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Adaptationism – how to carry out an exaptationist program[1]

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Abstract: Adaptationism is a research strategy that seeks to identify adaptations and the specific selective forces that drove their evolution in past environments. Since the mid-1970s, paleontologist Stephen J. Gould and geneticist Richard Lewontin have been critical of adaptationism, especially as applied toward understanding human behavior and cognition. Perhaps the most prominent criticism they made was that adaptationist explanations were analogous to Rudyard Kipling's *Just So Stories* (outlandish explanations for questions such as how the elephant got its trunk). Since storytelling (through the generation of hypotheses and the making of inferences) is an inherent part of science, the criticism refers to the acceptance of stories without sufficient empirical evidence. In particular, Gould, Lewontin, and their colleagues argue that adaptationists often use inappropriate evidentiary standards for identifying adaptations and their functions, and that they often fail to consider alternative hypotheses to adaptation. Playing prominently in both of these criticisms are the concepts of constraint, spandrel, and exaptation. In this article we discuss the standards of evidence that could be used to identify adaptations and when and how they may be appropriately used. Moreover, building an empirical case that certain features of a trait are best explained by exaptation, spandrel, or constraint requires demonstrating that the trait's features cannot be better accounted for by adaptationist hypotheses. Thus, we argue that the testing of alternatives requires the consideration, testing, and systematic rejection of adaptationist hypotheses. Where possible, we illustrate our points with examples taken from human behavior and cognition.

Keywords: adaptation; ADHD; brain allometry; constraint; epistemology; evolutionary psychology; exaptation; female orgasm; optimization; special design; waist-hip ratio (WHR)

1. Introduction

In the past decade, evolutionary psychology has emerged as an important theoretical perspective in psychology. Evolutionary psychology is a methodologically rich field that could be applied to a variety of interesting questions (e.g., phylogenetic analysis of psychological and behavioral traits). One approach receiving much attention in recent years predominantly involves the application of adaptationism to understanding the evolution and nature of human psychological design (Barkow et al. 1992; Buss 1995; Ciba Foundation 1997; Pinker 1997a). Adaptationism, as a research strategy, seeks to identify adaptations and to elucidate the specific selection pressures that forged them in an organism's evolutionary past. It has a long history within evolutionary biology that, in its current form, crystallized in the 1960s and 1970s (particularly influenced by the writings of George Williams 1966) and now dominates the study of animal behavior in biology (e.g., Krebs & Davies 1993; 1997). Adaptationists sometimes implement optimization models (formal mathematical theories of selection pressures) to decide whether a particular design serves some specific function (e.g., Parker & Maynard Smith 1990). Perhaps as often, however, they use intuitive arguments for how a particular feature must have served a goal responsible for its evolution (Williams 1966).

Everyone agrees that organisms have adaptations. Yet, adaptationism as a research strategy has not enjoyed consensual affection within evolutionary biology. In the 1970s, it became the target of criticisms by paleontologist Stephen Jay Gould and geneticist Richard Lewontin (e.g., Gould & Lewontin 1979; Lewontin 1978; 1979). Perhaps the most prominent criticism they made was that the explanations that adaptationists gave for traits were analogous to Rudyard Kipling's *Just So Stories* (outlandish explanations for questions such as how the elephant got its trunk). Of course, the criticism is not against storytelling in science per se. The generation of hypotheses and the making of inferences is an inherent part of science. Rather, the criticism refers to the acceptance of stories without sufficient empirical evidence. Gould, Lewontin, and their colleagues have made two important epistemological criticisms of the story telling that adaptationists do. First, adaptationists often use inappropriate evidentiary standards for identifying adaptations and their functions. Second, adaptationists often fail to consider alternative hypotheses to adaptation.

Many have responded to the criticisms of Gould and Lewontin (e.g., Alcock 1987; 1998; Alexander 1987; Borgia 1994; Buss et al. 1998; Cronin 1993; Dawkins 1986; Dennett 1995; 1997; Houston 1997; Maynard Smith 1978; 1995; Mayr 1983; Parker & Maynard Smith 1990; Pinker 1997b; Pinker & Bloom 1992; Reeve & Sherman 1993; Sherman 1988; 1989; Thornhill 1990; Thornhill & Palmer 2000; Tooby & Cosmides 1992; Wright 1997) and Gould has responded to at least some of these arguments (e.g., Gould 1997a; 1997b; 1997c; 1997d). Most recently, the debate between Gould and adaptationists has been carried to outlets intended for the lay public, including exchanges about evolutionary psychology in the *New York Review of Books* (Dennett 1997; Gould 1997a; 1997b; 1997c; 1997d; Pinker 1997b; Wright 1997). Despite

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emerging nearly a quarter-century ago, these debates persist with no consensual resolution (though each side appears to think matters have resolved in their favor). Few debates are more central to evolutionary biology and, in particular, evolutionary psychology – the arena in which skirmishes have most recently been staged. Our purpose is not to review the entire literature on this debate. Rather, some confusion about the nature of the debate persists, and we attempt to clarify the major issues. In particular, the major criticisms of adaptationism advanced by Gould and Lewontin have been largely epistemological in nature, rather than ontological; a point not always appreciated.

By way of background, we first discuss traits and how they evolve (sect. 2). Next, we discuss the primary goal of adaptationism – to determine whether traits are adaptations; and, if so, to determine the specific selection pressures that shaped them (sect. 3). In this section we also discuss problems with different standards that adaptationists could use (and sometimes have used) to classify traits as adaptations and make inferences about the specific selective forces that shaped them, especially in light of the criticisms made by Gould and Lewontin. Playing prominently in these criticisms, are the concepts of constraint and exaptation. A constraint opposes the modifying influence of selection on the phenotype, whereas an exaptation is a preexisting trait that acquires a new beneficial effect without modification to the phenotype by selection. To Gould and his colleagues, constraint and exaptation are so prevalent in selection that it is difficult to infer selective history with the use of traditional adaptionist tools. Thus, we also discuss the ways in which even the best adaptationist evidentiary standards can fail to identify adaptation (sect. 4). In the last major section (sect. 5), we note that problems with storytelling are not unique to adaptationism. Gould and Lewontin insist that adaptationists consider alternative hypotheses, but they have not provided any evidentiary criteria for accepting the alternatives that they ask adaptationists to consider. In the absence of rigorous evidentiary standards, exaptationist story telling is "Just So" storytelling. We argue that an adaptationist approach is crucial to providing empirical support for the alternative hypotheses about trait design that Gould, Lewontin, and their colleagues insist should be considered. Where possible, we illustrate our points with examples about human behavior and cognition.

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2. The effects of traits and how they influence trait evolution

Biologists use the term "trait" to refer to aspects of organisms' phenotypes. The question of what qualifies as a trait is not so straightforwardly answered as it might seem, a point emphasized by Gould and Lewontin (1979). Because all aspects of the organism's phenotype are integrated with one another, organisms are "not collections of discrete objects" (Gould & Lewontin 1979). Genes often have pleio-tropic effects (i.e., a single gene may influence many aspects of the organism's phenotype) and they often epistatically interact with each other (i.e., an allele at one locus may influence the phenotypic expression of an allele at another locus).

Nevertheless, biologists interested in how an organism's phenotype evolved are forced to discriminate between aspects of the phenotype. A liberal definition would allow a trait to be any aspect of the phenotype that can be discriminated on the basis of any criterion – its causes, its effects, its appearance, and so on – and would include dispositional traits (e.g., the disposition to develop callouses with friction). The subset of such traits that could *potentially* qualify as adaptations, are those that have *effects* (a conceptualization that follows from Williams 1966; see also Gould & Vrba 1982). An effect refers to the way (or ways) in which an aspect of the phenotype interacts with the environment. This approach does not imply that traits are completely genetically distinct from each other, as two traits with very different effects may have common genetic underpinnings. This is not a problem, however, because adaptationism is concerned with how traits come into being on account of the effects that they have.

2.1. Should behavioral and psychological phenomena be considered traits?

Behaviors and psychological phenomena are often responses of the organism to aspects of the environment. They are not traits in and of themselves because they are not constructed from genes or their products. Rather, they are effects of components of the nervous system interacting with each other (e.g., emotional experience), or effects of the nervous system interacting with the muscular-skeletal system (e.g., behaviors). However, behaviors and psychological processes are like traits in that they produce effects of their own (e.g., the movement of a hand that shapes the environment to create a tool), and these effects are of-

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ten functional. Throughout the article we will speak of behaviors and cognitive processes as if they were traits. But when we do so, we are implicitly referring to the underlying decision-rules and information processing algorithms encoded into the structure of the nervous system either through genetics, learning, or some other process.

2.2. How the effects of traits influence their evolution

Traits evolve as the genes from which they develop evolve. Genes evolve from any one of four evolutionary forces – mutation (the original source of all genetic variation), migration, drift or chance, and selection (often partitioned into natural selection and sexual selection). An effect influences the evolution of a trait if it either enhances or inhibits the replicative success of the genes from which it develops. Thus, selection results in modifications to the phenotype by virtue of the differential effects on replicative success that are generated by allelic variation.

2.2.1. Some beneficial effects drive a trait's evolution, whereas others do not. The word *adaptation* has two meanings in evolutionary biology (Gould & Vrba 1982). It refers to the process by which natural selection modifies the phenotype and generates traits whose effects facilitate the propagation of genes. It also refers to the endproducts of that process – that is, the traits that have been constructed by a process of phenotypic modification by natural selection for a particular gene-propagating effect. The effect that causes the trait to evolve is called the *function* of the trait.

Gould and Vrba (1982) were the first to define and discuss the concept of exaptation. An *exaptation* is a pre-existing trait (i.e., one that has already evolved) that acquires a new beneficial effect without being modified by selection for this effect (i.e., it takes on a new role, but was not designed for it by selection). Because the beneficial effect did not contribute to the trait's evolution, the effect the trait is exapted to is not a function but just an *effect:* "Adaptations have functions; exaptations have effects" (Gould & Vrba 1982, p. 6).

Modification of the phenotype is essential to the concept of adaptation. Natural selection cannot bring about adaptation (the process or the end product) without the changes that new genes make to the phenotype. However, for a trait to become exapted to a new beneficial effect, it must have acquired it without being phenotypically modified by selection for the effect. This point is not always appreciated. For instance, in an article explaining the differences between adaptations, exaptations, and spandrels, Buss et al. (1998) stated, "Selection is necessary . . . 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" (p. 542). If a trait undergoes a process of structural modification to facilitate a new beneficial effect, it has undergone a process of adaptation and the resultant structural changes are referred to as adaptations. Gould and Vrba (1982) are clear on this point. They refer to an initially exapted trait as a *primary exaptation* and any subsequent adaptive structural modifications as *secondary adaptations.*

Some traits are complex, meaning that subcomponents can be discriminated and interact in ways to produce effects. The hand is a complex trait, one that has particular effects (e.g., grasping) by virtue of the organization of subtraits (e.g., fingers, bone structure, musculature that permit grasping). Technically, complex features are probably mixtures of exaptations and secondary adaptations. With regard to the skeletal structure and musculature of land-living vertebrates, "The order and arrangement of tetrapod limb bones is an exaptation for walking on land; many modifications of shape and musculature are secondary adaptations for terrestrial life" (Gould & Vrba 1982, p. 12). Naturally, one expects that the finer details of a complex feature that are most subject to secondary modification are those that do not serve the new exapted effect well: "Any coopted effect (an exaptation) will probably not arise perfected for its new effect. It will therefore develop secondary adaptation for the new role. The primary exaptations and secondary adaptations can, in principle, be distinguished" (Gould & Vrba 1982, p. 13).

2.2.2. The genesis of exaptation. There are two scenarios under which a trait may become an exaptation. In the first, the trait initially evolves as an adaptation for a particular effect, and then subsequently becomes exapted to another effect (Gould & Vrba 1982). For example, feathers may have evolved initially for their insulation properties rather than for flight (Gould & Vrba 1982). Nevertheless, many of the feathers on a bird (such as wing and tail feathers) have been modified specifically for flight and so represent at least secondary adaptation for flight. Other feathers on a bird do not exhibit obvious modification for flight. Contour feathers are surface feathers covering all parts of the body except for the wings and the tail (Gill 1990). At the proximal end of the feather, close to the skin, they have soft, plumaceous, fluffy barbs that suggest special design for trapping air that has been heated by the body, and keeping it close to the skin. Toward the distal end of the feather that is exposed to the air, the barbs form a relatively cohesive flat surface. This feature may contribute both to heat insulation (by protecting the underlying thermal layer from being disturbed by wind) and flight facilitation (by reducing drag while flying). If contour feathers have not been modified by selection specifically for facilitating flight, they may be pure exaptations to flight as well as adaptations for insulation.

Under the second scenario by which exaptation can occur, the trait is a by-product of selection for another trait. The by-product evolved, not because it was selectively advantageous, but because it was inextricably linked (either through pleiotropy or linkage disequilibrium) to another trait that was reproductively advantageous. Such traits, called *spandrels* (Gould & Lewontin 1979), can subsequently become exapted to new beneficial uses. For example, some species of snails have a space in their shell that they use to brood eggs (Gould 1997e). The space exists even for snails that do not use the space, and is presumably a necessary consequence of a plan for shell development that was the product of selection. Those snails that use the space for egg brooding apparently evolved after ones not using it. The space then appears to qualify as a spandrel that was later exapted to brooding eggs.

Systematic processes rather than mere coincidence may lead to exaptation. As argued by Lewontin (1983), organisms not only adaptively respond to adaptive problems posed by autonomous environments; they also construct them (see also Laland et al. 2000). One of the ways by which

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organisms can adaptively create and successfully move into new niches is by exapting existing structures – putting old features to new uses. In this view, birds were able to move into a world of flight precisely because they possessed structures that could be exapted (and only subsequently, adapted) for flying. Similarly, modern humans may live in a world very different in many ways from the ancestral ones that shaped us, but it is far from coincidence that we fit this new world in interesting ways. Thus, although we did not evolve in a world in which transportation involved driving vehicles at high speeds, we would not now live in such a world did we not possess features that could be exapted for driving. As recognized by Mayr (1963), shifts into new adaptive zones are often behaviorally led, with secondary adaptation of exapted morphological and other structures following behind. From this perspective, exaptations may not be rare fortuitous "accidents," but rather regular occurrences. (Parenthetically, however, we emphasize that organisms may also possess specific features highly maladapted to the new environments they construct [e.g., Daly & Wilson 1999]. Thus, modern humans would perhaps survive longer were they to exhibit less of a preference for fatty foods.)

2.3. Constraints limit the phenotypic outcomes of selection

A *constraint* opposes the modifying influence of a selective force on the phenotype. In the absence of constraints, directional selection will continuously modify the phenotype over evolutionary time and there will be no stable phenotypic outcome of the selective process. To oppose the effects of selection on phenotypic modification, a constraint either must limit the phenotypic outcomes that alleles could produce, or it must be an opposing evolutionary force.

Physical laws are examples of constraints that limit the possible outcomes that alleles could produce. No allele could ever arise that will allow an organism to have zero mass or violate the laws of conservation of mass or conservation of energy. Also, the epistatic effects of genes may limit the suite of possible phenotypic outcomes. For example, since a new allele arises in the context of a pre-existing genome, the range of possible phenotypic modifications that a new allele could produce may be limited by the prior evolutionary history of the organism.

A selective force on a trait may constrain other selective forces on the same trait if they have opposing effects. For example, selection favors large clutch size in birds because a larger clutch size will increase fitness in the absence of an opposing selective force. But because parents find it difficult to raise all offspring from a large clutch to weaning, there is an opposing selective force favoring smaller clutch sizes. Actual clutch sizes should then be influenced by the tradeoffs between these two selective forces (see, e.g., Seger & Stubblefield 1996).

A selective force on one trait may also indirectly constrain a selective force on another trait if the traits are inextricably tied to each other. For instance, when a new mutation arises, it arises in a genome that has been subject to a long history of selection. As such, much of the genome will be highly conserved because it results in advantageous phenotypic effects. It is possible that the only new mutation that could result in a given beneficial trait also interacts with the existing genome to produce costly effects that outweigh the beneficial effects. Selection will then disfavor the evolution of the new trait and the design of the organism will be constrained. This is referred to as a *genetic constraint* because there is no possible mutation that favors the new trait within the context of the existing genome. A genetic constraint should be understood as a selective tradeoff between the new mutation and the existing genome. Because the advantages afforded by the preexisting genome outweigh the beneficial effects of the new mutant, the new mutant cannot evolve, and the trait is constrained from reaching optimal design for its function.

A particular form of a genetic constraint is a *developmental constraint.* The construction of an organism through the developmental process depends on the coordinated action of many different genes. It is possible that a new mutation could only code for a beneficial new trait by interfering with the developmental process, thereby disrupting the development of the rest of the organism. If the costs of developmental disruption outweigh the advantages provided by the new mutant, the new mutant will be disfavored and the trait's design will be constrained.

2.4. The concept of evolvability

A concept related to genetic constraint is *evolvability.* Evolution by natural selection can occur when new mutations can possibly lead to fitter phenotypes. "Evolvability" is the genome's ability to produce adaptive variants, which depends on the mapping of genotypes to phenotypes. While genetic constraints entail mappings of genotypes (both actual and potential, through mutation) to phenotypes that prevent evolution toward certain phenotypic configurations, evolvable genetic systems are those that allow incremental, stepwise improvement. A key feature is that further improvements in one part of the system must not compromise past achievements. Modularity of genotype-phenotype mapping functions – a relative absence of pleiotropic effects of gene action – therefore facilitates evolvability (Wagner & Altenberg 1996).

