examples of Empirical Discoveries About Humans Generated by Thinking About Adaptation and Selection

Example	Source
Evolved landscape preferences	Orions & Heerwagen (1992)
Sexually dimorphic mating strategies	Thiessen (1993); Thiessen, Young, & Burroughs (1993)
Waist-to-hip ratio as a determinant of attractiveness judgments	Singh (1993)
Standards of beauty involving symmetry	Grammer & Thornhill (1994)
Women's desire for mates with resources found in 37 cultures	Buss (1989)
Men's preference for younger mates documented in 37 cultures	Buss (1989)
Cheater detection procedure in social exchange	Cosmides (1989)
Stepchild abuse at 40 times the rate of nonstepchild abuse	Wilson & Daly (1987)
Relationship-specific sensitivity to betrayal	Shackelford & Buss (1996)
Sex-linked shifts in mate preference across the life span	Kenrick & Keefe (1992)
Predictable patterns of spousal and same-sex homicide	Daly & Wilson (1988)
Pregnancy sickness as an adaptation to teratogens	Profet (1992)
Mother–fetus conflict	Haig (1993)
Predictably patterned occurrence of allergies	Profet (1991)
Different human sperm morphs	Baker & Bellis (1995)
Superior female spatial location memory	Silverman & Eals (1992)
Design of male sexual jealousy	Buss et al. (1992); Daly et al. (1982)
Sex differences in sexual fantasy	Ellis & Symons (1990)
Deception in mating tactics	Tooke & Camire (1991)
Profiles of sexual harassers and their victims	Studd & Gattiker (1991)
Sex differences in desire for sexual variety	Clark & Hatfield (1989)
Facial asymmetry as an indicator of poor psychological and physical health	Shackelford & Larsen (1997)
Frequentist reasoning in human cognition	Cosmides & Tooby (1996); Gigerenzer & Hoffrage (1995)
Predictable causes of conjugal dissolution in 89 cultures	Betzig (1989)
Socialization practices across cultures differing by sex and mating system	Low (1989)
Patterns of risk taking in intrasexual competition for mates	Wilson & Daly (1985)
Shifts in grandparental investment according to sex of grandparent and sex of parent	DeKay (1995); Euler & Weitzel (1996)
Perceptual adaptations for entraining, tracking, and predicting animate motion	Heptulla-Chatterjee, Freyd, & Shiffrar (1996)
Universal perceptual adaptations to terrestrial living	Shepard (1984, 1992)
Mate guarding as a function of female reproductive value	Buss & Shackelford (1997); Dickemann (1981)

ucts—should be formulated in a precise enough manner to produce empirical predictions that can then be subjected to testing and potential falsification.

It should be noted that evolutionary hypotheses range on a gradient from well-formulated, precise deductions from known evolutionary principles on the one hand to evolutionarily inspired hunches on the other (see, e.g., Symons, 1992). Evolutionary psychology often provides a heuristic, guiding scientific inquiry to important domains that have a priori importance, such as events surrounding reproduction (e.g., sexuality, mate selection). Just as with a precise evolutionary hypothesis, an evolutionary hunch may turn out to be right or wrong. It would seem reasonable to hypothesize, for example, that men would have evolved mechanisms designed to detect when women ovulate, because such a mechanism would help to solve the adaptive problems of identifying fecund women and channeling mating effort more efficiently. But there is little solid empirical evidence that such a mechanism exists (see Symons, 1995). Such hunches, however, can often be useful in guiding investigations. Thus, evolutionary psychology, at its best, has both heuristic and predictive value for psychological science.

Discussion

In principle, we agree with Gould's (1991, 1997b) suggestion to be pluralistic about the conceptual tools of evolutionary psychology, although it is clear that many evolutionary psychologists already embody the pluralism advocated (e.g., Tooby & Cosmides, 1990a, 1992). Researchers may differ about which of these tools they believe are most scientifically valuable for particular purposes. One reasonable standard for judging the value of such conceptual tools is the heuristic and predictive empirical harvest they yield. Table 1 shows 30 recent examples of the empirical findings about humans whose discovery was guided by hypotheses anchored in adaptation and natural selection.

From this empirical evidence, hypotheses about adaptations appear to have considerable value. In some cases, adaptation-minded researchers have generated and tested specific empirical predictions not generated from nonadaptationist theories, such as sex-linked causes of divorce (Betzig, 1989), causes of the intensity of mate retention effort (Buss & Shackelford, 1997), predictable conditions under which spousal homicide occurs (Daly & Wilson, 1988), sex differences in the nature of sexual fantasy (Ellis & Symons, 1990), and shifts in mate preferences across the life span (Kenrick & Keefe, 1992). In other cases, adaptation-mindedness has proved heuristic, guiding researchers to important domains not previously examined or discovered, such as the role of symmetry in mate attraction (Thornhill & Gangestad, 1993), the role of deception in mate attraction (Tooke & Camire, 1991), and the specific conflicts of interest that occur in stepfamilies (Wilson & Daly, 1987). Using the same criterion, we could not find a single example of an empirical discovery made about humans as a result of using the concepts of exaptations or spandrels (but see MacNeilage, 1997, for a testable exaptation hypothesis about the origins of human speech production). Of course, this relative lack of fruitfulness at this time does not imply that over time, the concepts of exaptation and spandrels cannot be useful in generating scientific hypotheses and producing empirical discoveries.