Kirschner and Gerhart (1998; Gerhart & Kirschner 1997) argue that developmental systems that display versatility also have high evolvability. Versatility is the ability of the development plan to be open to new adaptive possibilities. Kirschner and Gerhart argue that certain simple developmental processes (e.g., those giving rise to a common body plan, or Bauplan, within a taxonomic grouping) are conserved because they allow for versatility while also giving rise to robust developmental outcomes. Perhaps ironically, these processes themselves constrain evolutionary outcomes. Kirschner and Gerhart argue that constraint is inevitable, and that these simple constraining processes are conserved "because they deconstrain phenotypic variation in other processes, and hence facilitate evolutionary change" (p. 8426). (See also West-Eberhard 1998.)

Evolvability may not be selected for at the individual level, for its benefits are in a currency of *future* evolutionary adaptation, and selection cannot anticipate what traits are likely to be beneficial in the future. Within a species, individual selection should favor increasing specialization of traits because specialized traits will usually outperform more generalized ones (Symons 1992). Possibly, evolvability (e.g., in the form of a conserved developmental plan) is selected as a by-product of the other, adaptive evolutionary changes it allows. In this view, conserved developmental plans are not adaptations for evolvability, but their versatility makes it more likely that they will be exapted to new uses, and at the same time makes it easier for selection to

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build adaptations for these new uses. (In their seminal article on exaptation Gould and Vrba [1982] make a similar claim about repetitive copies of DNA, whose existence allows for [and is exapted for] a flexible future [evolvability], but whose existence cannot be due to its role as such.) Alternatively, evolvability may be subject to clade selection (Williams 1992). That is, even though there should be an increasing tendency towards specialization for species within existing niches, those taxa that happen to maintain more versatile, more evolvable developmental plans may be more effective at entering and exploiting new niches precisely because they are most open to new adaptive possibilities.

3. The possible evidentiary standards for identifying adaptation and function

The goal of adaptationism is to determine whether traits are adaptations (Mayr 1983). To classify a trait as an adaptation is to identify its function (Thornhill 1997; Williams 1966). To identify a trait's function is to determine the specific selection pressures (if any) that were at least partially responsible for the evolution of the trait.

Over the years, Gould, Lewontin, and their colleagues have argued that adaptationism is not only a flawed methodology for understanding the outcomes of evolution in general, but even for understanding the specific outcomes of its core concern, selection (e.g., Gould 1984; 1987; 1989a; 1989b; 1991a; Gould & Lewontin 1979; Gould & Vrba 1982; Lewontin 1979; 1983). Their arguments all involve a similar complaint. *Adaptationism is built on a view of evolution that overemphasizes the power of selection and under-appreciates the constraints on selection and other evolutionary processes.* They do not deny that selection is responsible for workable design. Gould (1997d) acknowledges that "natural selection is the only known cause of eminently workable design" and that "adaptive design must be the product of natural selection" (p. 57). Nor does Gould deny that natural selection is the primary force responsible for evolutionary change (Gould 1984). Rather, the point is that factors other than selection can lead an adaptationist to misunderstand the selective processes that gave rise to the trait. Thus, the explicit object of Gould's criticisms of adaptationism is its attempt to make inferences about the specific selective forces that shaped a trait over evolutionary time (Gould 1991a; Gould & Lewontin 1979; Gould & Vrba 1982).

There are two inferential errors that adaptationists can make when attempting to identify adaptations and their functions. First, they can infer that a trait is an adaptation for a proposed function when it is not. Second, they can infer that a trait is not an adaptation for a proposed function when in fact it is. Both sides in the debate agree that the worse error is to classify a trait as an adaptation when in fact it is not (Gould & Lewontin 1979; Gould & Vrba 1982; Thornhill 1990; 1997; Williams 1966). The point of disagreement centers around the probative value of the evidentiary standards that adaptationists use to classify a trait as an adaptation.

In particular, Gould and Lewontin (1979) have argued that adaptationists use *mere consistency* with adaptationist hypotheses as evidence for function. As such, adaptationists often fail because mere consistency does not test the relative likelihood of alternatives.

> We would not object so strenuously to the adaptationist programme if its invocation, in any particular case, could lead in principle to its rejection for want of evidence. We might still view it as restrictive and object to its status as an argument of first choice. But if it could be dismissed after failing some explicit test, then alternatives would get their chance. Unfortunately, a common procedure among evolutionists does not allow such definable rejection . . . The criteria for acceptance of a story are so loose that many pass without proper confirmation. Often, evolutionists use consistency with natural selection as the sole criterion and consider their work done when they concoct a plausible story. But plausible stories can always be told. (Gould & Lewontin 1979, pp. 587–88)

Actually, no adaptationist has ever suggested that mere consistency should be the standard of evidence used to identify function. Rather, the criticism seems to be that the evidentiary standards used by adaptationists are, in reality, no better than mere consistency. Below, we discuss various possible standards and argue that the last of them, special design, is clearly better than mere consistency.

3.1. Six possible evidentiary standards for identifying adaptation

3.1.1. Standard 1: The comparative approach. Phylogenetic comparisons seek to demonstrate a correlation between trait variation and the environment among a large number of related species in a way predicted by a selective argument (Leroi et al. 1994; Martins 2000). Some biologists have argued that phylogenetic comparisons are necessary to any argument for adaptation (Larson & Losos 1996). In its simplest version, the comparative approach suffers from the problem of inferring causation from correlation. Various methods have been suggested to address the causation issue, but phylogenetic analyses, by themselves, only provide weak evidence of adaptation at best (Martins 2000). Still, there appears to be a growing consensus that they are useful when used in conjunction with other approaches, a point to which we will return (see sect. 3.3).

More important for our purposes, the use of phylogenetic comparisons is problematic when making inferences about adaptation within a single species (see also Thornhill 1997). The existence of a correlation between trait variation and environmental circumstances for a large number of species cannot be used to conclude that the trait variant for a *particular* species in the data set has been influenced by a particular selective force. Moreover, the comparative approach, by itself, cannot be used to classify traits that are unique to a single species because it requires data on a large number of species to make statistical tests. Thus, it cannot classify any uniquely human trait (morphological, psychological, or behavioral) as an adaptation. The next five standards attempt to identify adaptations within a single species.

3.1.2. Standard 2: Fitness maximization. One standard that has been advocated by some adaptationists is that an adaptation is a trait that, among a suite of variants, maximizes fitness in a particular environment (Reeve & Sherman 1993). However, there are several problems with this standard (for reviews, see Symons 1992; Thornhill 1997). First, it requires the scientists to actually measure the fitness of organisms over time. This is a problem because selection is a statistical process. Fitness can vary temporally in such a way that a measurement of fitness over a particular period of time may not reflect statistical trends over evolutionary time.

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Second, the standard fails because it does not incorporate the notion that adaptations maximize fitness only in the environments in which they evolved. The environment in which an adaptation evolved and the modern environment that it is currently in, may be very different from each other, although this is not always the case. If the two environments are meaningfully different from one another, then this standard would leave scientists without any means for determining whether or not a trait is an adaptation, because it is impossible to directly measure fitness in ancestral environments.

Even if these other problems could be solved, the fitness maximization standard does not allow one to determine the function of a trait. The standard could allow one to determine which variant that selection is currently favoring, but by itself it gives little insight into what the trait does so that selection favors it. Many adaptationists have long known that they need some standard that allows them to make an inference about the specific effects that drove the trait's evolution by selection in ancestral environments (e.g., Symons 1992; Thornhill 1990; 1997; Williams 1966).

3.1.3. Standard 3: Beneficial effects. One possible standard for making an inference about function is whether the trait has any effect that would have been beneficial in ancestral environments. However, this standard fails because it is also possible that traits that had beneficial effects in ancestral environments were exapted to those effects. For instance, Singh (1993a; 1993b; 1994a; 1994b; Singh & Luis 1995) has reported that men find women who exhibit a waist-hip ratio (WHR) of 0.7 or less to be more attractive than women who exhibit a waist-hip ratio of 0.8 or higher. Whether WHR is a real component of men's mating preferences (Tassinary & Hansen 1998), or possibly a contingent preference varying with ecology (Marlowe & Wetsman 2001; Wetsman & Marlowe 1999; Yu & Shepard 1998), has recently been called into question. For instructional purposes only, we assume throughout the article that it is a real preference. If so, the preference could have evolved for any number of reasons: women who have lower WHRs tend to have fewer health problems, are young and have greater reproductive value, are more fertile, are less likely to be pregnant, and may be less likely to have an infectious disease. It is quite possible that the preference could have evolved as an adaptation for one of these effects and was exapted to the remaining effects. Using the beneficial effect standard would lead one to the conclusion that the trait was an adaptation for each of these effects.

The next three standards attempt to infer a trait's function by examining its features in relation to its effects. The idea is that selection often leaves its mark on traits when it designs them to perform functions. Thus, it should often be possible to reconstruct the selective history of a trait by examining the features of the trait in relation to what it does. Arguments from design have been described as projects of "reverse engineering" (e.g., Dawkins 1982/1983; Dennett 1995). In building a piece of machinery to solve a particular problem, an engineer thinks about what kind of design would solve the problem efficiently and economically. The evolutionary biologist is faced with the reverse task. He or she is looking at a trait that is the product of evolutionary forces. If the trait was produced by selection, it has already been "designed" for a special purpose. The goal of reverse engineering is to figure out what nature designed the trait for.

3.1.4. Standard 4: Optimal design. Adaptationists often use optimization models to analyze traits. An optimization model quantitatively models the selection pressures on a particular trait or suite of traits (Seger & Stubblefield 1996; Winterhalder & Smith 2000). The model has one or more *actors* (e.g., a gene, a plant, two or more individuals engaging in social interaction, etc.) expressing the phenotypes that the theoretician is trying to understand. The payoffs of the model are expressed in a *currency,* such as actual fitness units or some correlate of fitness (e.g., units of energy). The *goal* of the optimization model is to maximize the actor's net benefit as measured by the currency. The *decision set* is the suite of phenotypic or behavioral options available for pursuing the goal, and the *selective constraints* delineate how these options are translated into costs and benefits. The optimal phenotypic or behavioral option is the one that satisfies the goal. Complexities can be taken into account, such that optimal strategies may be contingent on the relative frequencies of each strategy in the population (frequency-dependent optima) or the condition or phenotype of the individual (conditional or phenotype-limited optima). (See Parker & Maynard Smith 1990 for more discussion.)

Optimization models may allow either a single trait to evolve (*atomistic* models), or allow multiple traits to evolve simultaneously (*coevolutionary* models). Atomistic models do not necessarily neglect other traits of the organism. Rather, they may make assumptions about other traits and treat them as inputs in the model, as in models of sex ratio evolution in which the genetic system itself is a trait that exerts a selective force on sex ratio (e.g., Charnov 1982). A coevolutionary model looks at a larger chunk of the organism than an atomistic model. However, even in coevolutionary models, only a small number of traits are ever really allowed to coevolve. In coevolutionary models, traits may drive the evolution of each other, as in some models of signaler-receiver interactions (e.g., Grafen 1990). Often, traits will exert opposing influences on each other and force selection to make tradeoffs between them, as in some life history models (e.g., Stearns 1992).

3.1.4.1. Design arguments based on atomistic optimization models. In a sense, atomistic models presuppose that selection builds traits in the same way that an engineer would design a piece of machinery to perform a task. They can then be used to make predictions about how traits should be designed if they were to perform their functions optimally. A reasonable fit with these expectations is taken as evidence that selection designed the trait to solve the problem.

However, Gould and Lewontin (1979) have argued that the underlying premise that selection works like an engineer is flawed. Evolution does not result in solutions to problems similar to what an engineer would achieve. Rather, adaptations are jerry-rigged solutions. Whereas an engineer would be sure to specify the steps of construction of an optimal piece of machinery to achieve a particular end, natural selection adds features in unplanned steps. The analogy between human engineering and organic selection is therefore flawed. In the words of Jacob (1977), "Selection does not work like an engineer. It works like a tinkerer" (p. 1163).[2]

By considering traits in isolation from each other, adaptationists merely consider how a trait would optimally perform a particular function. The tinkering process of pheno-

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typic modification could still yield traits that are optimally designed to perform their functions in the absence of genetic constraints. But the organism is not a blank slate on which new traits can be constructed. New alleles arise in the context of an existing genome. If the new alleles that could give rise to an optimally designed trait would interact with the existing genome to produce costly effects, then the tinkering process may actually favor alleles that produce less costly effects but would build a less than optimally designed trait. An atomistic approach causes adaptationists to neglect how genetic constraints force selection to make design tradeoffs between traits (Gould & Lewontin 1979).

If selection should be thought of not as an engineer but rather as a tinkerer, the evolutionary biologist confronted with understanding the outcomes of selection faces a task not of reverse engineering, but rather, of "reverse tinkering." The existing genome may impose genetic constraints on the body plan such that trait design may be far from the predicted optimum and optimization models will be impotent to explain phenotypic outcomes (Gould & Lewontin 1979).

For example, Gould (1989a) has argued that the shell shapes in the West Indian land snail *Cerion* are constrained by an allometric relationship between whorl number and whorl size; the larger the whorls, the fewer there are. This constraint has implications for relationships between whorl size and shell shape; shells with larger whorls tend to be squatter. An adaptationist account of why shells with larger whorls should be designed to be squatter, would fail to account for them, for this association apparently has no adaptive value. Perhaps more important, the constrained relationship between whorl width and shape may prevent optimal designs (whatever they may be) from evolving. Human brains may be subject to similar allometric constraint (Finlay & Darlington 1995). Brain features may be forced to evolve together in developmentally constrained ways, with their structure nonoptimal as a result.

Predictions about optimal trait design will often fail to identify adaptations because optimality is too conservative a standard. Due to genetic constraints, there is probably no adaptation that (when examined closely enough) exhibits optimal design for its function. For instance, the vertebrate eye is a marvel of machinery for processing light information. Yet, even the eye exhibits a flaw – the optic nerve attaches to the front side of the retina in such a way that there is a blind spot in the vertebrate eye (Dawkins 1986). This is because the wiring from each photocell leaves the cell from the side that is nearest the light such that the wiring interferes with the path of light. The blind spot exists at the place where all the wires aggregate into a bundle to leave the retina. The evolutionary reason for this peculiar design appears to be a historical accident in which the earliest photocells randomly oriented in this "backwards" fashion. Now, the vertebrate eye is constrained from reaching a better design because it would entail the evolution of intermediate forms that would leave the organism worse off than it currently is.

3.1.4.2. Design arguments based on coevolutionary optimization models. If the scientist is familiar with all of the precise developmental and genetic constraints imposed on the possible solutions, he or she may be able to see that the solution is optimal *relative to all other possible solutions given the constraints.* In principle, coevolutionary models have the potential to remedy the concerns of Gould and Lewontin by incorporating genetic and developmental constraints. Unlike atomistic models, coevolutionary models allow theoreticians to make predictions about how selection would optimally make tradeoffs between traits if the actor were subject only to the selection tradeoffs included in the model. Traits, as outcomes of coevolutionary models, are not necessarily designed to optimally perform their functions. Rather, the optimization parameter is how the actor maximizes fitness by trading off the design features of one trait against those of another trait.

However, in practice, there are two problems that limit the incorporation of such constraints into such models. First, the mathematics becomes increasingly difficult to solve as the number of constraints increases. Second, the scientist often has little or no *a priori* understanding of how organismal design is integrated to generate constraints on the evolution of traits. These constraints arose due to the historically contingent events of the tinkering process (e.g., what mutations happened to arise, what features evolved first, what evolved traits were later exapted for other purposes) that the scientist has no clear view of. Thus, coevolutionary optimization models will usually fail to fully explain trait design because, even if adaptationists are able to include some genetic constraints in their models, they will be unable to include all the organism's traits and all the genetic constraints acting on them.[3]

3.1.5. Standard 5: Tight fit. In part, selection chooses among variants of a trait on the basis of how well they facilitate a particular gene-propagating effect. Often, this process generates a tight fit between the features of a trait and its function. Thus, it is often said that a tight relationship between a trait's features and some problem or opportunity in the environment, is demonstrative of function (e.g., Cosmides & Tooby 1995). For instance, there is a tight fit between the features of the eye and its function of sight (Williams 1966).

There are two reasons why tight fit may not be sufficient to establish adaptation. First, as noted earlier, many organisms have been under selection to modify their environments in ways that allow them to use their pre-existing traits in novel ways (Dawkins 1982/1983; Laland et al. 2000; Lewontin 1983). For instance, the hand fits very well inside a glove, yet this mere fact cannot be taken as evidence that hands evolved to fit inside the glove. This is precisely the sort of erroneous conclusion that the tight fit standard could lead us to make. Selection is responsible for the fit between trait and effect, but selection has not modified the hand to fit inside the glove. Rather, selection on some other aspect of the phenotype has given human beings the ability to modify the environment in a way that protects or insulates the hand.

Second, fit between behavioral performance and an adaptive problem can arise because of learning. Learning is a process in which feedback from the environment modifies the neurological structures that give rise to behavior and cognition. Learning mechanisms are themselves adaptations that allow the organism to adaptively modulate behavior with changing environments. As adaptations they have functions (e.g., to learn a language, to fear a predator, to get along with others, etc.). However, by their very nature, learning mechanisms are somewhat flexible with respect to outcome. It is possible that a learning mechanism can be so flexible that it can develop behavioral and cognitive

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traits that perform tasks that are not the function of the mechanism. For instance, being able to drive a car or play the stock market must in some sense represent the output of learning mechanisms that evolved for other purposes. Moreover, neural network models suggest that a single learning mechanism may be able to generate different cognitive mechanisms, each of which exhibits good design for performing a different task (e.g., Kruschke 1992). For these situations, the learning mechanism has been exapted to a new problem and so we refer to the trait as the output of an *exapted learning mechanism* (ELM).[4] Thus, the tight fit standard is consistent with adaptation, but it is also consistent with the possibility that the fit between trait and effect was the result of environmental modification or generated by an ELM (see Gould & Lewontin 1979, for a similar point).

3.1.6. Standard 6: Special design. The leading evidentiary standard for inferring function from the analysis of a trait's features in relation to its effects is special design (Symons 1992; Thornhill 1990; 1997; Tooby & Cosmides 1992; Williams 1966). Sometimes the special design standard appears to be a pre-specified list of criteria that must be satisfied (e.g., specificity, proficiency, precision, efficiency, economy, reliability of development, complexity of design, etc.). Satisfaction of these criteria is surely sufficient to demonstrate that a trait has been designed *by something* to perform a task. But if we are to take the lessons of neural network modeling to heart, these criteria are also consistent with behavioral and cognitive traits that develop from an ELM that evolved for another purpose. With sufficient feedback from the environment, traits that develop from ELMs can come to exhibit specificity, proficiency, and even complexity of design for performing a task.

Moreover, a research strategy that attempts to demonstrate adaptation and function by the satisfaction of a pre-specified list of criteria misunderstands the burden of proof. Williams (1966) wrote the leading account of how to demonstrate adaptation and function from the features of traits and their effects. Rather than proposing a pre-specified list of criteria, Williams (1966) advocated an approach in which the scientist makes an inference of adaptation and function only after demonstrating that all alternative hypotheses to adaptation for a particular effect are highly unlikely as complete explanations for the trait. Demonstrating adaptation, Williams argued, carries an onerous burden of proof. Moreover, "This biological principle [adaptation] should be used only as a last resort. It should not be used when less onerous principles . . . are sufficient for a complete explanation" (p. 11). Williams did suggest qualities of trait design that could help build a case for adaptation (e.g., precision, efficiency, economy) and claimed that formulation of "sets of objective criteria [of special design]" is a matter of "great importance" (p. 9). Yet, he himself applied only an informal probability standard: "whether a presumed function is served with sufficient precision, economy, efficiency, etc., to rule out pure chance [i.e., any possibility other than adaptation for a particular effect] as an adequate explanation" (p. 10, brackets added).

There may be no uniform list of criteria that must be satisfied to demonstrate that a trait has been specifically designed by selection for a function. Different traits may require satisfaction of different criteria. Nevertheless, it would be useful to have some guidelines about the sorts of criteria that can help build a case for adaptation. For instance, it is difficult to see how the function of a trait could be elucidated if it did not perform its function with specificity and proficiency and, hence, these criteria appear to be necessary components of a special design argument. If a trait's features produce multiple effects with equal proficiency, then it will be difficult (if not impossible) to determine which effect (if any) drove the trait's evolution. Within evolutionary psychology, specificity and proficiency interact in the concept of *domain specificity.* A cognitive mechanism exhibits domain specificity if it is good at processing information relevant to certain problems, but not other problems to which the mechanism might be applied. Domain specificity is often demonstrated by showing that certain stimuli facilitate the performance of a cognitive mechanism and other stimuli do not (see, e.g., Cosmides & Tooby 1992).

As argued above, however, specificity and proficiency merely demonstrate a good (or tight) fit between the trait's features and an effect of the trait. By themselves, they do not test whether the fit could have been caused by modification of the environment to fit the trait, or whether the trait is the developmental output of an ELM. The scientist may then want additional evidence demonstrating that the trait's features have been phenotypically modified by selection for the proposed function.

For morphological (i.e., non-neurological) traits, it is often sufficient to demonstrate that the trait also exhibits complex design for the proposed function. These traits cannot have developed from an ELM. For behavioral and cognitive traits, however, the lesson of neural network modeling is that ELMs may be able to generate behavioral and cognitive traits that perform tasks with specificity and proficiency, and these traits may even exhibit complex design for those tasks (e.g., Kruschke 1992). Fortunately, there are several forms of evidence that could, along with specificity and proficiency, bolster an argument that the trait's features have been constructed by selection for the proposed function.

3.1.6.1. The role of developmental specificity and biased learning in testing adaptationist hypotheses. For behavioral and cognitive traits, adaptationists sometimes build arguments for adaptation by showing that the trait is the biased outcome of a developmental or learning mechanism (Cummins & Cummins 1999). Biased outcomes indicate that the mechanism is biologically *prepared* (*sensu* Cummins & Cummins 1999; Seligman 1971) to produce the trait relative to other traits it could produce. When a trait exhibits developmental specificity (or learning specificity), it suggests that the function of the mechanism is the biased outcome. It can be demonstrated by showing that the trait develops (or is learned) more easily, more reliably, or serves its function with greater proficiency than other traits that could arise from the same mechanism.

Examples of psychological traits for which adaptationists have invoked the criterion of developmental specificity are language facility and intuitive ontologies. Pinker (1994) has argued that the ease with which children learn new words and the ways by which they generate syntactic structure indicate a biological preparedness and, hence, adaptation for language learning. Others have argued that the specific evidence that Pinker cites does not firmly establish the nature of the developmental specificity for all aspects of language and suggest that more general learning capacities play important roles, but appear to accept the general criterion of

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developmental specificity (e.g., Gomez & Gerken 2000). The work of developmental psychologists (e.g., Baillargeon 1987; Spelke 1990) suggests that humans have an "intuitive physics," a set of expectations about the physical world that reliably develop, on the basis of work suggesting that learning from specific instances cannot account for infants' perceptual expectations. Keil (1994) has argued for an intuitive biology on the basis of similar reasoning, though he cautions that the evidence for developmental specificity is not yet fully compelling (see also Atran 1998).

While intuitive ontologies often involve learning, they also consider the timing of development of learning capacities. Most learning bias experiments do not take into account the development of learning capacities. For this reason, some learning biases could be the result of prior learning history (e.g., learning algebra first may make it easier to learn calculus). Still, it is possible to devise experiments that are difficult for ELM hypotheses to explain. In one important experiment, rats were able to associate a sound with an electric shock but were unable to associate it with nausea. Similarly, rats were able to associate a taste with nausea but not with an electric shock (Garcia et al. 1974). This demonstrated that the learning mechanism involved in the perception of taste is biased towards providing information about the quality of food, and the learning mechanism involved in audition is biased toward providing information about external threats. Because the experimenters used novel stimulus-punishment associations, it is not immediately clear how any prior learning history could have caused the biased learning patterns that the rats demonstrated.

3.1.6.2. The trait's features exhibit a good fit with a proposed ancestral environment, but exhibit more of a mismatch in the modern environment in which the trait develops. It is often impossible for scientists to perform the experiments needed to test developmental specificity. In that event, it is sometimes possible to make inferences about developmental specificity from how the features of the trait interact with the environment. For example, if a particular behavioral or cognitive trait is the output of an ELM, it will have developed in response to modern environmental input. If such a trait exhibits specificity and proficiency for a task, it will do so in modern environments.

However, if the trait is an adaptation it will exhibit specificity and proficiency when in its evolutionary environment. Sometimes the pertinent aspects of the modern environment are very similar, if not identical, to the environment in which a trait evolved. If so, one would expect that the trait's features match the modern environment very well if it is an adaptation. If the modern environment is different in some pertinent way from the proposed evolutionary environment, the prediction is that the trait will fit better with the evolutionary environment than the modern environment if it is an adaptation.

For instance, people often experience a craving for foods that are high in sugar and fat, and these preferences are particularly robust in small children (for a review, see Drewnowski 1997). The sweet tooth exhibits specificity and proficiency for motivating people to seek out such foods or to choose these foods when given a choice. This evidence by itself, however, is not enough to demonstrate that the sweet tooth's evolved function was to motivate people (perhaps particularly children) to eat foods that are rich with sugar and fat. Food preferences are modifiable by learning (Drewnowski 1997), and it is possible that the near universal prevalence of the sweet tooth is an artifact of modern environments in which everyone develops a preference for sweet foods from an ELM that evolved for some other purpose.

One of the interesting characteristics of the sweet tooth is that it motivates us to eat sweets even when we become obese and our health is endangered. Ironically, this maladaptive characteristic actually suggests developmental specificity. If preferences for sweet and fatty foods reflect adaptation, they evolved in response to calorically limited ancestral environments in which sugar and fat were sporadically encountered, and there was little selection for limiting consumption. If, however, the preferences are the output of an ELM, presumably they are reinforced by specific experiences in the modern world. Although adults often avoid sweet, fatty food because they have been extensively educated about the health risks of high consumption, they do so despite their taste preferences for these foods. Similarly, in recent years small children have been increasingly exposed to adult models who encourage them to eat the "right" foods, yet still have strong preferences for sweet foods (Drewnowski 1997). The fact that the features of the sweet tooth cannot readily be accounted for by adaptive learning in a modern environment, but exhibit evolutionary adaptation within a calorically limited ancestral environment, suggests that the sweet tooth is the biased output of a developmental mechanism and not the output of an ELM.

3.1.6.3. Arguments for behavioral or cognitive adaptation are bolstered by empirical evidence that would be difficult to account for by an ELM. More generally, the case for adaptation may be strong when it is difficult to see how an ELM could account for the empirical evidence. Direct evidence for developmental specificity is one example. In other instances, the evidence against an ELM account need not directly imply developmental specificity. For instance, women's preferences for the scents of men shift over the course of the menstrual cycle so that they prefer the scents of more symmetrical men at mid-cycle (Gangestad & Thornhill 1998; Rikowski & Grammer 1999; Thornhill & Gangestad 1999; Thornhill et al. 2001). It is not clear how the preference could be learned, or why it would shift over the cycle were it the output of an ELM.

Another instance in which one could make a case against the trait being the output of an ELM, is when there are several other traits that converge on the same function as the trait in question. The burden may then shift to ELM advocates to show how an ELM could plausibly account for the entire pattern. Gangestad and Thornhill (1998; Thornhill & Gangestad 1999) suggest that the shift in female olfactory preferences toward the scent of symmetrical men when fertile may be an adaptation for seeking genetic benefits for offspring in the context of extra-pair sex, wherein women may pay a cost (e.g., loss of an in-pair mate's investment in offspring) and can only reap the genetic benefit when fertile. Other evidence indicates that: (1) Men with more symmetrical faces are perceived to be healthier (Rhodes et al. 2001); (2) More symmetrical men sexualize other women more and they invest less time and emotional support in their primary partner (Gangestad & Thornhill 1997a); (3) More symmetrical men are more likely to have extra-pair sex partners and are more likely to be chosen as extra-pair sex partners (Gangestad & Thornhill 1997b); (4) Women

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are more likely to have extra-pair sex mid-cycle, a pattern not observed for sex with a primary partner (Bellis & Baker 1990); and (5) Women report greater feelings of sexual attraction to and fantasy about men other than a current primary partner when fertile, a pattern not observed for feelings about in-pair partners (Gangestad et al. 2001). These effects are all consistent with the proposed function of the shift in olfactory preference.

Moreover, women also prefer the scent of men with heterozygous major histocompatibility (MHC) alleles, a trait that may be particularly valued in a primary mate, as it should increase the diversity of MHC alleles within a set of offspring and reduce spread of an infection within a family (Thornhill et al. 2001). As this preference is purported to have a function different from the preference for symmetrical men, it should not increase during the fertile phase. In fact, it appears to increase during the non-fertile phase, when, according to this reasoning, selection for long-term mates should dominate. It is difficult to see how an ELM could plausibly account for the complex and multiple patterns of evidence (although even more work may be required to satisfy the onerous standard of special design and convincingly demonstrate the precise functions of the preference shifts; Thornhill & Gangestad, in press).

3.2. The role of optimization analyses in the adaptationist program

Complete consistency with optimization models is too strict a standard for identifying adaptation and function, because optimization models are generally not capable of including all the constraints that influence the trait's design. Nevertheless, optimization models are, in practice, one of the most useful instruments in the adaptationist toolbox. The primary goal of such models is not to determine whether a trait is optimally designed, but to determine whether ancestral selective pressures have acted on the trait in ways predicted by the model. The approach admits that genetic and developmental constraints may influence trait design, but gambles that they will not obscure the patterns that selection would have on trait design in the absence of those constraints. Thus, the optimization analysis may yield predictions about the modulation of phenotypes or behavioral decisions with the environment that could not be made in the absence of a formal mathematical analysis. If these predictions are particularly novel or non-intuitive, and are empirically borne out, they may provide powerful special design evidence that the selection tradeoffs included in the model have, in fact, been operating on the trait.[5]

For example, optimization models predict parent-offspring conflict over parental resources (e.g., Parker & McNair 1978; Trivers 1974). Haig (1993) used this theory to explain why specific features of the fetus and mother exhibit special design for extracting and avoiding the extraction of resources by the fetus, respectively. In the absence of a cost-benefit analysis showing that selection pressures should result in a conflict over parental resources, no argument from design would have been possible.

3.3. The role of the comparative approach in the adaptationist program

While the comparative approach cannot demonstrate adaptation by itself, it is another important instrument in the adaptationist's toolbox. Examining how a trait functions in one species can be useful in generating testable hypotheses about how it functions in another species. The comparative approach can also help determine whether adaptation has taken place when used in conjunction with other methods (Leroi et al. 1994; Martins 2000). One important approach is to use comparative data with optimization models to demonstrate a broad pattern of selection across species (Charnov 1993; West et al. 1997).

When used in conjunction with design evidence, the comparative approach can also demonstrate that a trait within a single species is an adaptation. As we describe in more detail below (sect. 4), the special design standard is very conservative and so will sometimes fail to correctly classify a trait as an adaptation. The comparative approach can be used to supplement design evidence when the trait cannot be classified as an adaptation for a particular function based solely on its design features. For instance, compared to invertebrates, vertebrates have evolved a metabolism that places greater reliance on the quick mobilization of energy through anaerobic respiration. However, vertebrate skeletons also dissolve slightly from the lactic acid that is generated from this process (Ruben & Bennett 1987). The dissolution process is very detrimental to the organism because it interferes with the supportive and protective functions of the skeletal system. If one were to examine the skeletal dissolution process in a single vertebrate species, one would probably be unable to conclude that the skeletal system has undergone adaptation for dealing with the problem. Yet, when one examines those invertebrates that have skeletal systems, one finds that they are almost always composed of calcium carbonate, whereas those of vertebrates are composed of calcium phosphate. Calcium phosphate appears to be much less soluble than calcium carbonate in salt solutions and more complex biological media. Since vertebrates generate greater amounts of lactic acid than invertebrates, their skeletons may be composed of calcium phosphate because it resists the dissolving effects of lactic acid better than calcium carbonate (Ruben & Bennett 1987). The comparative analysis is useful in this instance because it suggests an alternative substance that vertebrates could have used to construct their skeletal systems. Comparing the design features of both substances strongly suggests that vertebrate skeletal systems exhibit adaptation for resisting the dissolving effects of lactic acid.

3.4. Special design criteria: Summary

Gould and Lewontin have helped highlight many ways in which the evidentiary standards that adaptationists have used can lead them to erroneously classify a trait as an adaptation for a proposed function. First, the genes underlying the trait could have evolved by chance or mutation. Second, the trait could also be the developmental outcome of novel environmental input. Third, the genetic constraints operating on the trait may be so strong that selection is incapable of phenotypically modifying it for the proposed function. Fourth, the trait could be a spandrel that lacks the proposed effect. Fifth, the trait could be an adaptation that has a different function. Finally, the trait could be a spandrel or an adaptation for another function that has been exapted to the proposed function. Because of the ways by which errors could occur, it is important that the evidentiary standards used to infer adaptation exceed mere consistency with an

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adaptationist account. In many cases, Gould and Lewontin (1979) argued, they don't. Although this complaint may apply to certain standards that could and have been used, it clearly does not apply to the one advocated by Williams, the special design standard. Indeed, Williams argued that explanation through adaptation be used as a "last resort" only after "less onerous" accounts were found to be highly unlikely.

4. Ways in which the special design approach can fail

As noted above, erroneous inferences about adaptation can be of two sorts: Traits may be misclassified as adaptations, and traits that are adaptations may not be so classified. Any trait that satisfies the rigorous evidentiary standards of the special design approach is highly likely to be an adaptation for the proposed function. Because the special design approach is very conservative, however, some adaptations may fail to exhibit special design for their functions. Gould and Lewontin's arguments also have implications for the ways in which even the best evidentiary standards of adaptationism can fail to correctly identify a trait as an adaptation for a proposed function.

One way in which adaptation could fail to exhibit special design is when the trait could have been phenotypically modified by selection for the proposed function, but been so constrained that it fails to perform its function with sufficient specificity and proficiency. (See Note 5.) The calcium phosphate composition of vertebrate bones may be just such an example. Vertebrate bones by themselves do not appear to exhibit special design for resisting the dissolving effects of anaerobic metabolism, precisely because they do dissolve under lactic acid. It is possible that vertebrates are constrained from designing bones from materials that are even better able to resist dissolution under lactic acid.