In this article, we have attempted to elucidate the defining criteria of adaptations, exaptations, spandrels, and functionless by-products. Tables 2 and 3 summarize several important conceptual and evidentiary standards applicable to each of these concepts.

Adaptations and exaptations—in the form of either co-opted adaptations or co-opted spandrels—share sev-

Table 2
Conceptual and Evidentiary Criteria for Evaluating the Core Concepts of Adaptations, Exaptations, Spandrels, and Functionless By-products

Differentiation criteria	Adaptation	Exaptation: Co-opted adaptation	Co-opted spandrel	Functionless by-product
Origin and maintenance	History of selection	Selection operating on previous adaptation	Selection operating on previous by-product	History of selection for mechanism that produced by-product
Role of fitness	Correlated with fitness in past during period of its evolution	Currently correlated with fitness	Currently correlated with fitness	Not directly related to fitness
Critical features	Solved adaptive problem in past	Has new function	Has new function	No previous or current function

Note. *Exaptations* and *spandrels* are used here according to Gould's (1991) primary meanings, that is, as features co-opted for new current functions; *functionless by-product* is the term used for Gould's other and less common usages of exaptations and spandrels, that is, as incidental, nonfunctional consequences of other characteristics. In the evolutionary literature, these are usually called "by-products." In Gould's usage, "currently enhances fitness" presumably refers to the period of evolutionary time during which selection transformed a previous adaptation or by-product into a new function. Note also that Gould sometimes used the term *exaptation* to cover both co-opted adaptations and co-opted spandrels; we treat these separately.

Table 3
Standards Common to Adaptations, Exaptations (Co-opted Adaptations), and Co-opted Spandrels

Standards	Criteria
Conceptual	Hallmarks of special design for proposed function: complexity, efficiency, reliability, specificity, capability of solving adaptive problem, and evolvability
Empirical	Capable of generating specific and falsifiable empirical predictions; must account for known data better than alternative hypotheses

eral common features. All invoke selection at some point in the causal sequence. All invoke function. All must meet conceptual criteria for the proposed function—the hallmarks of special design, including specialization of function for solving a particular adaptive problem. And all must meet evidentiary standards, such as generating specific testable empirical predictions and parsimoniously accounting for known empirical findings.

These concepts differ, however, in the role of selective origins and fitness in explaining a feature. Although all three invoke selection, adaptations that arose de novo from mutations invoke selection in the original construction of the mechanism as a species-wide feature. Co-opted adaptations invoke selection in the original construction of the mechanism that is co-opted as well as in any reconstruction necessary for reshaping the mechanism for its new function and in maintaining the mechanism in the population because of its new function. And co-opted spandrels invoke selection in explaining the adaptations of which they are by-products, in explaining the reshaping of the by-product for its new function, and in explaining the maintenance of the by-product in the population because of its new function. Consequently, relative to initial adaptations, exaptations carry the additional evidentiary burden of showing that a current function is distinct from an earlier function or from a functional original structure.

The most important differences, however, center on the temporal aspect of function and fitness. Adaptations exist in the present because their form was shaped in the past by selection for a particular function (Darwin, 1859/1958; Symons, 1979; Tooby & Cosmides, 1990b; Williams, 1966). Exaptations, in contrast, exist in the present because they were co-opted from previous structures that evolved for reasons different from those of the later exapted function (Gould, 1991). Although all three concepts require documentation of special design for a hypothesized function, co-opted exaptations and spandrels carry the additional evidentiary burdens of documenting both later co-opted functionality and a distinct original adaptational functionality. To our knowledge, none of the items on Gould's (1991) list of proposed spandrels and exaptations—language, religion, principles of commerce, warfare, reading, writing, and fine arts—have met these standards of evidence. Moreover, even if they did meet such standards, this would in no way diminish the need to place such items within an overall evolutionary framework in order to adequately understand and explain them—a point agreed on by all sides of these debates.

Evolutionary psychology is emerging as a promising theoretical perspective within psychology. As with many emerging theoretical perspectives, there is often controversy about the meaning and scientific utility of the new explanatory concepts. Although most psychologists cannot be expected to become steeped in all of the formal complexities of the highly technical discipline of evolutionary theory, we hope that this article will serve as a guide to some of the most theoretically useful core concepts and some of the most interesting controversies within this emerging perspective in psychological science.

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