Another way is when it has been exapted to other beneficial effects in such a way that it lacks specificity for its function. Earlier, we discussed waist-hip ratio as a possible factor influencing men's mating preferences. If so, it could have evolved for any of the reasons that were discussed (indicator of general health, reproductive value, fertility, or a lack of pregnancy or infection). But, it could also have evolved for one of these reasons and subsequently been exapted to the other effects. If the characteristics of the preference fail to exhibit specificity for any of these effects, then it will be impossible to determine which effect is the function of the preference and which (if any) it has been exapted to.

Finally, a trait may undergo adaptation for one effect, be exapted to a second effect, and then undergo further adaptation for the second effect. Such a feature may not look well designed for either the original or the latter function. In other words, the trait could also have multiple functions that exert opposing influences on its design so that it lacks special design for either function. If a mixed design trait doesn't show some specificity and proficiency in performing its functions, it will be impossible to reverse engineer. In other instances, a mixed design trait may exhibit enough specificity and proficiency that it will be possible to identify its functions even if the trait is not optimally designed for those functions. The identification of the trait as a mixed design trait will then depend on being able to identify opposing influences on trait design such that it is suboptimally designed for its multiple functions.

Consider the human female orgasm as a possible example of a mixed design trait. (See Note 6 on Gould's [1987] own writings on the female orgasm.) One adaptationist hypothesis for female orgasm is that it functions as a selective sperm retention mechanism (Baker & Bellis 1993; 1995). The "upsuck" hypothesis originated with the work of Fox and his colleagues showing that the normally higher pressure in the uterus relative to that in the vagina reverses direction immediately following orgasm (Fox et al. 1970). On the basis of sexual selection theory, Baker and Bellis (1993) proposed that female orgasm selectively biases the retention of sperm of one male over another when a female has multiple mates. The selectivity aspect of the hypothesis predicts that female orgasm should not always occur during intercourse and will be associated with the characteristics of male partners. Provisional data suggest that female orgasm can, in fact, lead to sperm retention (Baker & Bellis 1993). If so, data also suggest that female patterns of orgasm would favor the sperm of men who are extra-pair partners (Baker & Bellis 1993) and who possess high developmental stability – a characteristic that may be associated with increased genetic fitness of offspring in ancestral environments (Thornhill et al. 1995). If this and other predictions that follow from this hypothesis are shown to be robust, female orgasm may exhibit special design for choosing sires who produce viable offspring.

However, other aspects of female orgasm may exhibit special design for pair-bonding with good social partners. During female orgasm the neurohormone oxytocin is released (Blaicher et al. 1999). As this hormone plays a role in pair-bond formation in non-human mammals (Young et al. 1998), it may play a pair-bonding role in women as well (Turner et al. 1999). However, the characteristics that make for a good pair-bonding partner (e.g., a highly investing male) may make for a suboptimal sire, and vice versa (Gangestad & Thornhill 1997a). Female orgasm may exhibit mixed design because it may sometimes cause women to be pair-bonded to men who make good sires but low-investment social partners. Similarly, it may also sometimes cause women to retain the sperm of men who make good social partners but poor sires. We stress that much empirical work would need to be done to demonstrate these points. Moreover, it may be the case that selection has reduced the incidence of mistakes by neurophysiologically decoupling the two possible functions of orgasm (e.g., Thornhill & Furlow 1998).

5. The exaptationist program

Gould and Lewontin have also argued that the focus on adaptationist hypotheses (even if rigorously put to the test so that erroneous inferences of adaptation are minimized) is not harmless. It leads scientists to ignore more prevalent, more important, and more interesting hypotheses for trait design. For instance, of the alternative explanations for trait design listed in the prior section, Gould and Lewontin have been particularly insistent that adaptationists consider hypotheses of constraint, spandrel, and exaptation (Gould 1991a; Gould & Lewontin 1979; Gould & Vrba 1982; Lewontin 1979; 1983).

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> [The constraint argument] holds . . . that the basic body plans of organisms are so integrated and so replete with constraints upon adaptation . . . that conventional styles of selective arguments can explain little of interest about them. It does not deny that change, when it occurs, may be mediated by natural selection, but it holds that constraints restrict possible paths and modes of change so strongly that the constraints themselves become much the most interesting aspect of evolution. (Gould & Lewontin 1979, p. 594)

Similarly, Gould has also argued that exaptations are both more numerous and more important than adaptations (Gould 1991a; Gould & Vrba 1982). Moreover, he argues that this is particularly true with respect to the evolutionary study of human behavior and psychology where the list of exaptive uses to which the human brain is put "is a mountain to the adaptive molehill" (Gould 1991a, p. 59).

The problem with the pluralistic approach is that Gould and Lewontin have not provided any evidentiary standards for testing these alternatives (Buss et al. 1998; Daly 1991). Indeed, Lewontin has acknowledged this problem (Lewontin 1978, p. 228): "In a sense . . . biologists are forced to the extreme adaptationist program because the alternatives, although they are undoubtedly operative in many cases, are untestable in particular cases." The lack of evidentiary criteria for testing alternatives has sometimes led participants in the debate to accept non-adaptationist explanations for traits very uncritically, and subsequent research has often vindicated adaptationist explanations for them (Alcock 1998). In the absence of rigorous evidentiary criteria for accepting alternatives, even exaptationist story telling is "Just So" story telling. Recently, Buss et al. (1998) have attempted to provide evidentiary criteria for testing alternatives to adaptionist hypotheses. The criteria we discuss next are complementary to many of their criteria.

5.1. Testing adaptationist hypotheses is a necessary part of the pluralistic program advocated by Gould and Lewontin

Several authors have suggested that testing adaptationist hypotheses might be a way to show that a trait has been constrained in its design (Dennett 1995; Mayr 1983; Sober & Wilson 1998). As noted above, adaptationists sometimes make predictions about trait design based on optimization models or special design arguments that generally assume no developmental or genetic constraints. If these predictions fail, one reason may be because trait design is influenced by genetic constraints that are difficult to identify and include in optimization models. If efforts to build in new assumptions about selection fail to produce a model that yields correct predictions, genetic constraints that limit the potential genotype-phenotype mappings and thereby force selection to make design tradeoffs between traits become a more likely reason for lack of model fit. Sober and Wilson (1998) make this point very well:

> Adaptationism is sometimes understood as a claim about nature – that organisms are well adapted (or even perfectly adapted) to their environments. At other times, however, adaptationism is understood as a method for investigating nature. This is the idea that a useful procedure for studying an organism is to ask, "What would the organism be like if it were well adapted to its environment?" Posing this question does not commit one to the position that the organism actually *is* well adapted. Perhaps the population inhabits a novel environment and has not had time to adapt. Perhaps the most adaptive behaviors never arose by mutation. Perhaps maladaptive behaviors spread by the process of random genetic drift . . . Even so, this kind of failure can be highly instructive because it allows deviations from the optimal phenotype to be discovered and interpreted. (pp. 11–12, citations omitted, emphasis in original)

Dennett (1995) uses an analogy of chess-playing to make this point. Sometimes, to even up a game with a weaker player, a strong player takes on a handicap, such as "no King's bishop." Suppose the handicap was to constrain movement of the pieces in some way (e.g., by not moving a piece twice in a row, by not moving a queen as a bishop, by not castling). The player writes down the limitation at the beginning of the game on a piece of paper, but does not tell the opponent. How should the opponent discover the limitation? By playing the game as if there were no limitation, with an eye toward seeing some limitation. Until the player makes some non-optimal move, there is no evidence of any specific limitation. So it is with figuring out the ways of Mother Nature. The adaptationist assumes no specific limitation, until seeing clear evidence of limitation because that is a good way of detecting limitations. Another way of knowing the limitation, of course, would simply be to peek at the piece of paper. But here the analogy clearly breaks down. Mother Nature, Dennett notes, doesn't write down her limitations. We cannot discover her limitations except by observing her ways.

This is, in fact, a general principle for testing alternative hypotheses to adaptation. Adaptationism is not only useful for discovering constraints on trait design, but empirical demonstration of constraint, exaptation, and spandrel *requires* an adaptationist approach. Commitment to the scientific enterprise requires that we not accept claims about constraint, exaptation, or spandrel in the absence of evidence. It is certainly possible that genetic constraints are so prevalent that optimization theory will be impotent to explain evolutionary outcomes and that exaptation is so common that traits will rarely exhibit special design for any particular effect. However, in the absence of evidence one way or another, we should be agnostic as to whether a given trait is optimally designed or constrained; exapted to a particular effect or specially designed for it. Building an empirical case that certain features of a trait are best explained by exaptation, spandrel, or constraint requires a demonstration that the trait's features cannot be better accounted for by adaptationist hypotheses. Confidence in alternative hypotheses for trait design only increases after consideration of all plausible adaptationist hypotheses and their failure to live up to special design scrutiny. We discuss several examples to make this point.

5.2. Example of spandrel

Spandrels differ from adaptations in that they were not reproductively beneficial in ancestral environments. Rather, spandrels must have been reproductively neutral or even costly over the period of their evolution. Spandrels evolved because they were genetically linked to other traits that were favored by selection. Many psychological phenomena currently thought of as pathologies, are good candidates as maladaptive spandrels (e.g., schizophrenia). Pathological spandrels of the psyche presumably are the byproducts of developmental mechanisms that evolved to produce particular psychological outcomes, but produce pathologies when subjected to stressful environmental or genetic per-

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turbations. Of course, adaptations can be costly (and they often are), but they evolved because they also had compensating beneficial effects in the ancestral environment that drove their evolution. Building an empirical case that a costly trait is a maladaptive spandrel thus requires some demonstration: (1) that the trait is not an adaptation; and (2) that the trait is linked (by pleiotropy or linkage disequilibrium) to another trait that presumably was favored by selection (Buss et al. 1998). The first requirement must involve rigorous testing of adaptationist hypotheses and a systematic failure to find special design evidence for any of the hypothesized functions.

Published arguments over whether attention deficit/hyperactivity disorder (ADHD) is an adaptation or a maladaptive spandrel illustrate our point. According to the Diagnositic and Statistical Manual of Mental Disorders, Fourth Edition (DSM-IV, American Psychiatric Association 1994), ADHD is diagnosed by showing that an individual displays "a persistent pattern of inattention and/or hyperactivity-impulsivity that is more frequent and severe than is typically observed in individuals at a comparable level of development," (DSM-IV 1994, p. 78). In addition to symptoms of inattention, hyperactivity and impulsivity, diagnosis requires that there be "clear evidence of clinically significant impairment in social, academic or occupational functioning."

Shelley-Tremblay and Rosen (1996) and Jensen et al. (1997) ask how this suite of costly traits could be present in five percent of the population. They argue that distractible, risk-taking individuals might have had a competitive advantage in two ancestral settings – intraspecific fighting and gathering as coastal waders. In these dangerous settings, survival would depend on being "response-ready." Response-ready individuals would be hypervigilant, rapid-scanning the visual and auditory environment, quick to pounce or flee, and motorically hyperactive. Conversely, "the excessively contemplative, more phlegmatic individual would have been 'environmentally challenged'" (Jensen et al. 1997, p. 1674) in these settings.

Special design evidence in favor of this hypothesis would indicate that individuals with ADHD respond better to cues of danger (perhaps particularly those encountered in ancestral environments; e.g., large animal movement or aggressive human movement). Do ADHD individuals respond more quickly and effectively to these cues? At present, the evidence suggests not. In a critical review, Goldstein and Barkley (1998) argue that, in fact, individuals diagnosed with ADHD appear to be deficient in response readiness (though, it should be noted that crucial tests of response readiness to ancestral cues of danger have not been performed). Because ADHD appears to lack special design for response readiness, the evidence seems to be more consistent with the hypothesis that ADHD is a maladaptive spandrel that persists despite selection, not because of it (e.g., Gangestad & Yeo 1997). Of course, a slower response to ancestral cues of danger, and demonstrating the precise adaptation to which it was linked, would enhance the empirical case that ADHD was a maladaptive spandrel.

Goldstein and Barkley (1998) dismiss Shelley-Tremblay and Rosen's (1996) adaptationist hypothesis as a "Just So story" (*sensu* Gould & Lewontin 1979). The fault with Shelley-Tremblay and Rosen's argument, however, lies not in the fact that they adopted an adaptationist approach, but rather that their approach was *insufficiently* adaptationist. Shelley-Tremblay and Rosen did not lay out evidence for special design of ADHD or even critical tests of special design. Ironically, it was the authors who doubted this adaptationist hypothesis, Goldstein and Barkley (1998), who rolled out the evidence pertinent to special design – illustrating that an adaptationist approach is critical to tests of hypotheses about adaptations, as well as hypotheses about alternative evolutionary scenarios.

5.3. Example of genetic or developmental constraint

Gould and Lewontin (1979) argue that there are some constraints acting on organismal design that cannot be included in optimization models because they are unpredictable and unquantifiable. Genetic constraints are often due to historical events that cannot be predicted beforehand from a general theory, and so the genetic constraint hypothesis does not readily lend itself to making positive predictions about trait design. The genetic constraint hypothesis does predict, however, that even after adaptationists have included all the constraints that they can, their models will still fail to accurately explain trait design. The hypothesis that genetic constraints have forced the organism to make design tradeoffs between traits is mutually exclusive with the hypothesis that the trait is optimally designed for its function. Before one can conclude that a trait is suboptimally designed for a function because of a genetic constraint, one must show a systematic failure of optimization models to explain trait design.

Gould has argued that allometric relationships sometimes exist because of constraints (Gould & Lewontin 1979). Adaptation that produces changes in the size of one trait may cause changes in the size of other traits (in a non-optimal fashion), simply because a developmental plan deeply ingrained in the genome does not allow unlinked growth of the traits. Of course, the existence of an allometric relationship by itself is not evidence of suboptimal trait design due to genetic constraint. The only way to demonstrate that the growth patterns of body parts could be genetically constrained is to show that the pattern of covariations between parts is inconsistent with *a priori* notions of what would be optimal growth patterns.

Consider the finding that the sizes of mammalian brain components are predictable with a high degree of accuracy from absolute brain size by a non-linear function (Finlay & Darlington 1995; Finlay et al. 2001). The authors suggest that these linked regularities are attributable to constraints on brain development. In testing their constraint hypothesis, the authors took an adaptationist approach by making an argument based on optimality. Because each species will be under selection for different cognitive abilities, Finlay and Darlington argued that the optimal response is for different species to invest in different brain components, which should result in a non-allometric relationship with overall brain size. This is a valid adaptationist hypothesis and its subsequent rejection with the finding of an allometric relationship increases confidence in the constraint hypothesis. By using an adaptationist approach, Finlay and her colleagues have made a *prima facie* case for constraint on mammalian brain development. (But see Barton 1999; 2001 on departures from perfect allometric relationships in primate brain size and for a critique of the analyses of Finlay et al. 2001.)

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5.4. Example of exaptation

Exaptation is not necessarily mutually exclusive to adaptation. A trait can first be exapted to a new beneficial effect and then subsequently be modified by selection for that effect. As we have noted, Gould and Vrba (1982) refer to the initial trait as a *primary exaptation* and the subsequent modifications as *secondary adaptations.* If some aspects of the initially exapted trait exhibit special design for the new effect, some reconstruction of the selective history of the trait is possible. For example, while feathers may have initially served a thermoregulatory function and later exapted to flight, flight feathers (found on the bird's wings and tail) are longer (Gill 1990) and stiffer (Corning & Biewener 1998) than necessary to serve a thermoregulatory function. Moreover, unlike body feathers, the vanes of wing feathers are asymmetrical, with the thinner vane being oriented toward the wind during flight (Gill 1990). Flight feathers clearly exhibit at least secondary modification for flight. We may then infer that flight exerted a selective force on the construction of flight feathers.

It is only when adaptationists fail to find any evidence of phenotypic modification for a particular effect that they will be unable to make inferences about the selective history of a trait. As such, all plausible adaptationist hypotheses must be considered, subjected to special design scrutiny, and rejected before a conclusion of exaptation without secondary adaptation (i.e., pure exaptation) may be drawn.

Consider again men's preference for a small WHR in women. A claim that the preference for small WHR is an exaptation for any specific effect requires demonstrating that the preference fails to exhibit special design for that effect. This requires considering what the trait would be like if it did exhibit special design for that effect. For instance, if the preference evolved because a small WHR ancestrally promised greater reproductive value, one might expect that men would specifically prefer it when choosing a long-term mate in whose offspring the man invests. A failure to support this prediction would strengthen a claim that the preference evolved for some other reason and was exapted to choosing a mate of greater reproductive value. Similarly, if the preference evolved because a small WHR suggested lack of pregnancy, one might expect that men would prefer women of low WHR as both long-term and short-term mates. If it has historically been a cue of infectious disease, one might expect men to actively avoid sex with women of high WHR. Moreover, one might expect that its importance would vary with the prevalence of disease (Gangestad & Buss 1993). Other predictions could be made about the special design implications of these adaptationist hypotheses. A systematic failure to support these predictions would strengthen claims that the preference is not the product of phenotypic modification by selection for these effects, but was instead exapted to these effects. Moreover, such a failure would make it impossible to make inferences about the selective forces that shaped men's preference for small WHR.

Parenthetically, if men's preference for small WHR does not exhibit special design for any of these possible functions, then it should be more evolvable than if it is specially designed for one of them. Traits that lack specialized design for a particular function are more likely to be versatile and therefore more evolvable (West-Eberhard 1998). In other words, once the preference becomes specially designed for a particular function, it may be more difficult to modify the preference for one of the other functions. Thus, inferences about the future evolvability of a trait could possibly be made by testing adaptationist hypotheses and subjecting them to special design scrutiny.

5.5. Testing alternative hypotheses for traits that have undergone adaptation

The problem with the approach we have advocated is that it assumes that one may make inferences about exaptation, spandrel, or constraint only after special design analyses or optimization arguments fail to explain the features of a trait. However, the relation between the trait's features and its effects may have been influenced by a combination of selection, genetic or developmental constraint, and exaptation: How, then, is the scientist to make inferences about the explanatory power of other hypotheses when special design or optimization analyses succeed in demonstrating adaptation for a particular function? First, the special design approach implies that a trait performs its function reasonably well, but it does not imply that the trait must perform it optimally. Even after demonstrating adaptation by special design, one may still build a case for constraint by showing that the trait is not optimally designed to perform its function, as in the case of the vertebrate eye.

However, we can only offer suggestions for demonstrating that a trait was initially exapted to an effect when it also exhibits special design for it. In some instances, it may be possible to make an inference of exaptation by examining the phylogenetic history of the trait, as in the case of birds' feathers evolving from reptiles' scales for a thermal insulation effect and subsequently becoming exapted to flight. If the trait is complex, the scientist may be able to do separate design analyses of its components in the hope that selection has only modified some of its components, but not others. If components fail to exhibit special design for the effect, they may have been exapted to it instead.

For instance, after further demonstrating allometric relationships between brain volumes across mammalian species (see above), Finlay et al. (2001) argued that mammalian brains develop from a fairly simple developmental plan with few parametric variations, a plan that is conserved because it promotes evolvability but necessarily also entails constraint. According to this plan, larger brains necessarily develop larger neo-cortical areas. One implication is that the large expansion of the human brain need not have been due to selection for existing neo-cortical functions, despite the fact that the neo-cortex accounts for most of the expansion. Rather, selection could have favored some larger subcortical feature, resulting in a large neo-cortex as a byproduct. Possibly, then, the large neo-cortex was exapted to its distinctly human functions (e.g., language, advanced toolmaking, certain theory of mind tasks, etc.). Testing this proposal requires adaptationist methodology. For one, it implies that increased size of a noncortical structure was favored, which means that some noncortical feature should be larger than expected on the basis of allometric relationships.

Second, it implies lack of special design of cortical structures for these distinctly human functions – unless secondary adaptation has also occurred. Demonstrating that the enlarged human neo-cortex has been exapted for its many beneficial effects and adapted for none, is admittedly

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a burdensome task that requires considering, testing, and systematically rejecting many adaptationist hypotheses for neo-cortical design. But then again, the claim is quite broad. For instance, it is possible that the neo-cortex has been constrained in its size relative to the rest of the brain and that selection has been free to play with how it is structured, a point raised by Finlay and Darlington (1995) in their initial paper. Components of the human neo-cortex seem to exhibit structural design for different tasks, such as language, planning, attention, and theory of mind tasks (Adolphs 2001; Damasio 1994; Pinker 1994). Many of these components could be adaptations that evolved sometime prior to the evolution of human beings, such that the increase in neo-cortex size over evolutionary time enhanced its performance at its pre-existing functions rather than leading to exaptation to new tasks. Testing this possibility will require identifying the functions for which selection initially designed the neocortex. This could be done by using comparative studies in conjunction with design analyses.

On the other hand, such tasks could be unique human functions: (1) for which selection designed the neo-cortex; (2) to which the neo-cortex was exapted; or (3) that arose by some combination of exaptation and secondary adaptation. Under the second scenario, the components of the neocortex presumably came to exhibit complex structural design for different tasks from developmental processes that evolved for other purposes (i.e., ELMs). We have suggested several lines of evidence that could be useful in building a case against ELM hypotheses (sects. 3.1.6.1–3.1.6.3). For instance, demonstrating that the neo-cortex exhibits developmental specificity for certain theory of mind tasks would strongly suggest that exaptation is not a complete explanation for neo-cortical design. Neonates and children do seem to exhibit a cognitive predisposition toward developing many theory of mind tasks (Flavell 1999), and presumably this reflects a structural predisposition in the neo-cortex (Adolphs 2001). The evidence of developmental specificity for some aspects of language learning is even stronger (Pinker 1994), even if it has not been demonstrated for all aspects (Gomez & Gerken 2000); and language is, of course, strongly rooted in the neo-cortex (Pinker 1994). However, other components of the neo-cortex may lack special design for their effects. Finding that other neocortical components having uniquely human effects generally lacked special design for those effects, might actually bolster the hypothesis that the neo-cortex was primarily exapted to theory of mind and language capacities and only adapted to them secondarily.

In the end, it seems likely that the design of the neo-cortex will probably be understood as a mixture of adaptation, exaptation, and constraint precisely because it is a complex trait. Determining which components are adaptations or exaptations for what effects, will undoubtedly take a great deal of work – work that must involve the testing of adaptationist hypotheses.

6. Conclusion

There is a great need for a consensus regarding the evidentiary criteria required to demonstrate that a trait is an adaptation for a particular function. While people may differ with respect to their expectations about whether a particular trait is an adaptation, exaptation, or spandrel, many arguments can be resolved with good data that bear on a commonly agreed upon standard of evidence. We have tried to incorporate the best ideas from both sides in the debate in the attempt to help forge a consensus.

Williams (1966) gave adaptationists three guidelines for how to build a case that a trait is an adaptation. First, the burden on the adaptationist is onerous. One must show that plausible alternative explanations for the trait are unlikely to generate the evidence about the trait. Second, one can acquire information about the relative likelihood of alternatives by examining the features of the trait in relation to what it does. Third, there is no fixed list of evidentiary criteria that must be met before the scientist can make an inference of adaptation. Williams did provide suggestions about the kinds of features of traits that could give insight into the relative likelihood of alternatives, and adaptationists have since expanded on those (specificity, proficiency, precision, efficiency, economy, complexity of design, reliable production, costliness, etc.). However, the scientist must not lose sight of the ultimate burden of proof. Different traits may require satisfaction of different evidentiary criteria (e.g., cognitive and behavioral traits may require satisfaction of more rigorous criteria than morphological traits). For instance, while we have argued that it will be difficult to identify a trait's function unless it exhibits some specificity and proficiency for an effect, it is possible that some cognitive and behavioral traits can come to exhibit specificity and proficiency for performing a task without having been designed by selection for that task (e.g., traits that develop from ELMs). Demonstrating that a behavioral or cognitive trait is unlikely to have developed from an ELM may require additional evidence (e.g., developmental specificity, etc.).

At the same time, advocates of an exaptationist program must live up to their own burden of proof. It is not enough to assert that a trait has been exapted, or that it is a spandrel, without meeting some rigorous standard of evidence. Good inference in any scientific field requires a serious consideration of alternative hypotheses. Because hypotheses about constraint, exaptation, and spandrel, and hypotheses about adaptation are often mutually exclusive to each other, we have argued that confidence in these alternatives increases only when plausible adaptationist hypotheses have been considered, subjected to special design scrutiny, and systematically rejected. Consequently, adaptationism is not an ontological commitment to the idea that traits or organisms are perfectly adapted to their environment (Sober & Wilson 1998). Rather, it is an epistemological approach for discovering whether *or not* they actually are adapted to their environment, and for making testable inferences about the causes of trait design.

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NOTES

1. The authors contributed equally to this paper. Order of authorship was determined alphabetically. Correspondence may be addressed to any of the authors.

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2. One may also object to the notion that engineers work in the way attributed to them by evolutionary biologists. Historically, engineers have been tinkerers that improve upon pre-existing design.

3. Indeed, we note that many of Gould's arguments generally do not imply that he is ontologically committed to the notion that organisms are suboptimally designed. It is possible to interpret Gould as saying that organisms may be optimally designed in fact, but that it is impossible to ever know this due to the inherent difficulty of including all of the constraints acting on the organism in optimization models.

4. We avoid the term "general learning mechanism" precisely because learning mechanisms are adaptations that have functions. When learning is proposed as an alternative to adaptation, what is implicitly claimed is that the behavioral or cognitive trait in question is merely the output of a learning mechanism that evolved for some other function.

We realize that, in some instances, whether an effect expresses the function of an adaptation or is a new beneficial, exapted effect is open to question. Is the use of optic flow to infer one's own bodily movement exapted for driving, or is it the case that people can drive partly because they have an adaptation for inferring bodily movement from optic flow? The answer partly depends on how one carves up the activities of the person (see also Cosmides & Tooby 1992). The specific task of driving is evolutionarily novel and so is the use of optic flow information exapted to it, but the more general task of inferring movement from optic flow (when driving or doing anything else) reflects adaptation. The same point can be made with many learning tasks. Learning to read is not a task to which humans are adapted and adaptations may be said to be exapted to it. The components of learning to read, however, may specifically function when an individual reads in much the same way as they were evolved to function (e.g., Spelke 2000). For convenience, however, we will use the term *exapted learning mechanism* to refer to the shaping of a good fit between behaviors or cognitive processes, and an evolutionarily novel problem that takes place through learning.

The main point we make here is that, given the learning capabilities of organisms, a good fit between behavior or a cognitive process, and a task, often does not constitute sufficient evidence for the function of the behavior or cognitive process, a point that stands whether or not we say that the trait has been exapted to a new task.

Some might argue that part of a tight fit assessment is to characterize the evolved domain of the psychological processes that underlie task performance at the correct level of description (Cosmides & Tooby 1992). This may lead the researcher to conclude that the underlying psychological processes are not evolved for the purpose of solving the task in such a way that the researcher avoids the mistake of saying that there is a tight fit. The problem is that one can confuse the lax standard (in which tight fit is demonstrated by a fit between task performance and an adaptive problem) for the more rigorous standard (in which tight fit also requires an examination of the psychological processes underlying the task performance), a problem that some evolutionary psychologists have fallen prey to (Cummins & Cummins 1999; Lloyd 1999). For this reason, we think it constructive to distinguish the tight fit criterion from other criteria that properly rule out the possibility that task performance is due to an ELM.

5. Earlier, we noted that Gould and Lewontin (1979) argued that separate traits are difficult to identify because all aspects of the organism's phenotype are integrated with each other. Adaptationists tend to identify traits on the basis of their effects. Due to genetic constraints, it nevertheless may be difficult for selection to independently change two traits that have different effects. The optimization modeler specifies certain constraints in the genotype-phenotype mappings of traits (usually in the form of cost-benefit trade-offs), and gambles that genotype-phenotype mappings do not seriously constrain evolution in ways not specified by the model. Although Gould and Lewontin are correct in pointing out that this assumption could be in error, it should be emphasized that the assumption is part of a theory that is subjected to rigorous empirical test under the special design standard. It is therefore unclear how an error in the assumption could lead one to misclassify a trait as an adaptation using this standard.

6. In one of his Natural History essays, Gould (1987) proclaimed that the female orgasm is *not* an adaption but a byproduct, and that this should have been clear simply on the basis of the fact (pointed out years previously by Kinsey) that the major site of stimulation, the clitoris, is homologous to the male penis. But as has been forcefully pointed out elsewhere (Alcock 1987; 1998; Sherman 1988; 1989), the mere fact that penis and clitoris are structurally homologous is insufficient justification for the conclusion that the clitoral orgasm in humans is nonadaptive. The clitoris obviously comes from somewhere. The genes whose expression in women specifically account for it must overlap considerably with those specifically accounting for the development of the penis. That fact itself does not answer the question of whether the expression of these genes to create the clitoris in women is under adaptive control and hence been selected for. Gould's conclusion may be correct but his argument does not warrant it. As we point out later, demonstrating that the female clitoris and orgasm are byproducts requires the failure to find evidence for its special design and, hence, an adaptionist testing strategy.

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Modest adaptationism: Muddling through cognition and language

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Abstract: Strong adaptationists would explain complex organic designs as specific adaptations to particular ancestral environments. Weak adaptationists don't assume that complex organic functioning represents evolutionary design in the sense of niche-specific adaptation. For some domain-specific competencies (folkbiology) strong adaptationism is useful, not necessary. With group-level belief systems (religion), strong adaptationism can become spurious pseudo-adaptationism. In other cases (language), weak adaptationism proves productive.

Recent cognitive experiments indicate that humans have specialized core mental faculties with privileged access to distinct but overlapping domains of nature, including: folkmechanics (object boundaries and movements), folkbiology (biological species' configurations and relationships), and folkpsychology (interactive agents and goal-directed behavior). These plausibly innate (but maturing), domain-specific cognitive faculties are candidates for naturally-selected adaptations to relevant and recurrent aspects of ancestral environments. Under analytic idealization they are "universal" and "autonomous" from other cognitive faculties, the way the visual system is universal and autonomous from other cognitive and biological systems (with significant individual genetic variation, and viability only in functional interaction with others faculties).

Folkbiology. A strong adaptationist stance helps to counter

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claims that folkbiology develops ontogenetically as an "exapted learning mechanism" (Andrews et al.'s term) from folkpsychology (Carey 1985). As Andrews et al. note, evidence for developmental specificity was lacking. Recent developmental and cross-cultural studies show that the apparent effects of folkpsychology on folkbiological development (e.g., anthropocentric construals of animals and plants) fade or disappear in "nonstandard" populations, that is, human groups other than those (students or children) linked to major research universities (Atran et al. 2001; Ross et al., in press). One interpretation is that nonstandard societies more closely approximate ancestral conditions of intimate interaction with nature. By contrast, standard populations (the near-exclusive focus of most developmental and cognitive psychology) need compensatory learning strategies for lack of sufficient exposure to triggering conditions that enable folkbiological knowledge, including strategies derived from folkpsychology and even folkmechanics (Au & Romo 1999).

Study of standard populations sometimes reveals more about effects of devolutionary cultural processes on innate knowledge than innate knowledge as such – much as study of language acquisition in feral children tells more about how the language faculty degenerates, than how it evolved to develop (Medin & Atran, in press). Evidence against exaptation in all populations stems from developmental and cross-cultural research; this may be compatible with strong prior or post hoc adaptationism but doesn't require it.

Religion. To illustrate strong adaptationism's epistemological stance, Andrews et al. cite Sober and Wilson's (1998) work on social traits as (group-selected) adaptations. Sober and Wilson reduce complex distributions of human behaviors to artificially coherent bundles of norms, termed "religion" or "culture." They then assume that social norms are actual behavioral traits that undergo Darwinian selection. Who holds these norms? An omniscient informant? Some expert(s)? Most people in society? In fact, purported norms are usually summary digests of lone analysts and anthropologists struggling to reduce the flux of observed social experiences into manageable proportions for report. Many social functional accounts (e.g., the Human Relations Area Files used by Sober & Wilson) purposely exclude information on individual variation, but without such information it is impossible to verify or falsify claims about the existence of norms, much less about their evolution.

These pseudo-adaptationist accounts are often historically tendentious, sometimes pernicious: for example, D. S. Wilson's (2002) notion of Judaism as a eugenics program designed to produce intelligent cabals that dominate other groups through intergroup competition (cf. MacDonald 1998). It's not that religious and cultural cognitions and behaviors lack interesting generalities that can't be productively investigated through evolutionary approaches (see Atran 2002); only, that religions and cultures as selectable objects simply don't exist (except in a loose, commonsense way), any more than do whole species (over and above constituent individuals) (Sperber 1996).

Language. Demonstration of biological preparedness *doesn't* directly imply "hence, adaptation for language learning," as Andrews et al. suggest. At best, strong adaptationist claims for syntax involve retrodictions of structures previously discovered (mainly through generative grammar). No novel predictions ensue. Reasonable people can argue over whether strong adaptationism has novel predictions or discoveries for *any* higher-order cognitive process (this excludes – perhaps artificially – "lower-order" cognitions, that is, those related to sex, kinship, and violence; and though I don't believe there's evidence for a "cheater-detection module" [Atran 2001], I'm less sure about adaptationist reworking of Kahneman and Tversky's [1979] "biases and heuristics" in human reasoning).

The one seriously strong adaptationist argument for language – natural selection of syntax for serial communication of propositions (Pinker & Bloom 1990) – may be circular, or at least, it lacks independent empirical support. No example I'm aware of indicates propositional subject-predicate structures in any creature save language-competent humans. Even that stellar bonobo, Kanzi, consistently fails to apprehend such structures; his novel "sentences" are maximally two concatenated arguments with no subjects, such as "chase bite," which humans shun (Atran & Lois 2001). So, Pinker and Bloom's proposal may reduce to this: Language was naturally selected to communicate what only language can formulate (propositions).

Strong and weak adaptationists accept natural selection as the only known (noncultural) explanation for functionally complex design. One possibility consistent with this is that much complex design has no presently known explanation (this includes most human cognitive architecture; Fodor 2001), and there may be some functional complexity that results largely from more general physical, chemical, or biological processes governing complex systems. One alternative, weak adaptationist approach assumes no direct natural selection (no task-specific adaptation to distinctive features of ancestral environments) for language's "creative core"; that is, the faculty of syntactic recursion that allows potentially infinite production of words and well-formed word-combinations with relatively few and finite means (Chomsky 2000). Putting aside the inference to adaptation from complexity of design as too vague or nearly circular, this "minimalist program" operates on the huge but bold assumption that language's creative core is a recently evolved accommodation to more general physical or biological processes – in ways analogous to the apparent optimization of information flow in a material medium through minimization of "wire length," as in microchip design, nematodes, and human brains (Cherniak 1995).

Perhaps recursion in language is a *physically optimal* sort of interface (internal accommodation) between two physically suboptimal (but perhaps genetically optimal and adapted) systems of more ancient evolutionary origins: the sensorimotor system (including phonation) and the conceptual-intentional system (including categorization, reference, and reasoning). The idea of physical optimality has a distinguished tradition in science generally (Galileo, Newton, Einstein), and in studies of biological form and development particularly (Maynard Smith et al. 1985). For evolutionary biology in particular, the primary objective is to discover and predict, through strictly physical and chemical means, the set of organic forms (molecular, morphological, neuronal) that are likely to emerge from a given starting point. Only then is it worthwhile to inquire into which of those forms might be selected and how. For example, extensive sharing of genomic structure among all vertebrates, and even vertebrates and invertebrates, suggests that many of the same "master genes" program body plan and the control mechanisms of development (Gehring 1998). Even eyes, which were thought to have evolved analogously and independently in different phyla, may be in each case a homologous derivation from the same DNA (*Pax-6*). Physical law and mechanical processes appear to be responsible for much of what follows: Development of each component of the eye is narrowly constrained by the laws of optics and mechanical contingencies involved in sharply projecting images of three-dimensional objects onto a planar surface of receptors.

In line with Turing's (1952) vision of biological explanation, much the same organic architecture and behavior may evolve in very different historical environments, just as basically similar cognitive architectures and behaviors may be developed in very different physical media (cf. Leiber 2002). If so, then it is plausible to attempt to explain significant aspects of the structure and emergence of these architectures and behaviors without considering how they have been accommodated to (selected for) particular historical environments and physical media. Indeed, further understanding of particular historical and physical accommodations (e.g., the "Cambrian explosion" of multicellular organisms, the "real-time" processing of information) may depend crucially on such nonteleological insights.

Worthiness of this approach depends on success in providing significant and surprising predictions and discoveries. In the min-

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imalist program, these arguably (if controversially) far exceed what its originators previously thought possible. At best, strong adaptationist arguments retrodict old discoveries. This isn't meant to deny that adaptationist arguments may ultimately prove insightful into language structure: Recent studies identifying multiple genetic loci for language disorders and delays seem to belie any monomutational account for language, and at least one of these genes (*FOXP2*) seems to have been a target for selection (although this gene concerns speech and processing of morphology, not syntactic recursion; Enard et al. 2002). Nevertheless, novel biological and evolutionary understanding of language (and other cognitive structures) may occur beforehand.

Weak adaptationist (though not necessarily minimalist) investigation of language crucially uses aspects of the strong adaptationist program, especially the comparative approach (Hauser et al. 2002). Therefore, arguments for natural selection of phonation have involved claims about the uniqueness of categorical auditory discrimination and descent of the larynx in humans. Comparative studies prove otherwise: Chinchillas and other mammalian species categorically discriminate human phones; deer and several bird species drop the larynx (possibly to exaggerate size; Fitch & Reby 2001). Perhaps human phonation is itself the by-product of a jury-rigged combination of other by-products and adaptations: The (originally prevertebrate) alimentary system and the respiratory system of terrestrial vertebrates interface at the larynx (which drops in humans), hence by chance enabling the production of phones later "exapted" to human language.

Other comparative studies show contrary evidence for prehominid antiquity in parts of the conceptual-intentional system. Intriguing experiments showing subordinate chimps taking the perspective of dominant chimps (Hare et al. 2001) have yet to be replicated in different laboratories (Povinelli 2001). Apparently, chimps can't repeatedly embed states of mind: for example,

> [Danny thinks that [Marc believes that [Brian knows that . . .]]] and so on.

Short-term memory typically limits iterated embedding of mental states to 5 or 6 levels (Barrett et al. 2002); however, as with "center-embedding" of linguistic clauses, computational machinery allows for indefinitely many embeddings (to any apparent limit; simply add: "You really think that . . . "). By giving a person more time and external memory, more embedding is interpretable in a unique and uniform way (not predicted by associationist models, connectionist or other). Other parts of the conceptual-intentional system may be more ancient in primates, including perceptually based reference (Gallistel 1990), categorization (Brown & Boysen 2000), and reasoning (Povinelli 2000).

In sum, combining strong and weak adaptationist strategies might profitably generate evolutionary insights into human cognition. Viewing progress in understanding the emergence of human cognition only (or principally) through a lens of either strong adaptationism or weak adaptationism could lead science into blind alleys. "Muddling through" with modest adaptationism may prove most effective.

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Are all bases covered?

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Abstract: In addition to ensuring that appropriate standards of evidence are employed when attempting to identify adaptations, researchers should investigate all nonevolutionary factors that could potentially explain their results. Evolutionary analyses may be undermined by alternative, nonevolutionary explanations either because not all relevant information is included in an evolutionary analysis, or because inappropriate methods incapable of detecting an adaptation are employed.

As Kelemen (1999a) recently pointed out, one of the most fundamental aspects of thought among Western-educated adults is the tendency to assume that objects have been designed for a purpose – that they exist "for" something. This teleological thinking is also seen from an early age in children but, unlike adults, who restrict their teleological thinking about the natural world to living things, children show a "promiscuous" teleology and believe that even non-living aspects of the world exist for a function, so that mountains are "for climbing" and clouds are "for raining" (Kelemen 1999b). While much research today focuses on why children are less restrictive than adults in attributing functions to objects, it is clear that, historically, such broad teleological thinking was also characteristic of adults prior to the European Enlightenment, with the nonliving world seen as carefully designed by God to furnish the needs of living things (Corey 1993).

Whether this teleological/functional tendency is a human cognitive adaptation or an exapted learning mechanism is open to debate, but that it even exists suggests our scientific endeavours are at risk of being biased, so that we do not see the wood for the well-designed trees. The apparent propensity to identify adaptations on the basis of insufficient evidence, which has so exercised Gould and Lewontin, may be partly a consequence of a basic human tendency to assume that objects are designed for a function. If so, then we need to be taught how to overcome this bias and pursue the adaptationist programme with proper scientific rigour. Andrews et al.'s article thus provides an extremely valuable guide to help us overcome our human frailty on such matters.

However, while the target article shows us how to distinguish true adaptation from exaptations, spandrels, and the like, it nevertheless assumes that the explanation will, in some sense, be evolutionary. Here, we suggest that we also need to be open to the possibility that some of our results may sometimes be explained by non-evolutionary factors, something that we miss, not merely because of a lack of appropriate evidence, but because our propensity to see design means that we fail to realize when inappropriate methodology is being used or fail to consider all the relevant evidence regarding the trait in question. We have two examples with which to illustrate our point, one drawn from study of current adaptiveness and one from a series of studies investigating adaptation.

In an elegant study of human reproductive decision-making, Blurton-Jones (1986; 1987; Blurton-Jones & Sibley 1978) demonstrated, with the use of both optimality models and empirical data, that the extremely long interbirth intervals (around four years) shown by !Kung San women could be explained by local ecological constraints and could be considered as evolutionarily adaptive. However, the fundamental assumption that !Kung women were displaying abnormally low fertility compared to other subsistence groups was questioned by Pennington (1992) and Harpending (1994). They showed that the !Kung populations in Blurton-Jones' studies came from an area of Botswana where overall fertility among *all* subsistence groups was low as a result of the prevalence of sexually transmitted diseases (STDs). For example, the young age at last birth shown by the !Kung women in the sample is a widely recognised signature of pathological sterility. Pennington (1992) and Harpending (1994) suggested that low fertility and

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long interbirth intervals (IBIs) could just as easily be a consequence of high levels of infectious secondary sterility rather than an adaptive response to local ecological conditions. Placing the !Kung into a wider geographical context thus allowed Pennington and Harpending to identify STD infection as another relevant variable in the analysis of !Kung birth spacing, and to proffer this as an equally valid, nonevolutionary explanation for the patterns shown.

Our second example concerns the issue of appropriate methodology. In a series of celebrated papers, Cosmides (1989; Cosmides & Tooby 1992; Fiddick et al. 2000) has used the Wason selection task as a means of testing whether humans possess a psychological adaptation for "cheat detection." The central result of these studies is that subjects generally solve a conditional reasoning problem easily when it is presented as a social contract infringement, but they consistently fail to do so when it is presented as an abstract logical problem. According to Cosmides, these results point to the operation of a content-specific mental algorithm devoted to social contract problems.

However, Sperber and colleagues (Sperber et al. 1995; Sperber & Girotto 2002; in press) have argued that Cosmides' results demonstrate nothing of the sort – not because her notion of a cheat detection algorithm is wrong; indeed, they suggest that it is highly plausible – but because the Wason selection task, and the variants that Cosmides has used, are simply not capable of testing whether such a thing exists. Although lack of space prevents a full discussion, the core of their argument is as follows. First, they consider the value of the selection task as a means of studying human inference to have been grossly overestimated. This is because, as Sperber et al. (1995) have demonstrated, the original Wason selection task is solved by what they call "relevance-guided comprehension processes" that preempt the use of other inferential capacities. In other words, the selection task does not tap into human inference processes in the way that Cosmides has assumed. Secondly, they argue that some of the variants of the Wason task that Cosmides has employed are not actually Wason tasks at all, and are even more inappropriate for the purpose of discovering a competence for social exchange – that is, they do not ask subjects about the truth/falseness or respect/violation of a conditional rule, but merely ask subjects to select cards that define a category (such as "cheater"), and so are trivially easy for subjects to pass. Sometimes this category selection task is mixed with the Wason task, giving rise to a task that is, in Sperber and Girotto's (2002) opinion, methodologically unsound. Backing this argument with convincing experimental results, they conclude that, to date, Cosmides' hypothesis has not been properly tested experimentally, least of all by Cosmides herself, and that "further investments of effort" in uses of the task should be discouraged (Sperber & Girotto 2002 p. 289).

Thus, while the adaptationist programme is indeed the best research strategy we have for detecting adaptations and testing for alternative explanations, we need to ensure that, as well as appropriate standards of evidence, we also adopt appropriate methods to provide this evidence and that all of the evidence appropriate to the issue is included in our analyses.

Use of phylogenetic analysis to distinguish adaptation from exaptation

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Abstract: One important difference between adaptive and nonadaptive explanations can be found in the evolutionary sequence of structural and functional modifications. Phylogenetic analysis (cladistics) provides a powerful methodology for distinguishing exaptation from adaptation, by indicating whether character traits have predated, accompanied, or followed evolution of particular functions. Such analysis yields falsifiable hypotheses that can help to distinguish causal relationships from mere correlation.

Critiques of adaptationism (e.g., Gould & Lewontin 1979; Lewontin 1978; Williams 1966) have focused on the scarcity of good criteria for recognizing adaptations, and on untested assumptions that natural selection optimizes structural features. Other work has developed alternative explanations for structural-functional correlations – notably exaptation and formation of architectural by-products (spandrels) (Gould 1991a; 1997e; 2002; Gould & Lewontin 1979; Gould & Vrba 1982). Although adaptationism gained a pejorative connotation in some circles (see Rose & Lauder 1996b, p. 2), adaptation remains a central concept in evolutionary biology (Gans 1988; Mayr 1982; 1988).

Andrews et al. have contributed usefully to ongoing dialogues by reviewing and refining criteria for the recognition of adaptations. Their analysis emphasizes the importance of rigorously testing adaptationist hypotheses, and of rejecting them in favor of alternatives when adaptationist explanations fail to conform to predictions. However, if exaptation and spandrel formation are to be treated seriously as evolutionary explanations, they too must be defined in falsifiable terms, and ideally, tested against adaptationist hypotheses. Otherwise, exaptation itself may become an untested assumption or a default explanation, despite other nonadaptive explanations for structural-functional relationships.

The principles and methods of cladistics (phylogenetic analysis) offer a powerful way to distinguish adaptation from exaptation. Cladistic methodology originally was developed to analyze phylogenetic relationships (Hennig 1950). In cladistics, lineages are recognized by presence of shared, derived (advanced) characteristics (Brooks & McLennan 1991; Eldredge & Cracraft 1980). Thus, derived neural and skeletomuscular features define bats (Baker et al. 1991), whereas hair defines the more inclusive mammalian group to which these chiropterans belong. The cladistic approach contrasts markedly with older approaches, in which organisms are grouped by overall similarity and taxa are defined by subjective criteria. Cladistics has revolutionized systematics, overturning some traditional taxonomic categories and firmly establishing others.

Phylogenetic analysis has also proven valuable as a means of reconstructing evolutionary history. By superimposing phenotypic features over accepted phylogenies, one can adopt parsimonious interpretations of evolutionary change. For example, application of cladistic principles has facilitated analyses of reproductive evolution in vertebrates (Blackburn 1992; 1999; Mess et al. 2003), as well as reconstruction of fetal membrane evolution in mammals (Freyer & Zeller 2001; Luckett 1977; Mess 2003) and reptiles (Blackburn 1998; Stewart 1997; Stewart & Thompson 1996; 2003). Cladistics requires us to document carefully the evolutionary sequences through which features evolve, with reference to particular phylogenies. Resultant evolutionary explanations therefore are testable, parsimonious, and relatively free from preconceptions about the nature and direction of evolutionary transformations.

One crucial difference between adaptation and exaptation lies in the chronological sequence of structural and functional modification. In adaptation, the modification of a phenotypic feature (e.g., a structure or behavioral trait) accompanies or parallels its evolutionary acquisition of a function. However, in exaptation, the feature originates first (either as a selected or nonselected attribute) and only later is coopted for the function in question. For example, the presence of elongate, vaned feathers in terrestrial saurischians (Qiang et al. 1998; 2001) implies that they are adaptations for endothermy or display, that only later became exaptations for avian flight. Likewise, mammary secretions may originally have functioned in immunological protection of offspring, and were exapted and secondarily adapted for nutrient provision (Blackburn 1993).

Phylogenetic analysis provides powerful methods for distin-

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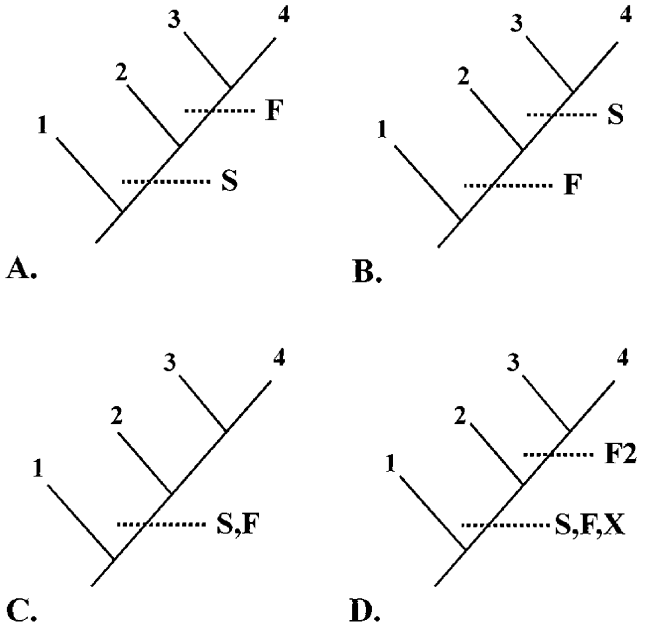


Figure 1 (Blackburn). Cladograms of four taxa, showing the timing of evolution of a given structure ("S") and function ("F"), as inferred from characteristics of the taxa. In A, the structure evolutionarily predates a function that it serves, indicating exaptation. In B and C, the function respectively predates or accompanies evolution of the structure; such sequences are necessary (but not entirely sufficient) indicators of adaptation. In D, a spandrel (X) has accompanied evolution of an adapted structure (S) as an architectural byproduct; here, the structure subsequently is exapted for a new function (F2).

guishing exaptation from adaptation by determining whether character traits have predated, accompanied, or followed evolution of their functional attributes (e.g., see Blackburn 2000; Larsen & Losos 1996). The enclosed figures illustrate acladograms of hypothetical taxa, with various possible phylogenetic distributions of a particular structure (or other phenotypic characteristic) and a function superimposed. The timing of evolution of a feature is inferred from its taxonomic distribution (Brooks & McLennan 1991). Thus, in Figure 1A, the presence of a derived structure ("S") in three of the taxa indicates that it probably characterized their common ancestor. When the structure originates first and only later takes on the function in question (as in the mammary example above), exaptation is indicated (Fig. 1A). When a function either predates (Fig. 1B) or accompanies (Fig. 1C) evolution of a structural feature, it may represent a case of adaptation. Phylogenetic analysis also may facilitate recognition of spandrels. An architectural byproduct should originate as an unselected correlate of a particular structure, regardless of whether the structure itself is selected (Fig. 1D).

In phylogenetic analysis, adaptation and exaptation have the status of mutually exclusive, competing hypotheses, each of which can be falsified or supported according to the sequence of evolutionary modification. That a structure antedated the function it performs, offers a sufficient criterion for recognition of exaptation. However, a function predating or accompanying evolution of a given structure is a necessary but insufficient criterion for recognition of adaptation; therefore, other criteria (such as those discussed by Andrews et al.) must also be brought to bear. In effect, phylogenetic analysis allows us to address, in an evolutionary context, difficult issues whose recognition dates to the writings of David Hume – notably the difficulty of distinguishing causation from correlation.

As a practical matter, phylogenetic analysis is useful chiefly where a robust cladogram can be constructed from taxa that vary in structural and functional features of interest. It therefore offers no panacea to evolutionary psychology, where inferences of genetically based behavioral attributes are problematic, particularly as applied to extinct hominids. However, in principle, phylogenetic approaches offer ways to analyze evolutionary sequences and transformations in historical contexts, and where sufficient data are available, they can provide clear evidentiary standards for distinguishing exaptation from adaptation.

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There is no evidentiary silver bullet for the frequency adaptation hypothesis

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Abstract: Special design criteria are largely unable to discriminate between claims that specific competencies in judgements under uncertainty are a result of an adaptation for representing naturally sampled frequencies, or due only to inherent properties of such a format. Because divisions between these perspectives are thin, evidence via additional criteria are persuasive only in combination, using inference to the best available explanation.

Andrews et al. point out, quite correctly, that different traits may require satisfaction of different evidentiary criteria in reaching some consensus on whether it is an adaptation. This may actually not be a strong enough statement of the case: In many situations, one or more of the usual evidentiary criteria may be used to argue against the case for adaptation. A case in point is the recent debates on the nature of statistical judgements under uncertainty.

The claim has been made that information in the form of frequencies, and in particular frequencies in a natural sampling framework, is privileged representational format (i.e., that it is the proper domain for a cognitive adaptation for making statistical judgements; Cosmides & Tooby 1996; Gigerenzer & Hoffrage 1995). Those in opposition to this claim have pointed out that naturally sampled frequencies create computationally less complicated situations simply by virtue of their inherent properties and they reject the claim of a specific adaptation (e.g., Evans et al. 2000; Girotto & Gonzalez 2001; Johnson-Laird et al. 1999). In particular, the counter-hypothesis to an adaptationist explanation is that, because the frequencies within a natural sampling system inherently preserve base-rate information, the set/subset relationships between classes of events become much more easily perceived (see Fig. 1). Instead of an adaptation for understanding and using frequencies, this explanation rests on claims for a basic appreciation of set relations (which happen to be expressible almost exclusively in frequentist terms).

In the context of this debate, criteria such as proficiency, efficiency, economy, and reliable production are unable to discriminate between these two explanations; and in fact, the presence of these features – attributed to the nature of the inputs (natural frequencies per se) – have been used to argue against an adaptationist interpretation. One can argue that the proficiency, efficiency, and economy of the behavior when using natural frequencies is purely the result of the properties of the numbers themselves (natural frequencies are simply easier), or one can argue that these characteristics are a result of a cognitive mechanism that is preferentially tuned to using these numerical formats in the first place (natural frequencies are particularly easy because the mind is designed to work with them).

Discriminating between these two theoretical perspectives is difficult because the divisions between them have become thin,

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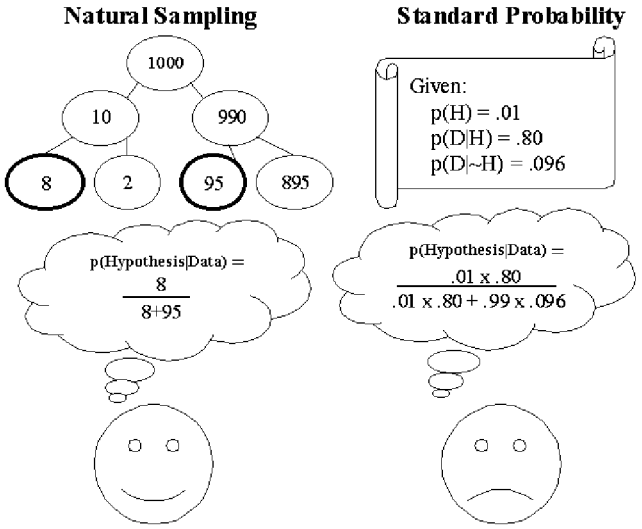


Figure 1 (Brase). Natural sampling versus standard probability. Differences in computational complexity in calculating the posterior probability (Bayesian inference), attributable to the information representation (natural sampling of frequencies versus single-event probabilities). (Figure adapted from Gigerenzer & Hoffrage 1995.)

and there is significant overlap in their predictions. Given this state, particularly, clear thinking about multiple, alternative evidentiary criteria is increasingly important. What evidentiary criteria can be used, then, in evaluating the adaptationist hypothesis that natural frequencies not only are computationally simpler (a point all parties agree on), but also constitute a privileged representational format?

Using the criteria of biased learning outcomes of developmental learning mechanisms would appear to clearly support the adaptationist view of frequencies. Children learn whole numbers (frequencies) relatively quickly and easily, but they often develop any of a number of characteristic difficulties when learning mathematical concepts that deviate from a frequentist perspective (Geary 1995; Geary & Lin 1998). For example, children often develop misconceptions about the nature of fractions and decimals, and a large number of these misconceptions are recognizable as misapplications of a frequentist interpretation of numbers (Brase 2002a). Because numbers and mathematics are an academic topic, however, the possible confounding influences of teaching techniques can be raised as a concern (e.g., Glassman 1996). It is unclear whether an early proficiency with frequencies is a result of the evolved structure of the mind or of the exposure to frequency information and subsequent learning to use such information.

The criteria of specificity may need to be revised to become even more precise, such that it again discriminates between predictions made based on different hypotheses. For example, based on the notion that an adaptation for tracking natural frequencies of objects, events, and locations in the real world must have some set of parsing rules for dividing the world into countable entities, Brase et al. (1998) proposed that such an adaptation should operate better on whole objects, events, and locations than on arbitrary aspects or features of such entities (i.e., the individuation hypothesis). Their subsequent experiments documented that, indeed, people's statistical judgements were hampered in tasks that required calculations about aspects of objects and the objects themselves, even if the information was presented in natural frequencies. Statistical judgements about individuated objects were consistently more successful.

Criteria such as fit with the ancestral environment, rather than the modern world, are difficult to assess because statistically informed judgements in ancestral circumstances would be translated directly into behavior without necessarily any explicit and conscious mathematical calculations. Although we know that bumblebees perform complex calculations of posterior probabilities, we know little about the performance of human hunter-gatherers in this respect. Related research, however, appears to support the idea of statistical judgement abilities adapted to an ancestral world. Isomorphic numerical information, presented in different formats, is evaluated and perceived in very different ways, and these phenomena can help in understanding the ways that such information is cognitively represented (Brase 2002b; Wang 1996). Specifically, some irrational and inconsistent responses in the face of statistical judgements become apparent only when using numbers on a scale that would never have been encountered at any time in evolutionary history (e.g., dealing with millions of people).

Ultimately, the adjudication about a trait being an adaptation must be made as an inference to the best available explanation, given all the evidence (preferably using multiple, independent, and converging lines of evidence). As troublesome as it may be, this means that weaker explanations can continue to survive in some quarters by selective attention to various lines of evidence (for example, by ignoring most of the information from outside one's own discipline). In this respect, one of the key obstacles to adaptationist descriptions of cognitive and behavioral traits is the narrowing of individual interests and knowledge within traditional academic divisions.

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Development: The missing link between exaptationist and adaptationist accounts of organismal design

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Abstract: To understand adaptation (and exaptation), a more comprehensive view of development is required: one beyond a constraining force. Developmental plasticity may be an adaptation by natural selection simultaneously favored (or sometimes in conflict) at multiple levels of biological organization (e.g., cells, individuals, groups, etc.). To understand the interrelationships between developmental plasticity and adaptive evolution I borrow heavily from West-Eberhard (2003) and Frank (1995; 1997). Developmental plasticity facilitates evolution, results in particular patterns of evolutionary change, and may produce exaptations by design rather than by chance.

Development is often viewed as a source of exaptation in nature. However, a comprehensive theory of adaptive evolution must feature development beyond a constraining force. Another way of elucidating apparent exaptations is the concept of "phenotypic accommodation" (West-Eberhard 2003). Phenotypic accommodation is the nongenetic adjustment among interacting and variable-evolved components attributable to phenotypic plasticity (West-Eberhard 2003). West-Eberhard's view of development and evolution incorporates the latest findings in the evolutionary study of behaviour, genetics, endocrinology, and molecular mechanisms. Indeed, terms like *exaptation* (used in isolation from the adaptationist programme) and *developmental constraints* may have impeded synthesis between evolutionary and developmental biology.

Developmental plasticity causes phenotypic variation, which in turn is screened by selection. Mutations must first influence development to influence evolutionary change. Andrews et al. have discussed development mainly in terms of constraints (although,

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see section 2.4, para. 2). A developmental constraint is simply a type of evolutionary constraint. So what is development, and how do we avoid slipshod metaphorical crutches (e.g., genetic programming, canalized epigenetic landscapes, recipes, and blueprints)? West-Eberhard suggests that we focus on developmental mechanisms (e.g., the inherited bridging phenotype – see next section) and natural selection.

Inherited bridging phenotype (IBP). Cross-generational continuity of the phenotype is a more productive starting point in elucidating development, than the outdated notion that continuity of the germ plasm is all that is required for understanding design. Development begins with an inherited bridging phenotype (IBP). An IBP is an organized but flexible cell provided by a parent in the form of an egg, a recently divided cell, or a collection of cells that is transmitted from the previous generation. IBPs are adapted for survival and "social" interaction within a gametic and embryonic environment. The IBP is transmitted maternally in several species, but paternal cross-generational transfers occur as well (Queller 1984; Westoby & Rice 1982).

A standard view in the behavioural sciences defines the life cycle of an individual as beginning with fertilization and ending upon death. Alternatively, an individual can be envisioned as only one cycle in a continuous string of ontogenies interconnected by phenotypic bridges across generations. According to West-Eberhard (2003), genetic and/or environmental resources are interchangeable, so organisms can adjust the frequency of trait expression under selection. Genes that respond to natural selection are the ones that influence the responsiveness of regulatory mechanisms (e.g., sensory systems) during development. Indeed, Andrews et al. rightly discuss the existence of general mechanisms mediating plasticity in some taxa, which may allow the exploitation of new niches because these are the organisms "most open to new adaptive possibilities" (sect. 2.4, last para.).

Plasticity and natural selection. How is plasticity itself an adaptive strategy, and how does selection simultaneously operate at a variety of levels to favour its spread? It is unfortunate that Andrews et al. imply that only *some* taxa maintain versatile and inherently evolvable development. This could suggest to some readers that plasticity is not pervasive in nature, which is clearly untrue (see West-Eberhard 2003). Flexible development is *not* an alternative to selection but rather, mediates selectable variation. The idea that evolved learning mechanisms in humans are sensitive to cultural influences (and are therefore flexible) must be explained rather than assumed. For example, Haig (1999) has argued that incest taboos cannot be assumed to have evolved using standard inclusive fitness considerations (where the coefficients of relatedness are averaged). Alternatively, asymmetries in paternal and maternal coefficients of relatedness may lead to conflicts within individuals over incest (Burt & Trivers 1998; Haig 1999). Specifically, paternal genes may have a lower threshold (compared with maternal genes) for influencing individuals to partake in incestuous relations (Haig 1999; Isles et al. 2001). Imprinting effects over fetal growth (Haig 2002), and cognitive decision rules for behaviour (Brown 2001a; 2001b), cannot be assumed to be optimally designed for the individual organism. A decision rule could be adaptive from a maternal or paternal gene's (or meme's) "point of view." Hence, the "noise" at the individual level of selection could reflect underlying intragenomic conflicts rather than exaptation per se. A potentially fruitful approach to the developmental complexity of living systems is multilevel selection theory (Frank 1995; 1997; Price 1972). Multilevel selection theory (MLS) is mathematically equivalent to inclusive fitness theory (Hamilton 1975; Queller 1992; Wade 1980). Partitioning selection into more than one component (e.g., inter-group and intra-group variation) could help elucidate developmental mechanisms and apparent exaptations.

Andrews et al. write: "if the trait is an adaptation it will exhibit specificity and proficiency when in its evolutionary environment" (sect. 3.1.6.2, para. 2). This thought is incomplete for a number of reasons. Adaptations could be designed to be vulnerable to unexpected perturbances. Indeed, this is one characteristic of development (which may be an adaptation). Flexibility is designed and not attributable to random chance. Over the course of evolutionary time, natural selection could favour flexible responses to cross-generationally inconsistent adaptive pressures (Wilson & Yoshimura 1994). In general, recurring adaptive problems select for specific solutions because specialists may be more efficient at the task. The tradeoff (as with all evolved attributes) is that a specialist is vulnerable to shifting environmental demands affecting problem structure. Perhaps the best way to view the problem of domain-specificity is to imagine a sliding continuum between specialized and generalized responses. The degree to which either is favored by natural selection depends on a number of factors: (a) the frequency of individuals adopting a specialized versus a generalized response, (b) environmental stability, and (c) the costs and benefits of each strategy.

Andrews et al. have ingeniously started a dialogue regarding the sources of exaptation in nature. Tension between adaptationist and exaptationist accounts of organismal design may be resolvable three ways: (a) partitioning short- and long-term evolution using multilevel selection theory (Frank 1995; 1997); (b) moving away from hypothetical constraints and studying how the mechanisms mediating flexibility evolved (West-Eberhard 2003); and (c) recognizing that there is a phenotypic continuity between generations.

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Troubles with exaptationism

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Abstract: There are two kinds of useful traits: adaptations, and all the others. Exaptations are just all the others. Exaptations are not for anything. Because there is such diversity in all the others, exaptation is not an explanatory concept. Its only real use is to block adaptationist excesses.

A cheetah's tail has a white tip. A mother cheetah on walkabout holds her tail aloft so that the white tip is clearly visible to her cubs. The cubs use the white tip as a visual marker in their mother-following behaviour. This is a beneficial set-up, especially when the family is in long grass or dense undergrowth.

Suppose, for the sake of argument, that the presence of white tips on cheetah tails for this particular beneficial use is not explained by selection. Suppose that there was selection for some of the characteristic pigmentation patterns on cheetah coats, but that this specific pattern, the white tip, is purely a side-effect of the chemistry. In that case, the tail would be white, regardless of whether it had ever been useful to have a white tail (though perhaps not if it had been harmful). The white tip is not an adaptation for cub signalling, even though it is put to that use by cheetahs. Is it then an exaptation for cub signalling?

There is a genuine adaptation hereabouts. A mother cheetah uses her tail as a signalling device by holding it aloft in a fashion that makes it plainly visible to her cubs. The cubs use the tail as a visual marker by looking out for and following it. Mother's behaviour is an adaptation, as is the behaviour of the cubs. The white tip has been co-opted (recruited) for use in these behaviour patterns.

Selection explains the presence of a trait in a population. Selection also explains function. The function of the trait is what it is for, and it is *for* the effect for which it was selected (Millikan 1984; 2002). Selection explains how it is that traits come to be *for* something, as distinct from merely producing effects, some of which happen to be beneficial. The behaviours of mother and of cubs are adaptations for keeping the cubs close to mother. What of the

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white tip? It is not an adaptation for this role in behaviour, because it has not been designed (selected) for that role. So it must be an exaptation, a trait that has been recruited for its current function. It is explained as an exaptation.

Andrews et al. write of the functions of exaptations (i.e., what an exaptation is for) and of the explanation of a trait as an exaptation. Adaptation and exaptation appear as different processes, both of which explain traits and their functions. This is wrong. Exaptations do not have functions. Exaptation is not an explanatory concept. Adaptation is an explanatory concept because of the connection to natural selection.

Perhaps exaptation could be viewed as an explanatory concept by virtue of its connection to recruitment. However, is recruitment the process that bestows function – that makes it the case that a trait is *for* some beneficial effect? Cheetahs have put their white tipped tails to good use. Is that what recruitment is, putting to good use a trait that is not an adaptation for that use? All behaviour involves uses of parts of the body. Some behaviours use parts of the body that have evolved for that specific use. For instance, carnassial teeth evolved in the carnivores as tools for slicing meat. Using the carnassials to slice meat is a behavioural adaptation, and the carnassial teeth themselves are adaptations for use in that behaviour. But all kinds of behaviour use some parts of the body in ways for which they have not been specifically designed. Hands are often used as chin rests but are not adaptations for that use. Still, chin resting is something useful for hands to do, so hands must be exaptations for chin resting. Hands are also useful for brushing flies off the face when in Australia, so they are also exapted for that task. And so on, indefinitely. So does exaptation give rise to new functions? If every exaptation is *for* something, then functions proliferate beyond all reason. Yet, it might be possible to assign functions to some exaptations but not to all the others, by adopting Ruth Millikan's concept of a derived proper function (Millikan 1984). The white tip on the cheetah's tail is a trait that has been recruited for use in a pattern of behaviour that is itself an adaptation. The white tip derives its function from the function of the behavioural adaptation in which it is put to work. The white tip is not an exaptation but a derived proper function. Perhaps Millikan's concept is sufficiently well-disciplined not to proliferate extravagantly in the manner of Gouldian exaptations, but some work would be needed to show this.

Gould rightly objects to panadaptationism. Many useful traits are not adapted for those uses. They are exaptations, not adaptations. So far, so good. But the living world is full of traits that are used in ways for which they are not specifically adapted. Instances of exaptations are far too many and much too diverse for exaptation to be a useful explanatory concept. A trait is an exaptation if it looks like an adaptation but isn't one. It looks like an adaptation because it has some use; but it wasn't designed for that specific use, so isn't an adaptation. Hence, the concept of exaptation is useful in a way, but only as a blocker of panadaptationist reasoning.

Adaptation is a good concept because all adaptations are explained through natural selection. Are exaptations similarly explained by a single kind of process, the process of recruitment? The presence of the white tipped tail in cheetah populations (we assumed) is explained as a side-effect of chemical processes. It is not explained by recruitment, any more than it is explained by selection. What recruitment refers to is just the fact that the trait has come to be used in some undesigned way. Unlike selection, recruitment never explains the presence of a trait. Nor does recruitment explain how the trait came to have a novel use: it merely reports the new use. There is no one kind of process through which old traits get new uses. The term *recruitment* subsumes a multitude of different ways in which traits come to be used in behaviour.

How does this bear on empirical issues? Find a trait that is useful. It is either an adaptation or it is not. In animals with extensive repertoires of learned behaviour, there are many more non-adapted uses than adapted uses. Statistically, the fact that a trait has a use, does not make it more probable than not that the trait is an adaptation. More work has to be done on the adaptationist hypothesis before it gets to the testing stage. Is ADHD an adaptation "for gathering as coastal waders"? (Cf. target article, sect. 5.2.) The hypothesis is, well, imaginative; and it yields testable predictions. But falsifiability is only a minimum necessary condition for a hypothesis to be deserving of scientific consideration. The hypothesis that a pest species can be controlled using a homeopathic concoction that includes trace elements from the ground-up remains of dead individuals of that same species is testable, but it is not deserving of scientific consideration. Its prior probability of being true is just too low. The ADHD adaptationist hypothesis is in the same boat. The fact that ADHD has useful effects in some context is not of itself sufficient reason to propose an adaptationist hypothesis for scientific consideration. We already have the makings of a sufficient genetic explanation for the presence of the disorder in a small proportion of the population. The fact that we can dream up a use for the associated behaviour is not sufficient to put a hypothesis on the table of science.

Musings on the concept of exaptation and "creationism"

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Abstract: I claim that our desire to be special motivates us to suppose that if we were not God created, we must be self-created. I also claim that Stephen J Gould's claims about punctuated equilibrium, the absence of directional selection, and exaptations, when taken together, lead to kind of secular creationism. I introduce the notion of "adaptive effects" and argue that a focus on the actual physiological and psychological mechanisms that produce adaptations provides a way out of the exaptation dilemma.

We human beings are a very special species. We have, moreover, a very strong desire to be special. In my view, this desire sometimes hinders our attempts to understand our nature and makes various types of creationism attractive to us. I see much of the debate about exaptations in this context. Some years ago I attended a public lecture by Stephen Jay Gould. When the audience was asked to submit written questions for him to answer, mine was: "Professor Gould, given that not all creationists are fools and naïves, why do you think so many of them cite your work in support of their cause?" I asked this question because of my belief that several aspects of Gould's work lead to a kind of creationism.

It is not the creationism of the Bible-thumping preacher, but a subtler set of intellectual propositions, which can lead to the belief in one's scientific respectability, on the one hand, and the view, on the other, that we are so special that, even if we were not divinely created, we must at least be self-created. The first of this set of propositions is the notion of punctuated equilibrium – bursts of evolutionary creativity in small subpopulations of ancestral species that produce new species relatively quickly (Eldredge & Gould 1972). The second is Gould's arguments in *Wonderful Life: The Burgess Shale and Nature of History* (Gould 1989b) that directional selection is of limited importance in evolution and that, if the tape of evolutionary history were replayed, a species like humans would be very unlikely to evolve. The third is the notion of exaptation: a preexisting trait that acquires a new beneficial effect without modification to the phenotype by selection (Gould 1991a). By themselves, each of these notions has some scientific merit. Taken together, however, they promote a romantic view of evolution by natural selection that panders to our desire to be special. The logic is further obfuscated by the use of architectural and (simplistic) anatomical metaphors for complex physiological and psychological adaptations, as well as by the lack of probabilistic thinking. The result is a kind of creationism that is attractive to scientific creationists, and also to those who are attracted by the idea of human self-creation.

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Clarifying and expanding some of the standard terminology (Dobzhansky 1951; Williams 1966) used in the study of adaptation may be helpful for dealing with the concept of exaptation. A *beneficial effect* is an aspect of an adaptation that increases the probability that its carrier's alleles will have copies in succeeding generations. A *detrimental effect* (Crawford 1998b) is an aspect of an adaptation that reduces this probability. Natural selection may be occurring in a population if an adaptation's expected beneficial effects are not equal to its expected detrimental effects. A *function* is a beneficial effect that existed in an ancestral population for an extended period of evolutionary time, and hence is a cause of the evolution of the adaptation. The "thumb-finger" grip that enables us to manipulate the mice on our computers (a beneficial effect), and the same grip which also enables us to inject dangerous drugs (a detrimental effect), affects our current reproductive fitness. Chipping stone tools may have been one of its beneficial effects in ancestral environments, and hence, one of its functions. Normally, natural selection fine-tunes adaptations to operate in expected ancestral environments. Therefore, it is unlikely that a trait can acquire a new beneficial effect without at least some modification by natural selection! Moreover, if it appears that a trait has acquired a new beneficial effect, the most likely explanation is that we do not fully understand its original operation and how that operation contributed to ancestral fitness. Should we call our ability to manipulate the mouse on our computers an exaptation because it contributes to current fitness and because the thumb-finger grip did not evolve to manipulate computer mice? Should we interpret the ability to learn American Sign Language as an exaptation because it contributes to fitness of deaf people but did not exist in ancestral environments? And what about the ability to learn languages, such as Esperanto, that are not natural? Should we interpret our ability to digest Coca Cola as an exaptation because our digestive system did not evolve to digest it? If we do not ask hard questions about how the original adaptation worked, base our logic on architectural and simple anatomical metaphors, and do not think probabilistically, we may conclude that they are exaptations.

However, the thumb-finger grip is not an adaptation to grasp stone tools. It is a set of muscular and nervous integrations enabling us to manipulate a variety of small objects. The language adaptation is not an adaptation to make particular movements of the tongue, mouth, and larynx. It is a set of mental adaptations that enables us to understand, create, and process symbolic information. At the level of adaptation, the digestive system is not a system for digesting particular foods, but a set of biochemical processes for transforming ingested substances into nutrients for an organism. Manipulating computer mice, learning American Sign Language, and digesting Coca Cola are direct products of ancestral adaptations. At the risk of muddying the conceptual waters, I would like to suggest that the term exaptation be replaced by two other terms: adaptive effect and fortuitous effect (Crawford 1998a). An *adaptive effect* of a trait is an effect that contributes to current fitness because its efficacy depends directly on physiological or psychological processes that evolved in the environment of evoluntary adaptedness to carry out similar, though not identical, tasks. A *fortuitous effect* of an adaptation is an effect that contributes to current fitness, but does not call on the physiological or psychological processes that, on the surface, appear to mediate it. Digesting Coca Cola is an adaptive effect of the digestive system. However, Coca Cola is not really a food, and its apparent digestive processing is not a function or adaptive effect of digestion adaptations; it is a fortuitous effect of them.

Finally, although an effect may be a fortuitous effect of one adaptation, it may be a function or an adaptive effect of a different adaptation. Thus, while the benefits of drinking Coca Cola or Diet Coke may not be an adaptive effect of the digestion adaptation, they may be an adaptive effect of, say, the courtship adaptation. Human polyandry, although it may not be a function or adaptive effect of mating adaptations, may be an adaptive effect of adaptations for resource acquisition and control. The concept of adaptive effect focuses attention on how the history of natural selection affected a current trait. In my opinion, that is what is important.

In conclusion, I believe that we have spent too much time bickering about concepts that obscure the study of adaptation, and I hope that the arguments of the target article, which seem sensible to me, put an end to the squabbles. Finally, I hope that those involved in the wrangling will spend some time introspecting on their deep motivations for the incessant attempts to undermine the application of evolutionary theory to the study of human behavior. We live in a troubled world and we need all the help we can get for understanding who we are and why we do some of the things that we do.

Lack of evidentiary criteria for exaptations?

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Abstract: Andrews et al. criticize Gould and colleagues for (1) failing to provide evidentiary criteria for accepting exaptationist alternatives to adaptationist explanations, and (2) seeing exaptations and spandrels as being far more frequent than adaptations in the evolutionary history of modern humans. I argue that the first of these criticisms is wrong, and the second reflects a bias for the classical version of Darwinian evolutionary theory, which Gould was trying to expand by proposing concepts like exaptation and spandrels.

Andrews et al. state that "Gould and Lewontin insist that adaptationists consider alternative hypotheses, but they have not provided any evidentiary criteria for accepting the alternatives that they ask adaptationists to consider" (target article, sect. 1, para. 4). In Gould (2002 p. 1235) we read:

> The relative timings for the origin of a form and for the inception of its current function – as inferred either from the branching points of a cladistic analysis, or from direct knowledge of historical sequences – provide the main criteria for distinction of exaptation from adaptation.

Additionally, in arguing that this distinction can be made in a majority of cases, we read in Gould (2002 p. 1,255) that:

> If direct knowledge of historical sequences from paleontological data established the only path to resolution, then imperfections of the fossil record would preclude resolution at sufficient frequency. But evolutionary biologists can also reach firm conclusions about historical sequences from cladistic reconstructions of phyletic topography based on the distributions of traits among living organisms.

In both of these quotations, contrary to what Andrews et al. say, it is evident that Gould was offering criteria for distinguishing adaptations from exaptations. The two criteria involve (1) comparisons among lineages of current organisms to determine which ones share certain derived characteristics, and which don't (cladistics); and, (2) the historical record as reflected in paleontological data. Now obviously, the paleontological record is going to offer less evidence for evolutionary psychologists interested in understanding the origins of a given behavioral trait than it is for an evolutionary biologist interested in understanding the origins of a physical characteristic. One can wish that this weren't so, and that evolutionary psychologists had access to such data to resolve their arguments, but wishing doesn't make it so. One simply has to acknowledge that making adaptationist arguments in evolutionary psychology is that much more difficult, because the fossil record does not provide the kinds of data necessary for adjudicating arguments over the origins of behavioral traits in the same way that it provides data relevant to the origins of physical structures.

This leaves cladistic analysis as one of the tools that could prove useful in making the distinction between adaptations and exapta-

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tions. Comparative psychology, therefore, assumes a more prominent role in evolutionary storytelling. Even here, however, it may be extremely difficult to perform such an analysis when the character that is chosen is a behavior (e.g., a preference among human males for low waist-to-hip ratios in human females) rather than a structure (e.g., the cross-sectional area of a particular bone). Such analyses can, in principle, establish the historical order of emergence of various characters.

As an example, consider the large and systematic difference in size between male and female spiders in some species (sexual size dimorphism, SSD). It is possible to make an adaptationist argument about why it would be beneficial for male dwarfism to have been selected, but in fact, cladistic analyses shows that in many lines of spiders it was actually female gigantism that has apparently evolved, and that the size advantage of females (dimorphism) in some lines has apparently reversed to monomorphism numerous times in the course of evolutionary history (Hormiga et al. 2000). This shows that the failure to consider these historical pathways can leave one with an overly simplistic and probably erroneous account of the origin of a particular trait. Indeed, Hormiga et al. (2000) argued that the multiplicity of phylogenetic patterns (origins and reversals) for SSD means that "Each pattern must be understood historically before its origin and maintenance can be explained in ecological and evolutionary terms" (p. 435). Adaptationist accounts of human psychological evolution would be strengthened to the extent that they could be more informed by such comparative phylogenetic analyses, which Gould argued were necessary for distinguishing adaptations from exaptations.

Andrews et al. also criticize Gould for seeing exaptations and spandrels as being far more frequent in human evolutionary history than adaptationists may be willing to admit. It is undoubtedly true that Gould was not as quick to jump to an adaptationist argument for the origins or maintenance of human characteristics, as are some evolutionary psychologists. I think that Gould's willingness to see many more human characteristics as exaptations and spandrels was a reflection of his program of expanding classical Darwinian theory to admit these extra-selectionist mechanisms into a strictly mutation-proposes/selection-disposes account of evolution. If one doubts that evolutionary psychologists have not wholeheartedly embraced exaptationist accounts of human charactereristics, one need only read in Buss et al. (1998) that "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." (p. 545).

If the types of evidence necessary for distinguishing among "aptations" (Gould 2002) are difficult to come by in the case of the evolution of human traits, then one may be left with an adaptationist bias for constructing one's evolutionary stories. This is precisely the nearly exclusive selectionist bias that Gould was arguing against in proposing the concepts of exaptation and spandrel. Evolutionary storytelling, whether it is focused on adaptations, or exaptations, or spandrels, will always make use of principles like fitness maximization, optimal design, and special design. It is analyses based on historical and cladistic criteria that, Gould argued, would ultimately be necessary to separate adaptations from exaptations, and which appear to be difficult to find in current evolutionary arguments about human behavior.

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Does past selective efficacy matter to psychology?

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Abstract: Andrews et al. subscribe to the view that distinguishing selectionist from nonselectionist hypotheses – or, distinguishing adaptations from mere spandrels or exaptations – is important to the study of psychology. I offer three reasons for thinking that this view is false; that considerations of past selective efficacy have little to contribute to inquiry in psychology.

Suppose you claim of some trait that it is an adaptation (that it was modified by past selective pressures to serve some ancestral function), and I claim that it is not an adaptation but merely a spandrel (that it was not modified by past selection for any ancestral function). What sorts of evidence differentiate our claims? Andrews et al. are concerned with answering this question. The concern is to describe standards of evidence that distinguish selectionist from nonselectionist hypotheses. This, according to evolutionary psychologists, is important to the study of psychology.

I want to challenge this last claim. I am skeptical that the study of psychology requires, or even benefits much from, standards of evidence that enable us to distinguish adaptations from nonadaptations. I grant that evolutionary theory can contribute in various ways to psychology and I cite one example below, but I deny that claims concerning past selective success or failure can contribute much. Three considerations are relevant.

1. Everyone agrees that adaptations are functional relative to some past selective regime and that spandrels are functionless relative to some past selective regime. Both *adaptation* and *spandrel* refer to categories of traits classified on the basis of past selective efficacy or inefficacy. If the current environment differs from the past regime, or if the psychological economy of descendent organisms differs from that of ancestral organisms, the functional status of these traits may differ as well. Everyone agrees, therefore, that present functional standing cannot be inferred from past selective success or failure.

Why, then, the concern to distinguish selectionist from nonselectionist hypotheses? If the aim of psychology is to uncover the current architecture and functioning of our mental capacities, why worry about the precise causal mechanisms that drove evolution among distant ancestors? If we know, for example, that female preference for male scents changes throughout the menstrual cycle, and if we can trace the implications these changes have on our psychology, why should we *qua psychologists* care whether this preference was adaptive or merely a spandrel? We already know that this trait has a function in our current psychology; its past functional standing seems superfluous.

Of course, historical knowledge is sometimes of value to psychology. Recent neurological studies of emotional systems are illustrative. Panksepp (1998) claims that several subcortical structures in humans are homologous with morphologically similar structures in other mammals. The value of this claim consists in the broadening of relevant data: We can experiment on rats and cats to support hypotheses about homologous structures in humans. There is, however, no requirement that we distinguish selectionist from nonselectionist hypotheses. One trait is homologous to another just in case both descended from a common ancestor; discovering the precise mechanisms that drove the evolution of these traits is irrelevant.

2. The response, I suppose, is that although conjectures about past selection cannot support any direct inferences about our current cognitive architecture, they nevertheless may suggest a range of plausible hypotheses. But even this is doubtful. First, everyone will agree that *general* claims about our evolutionary past can be suggestive, even if unexciting: *Homo sapiens* evolved and hence we probably have cognitive capacities for finding food, warmth,

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and mates; *homo sapiens* is related by descent to other primate species and hence we, like other primates, probably have capacities for participating in social dominance hierarchies; and so on. Once again, however, there is no need to distinguish selectionist from nonselectionist hypotheses. The mere fact that we are closely related by descent to certain other species is enough to generate the conjectures.

Second, as Andrews et al. emphasize, the evidence required to substantiate claims about past selective success is usually difficult to ascertain, especially for psychological traits. Only a convergence of evidence based on special design, optimality, and comparative studies will do the job. Since we are unlikely to achieve such convergence for a wide range of psychological traits, the search for adaptations is hard to justify. Moreover, insofar as a convergence is unlikely, we should wonder why hypotheses in evolutionary psychology ever strike us as plausible. Is it because the evidence really converges on an adaptationist hypothesis? Or is it, instead, that certain general claims about our evolutionary history, without considerations of past selection, are plausible on their face?

Third, and most pressing, all of the traits discussed by the authors illustrate the following fact: To inquire into the past selective success of any trait – to discover special design, generate optimality models, construct comparative hypotheses – we must already know a good deal about the trait's architecture and function. With respect to psychological traits, we must have already accomplished, to a significant extent, the central task of psychology to commence with the question concerning past selective efficacy. In the case concerning scent preferences and the menstrual cycle, we would have no idea what to look for in the historical record if we had not first discovered the function of this trait within our psychology. Speculations concerning past selective success, therefore, do not generate important psychological hypotheses; to the contrary, we must already have well-confirmed psychological hypotheses before we can seek a convergence of historical evidence. (See Davies 1996; 1999.)

3. A further problem is that the methods employed in evolutionary psychology flout two important lessons from the history of modern science. The first (i) is that progress in understanding natural systems is accomplished by analyzing inward, tracing higher-level systemic capacities to the structured or integrated effects of lower-level mechanisms (Bechtel & Richardson 1993; Davies 2001). The second (ii) is that as inquiry proceeds – as we uncover lower-level mechanisms – the categories in terms of which we initially understand the higher-level capacities of the system will likely be revised or replaced.

Evolutionary psychology, like cognitive psychology generally, aims to discover the information-processing algorithms that underwrite our psychological capacities. Studies of the brain are accorded secondary importance at best, given the assumption that such algorithms can be implemented in diverse hardware. The obvious problem, however, is that distinct sets of algorithms can produce the same higher-level capacity; we all learned, for example, more than one procedure for solving division problems. To show that one algorithmic description is in fact correct, we must analyze further and confirm that the requisite lower-level mechanisms exist in the system. Hence the importance of point (i).

Evolutionary psychologists further claim that the best way to discover the relevant algorithms is to first develop a functional taxonomy – a list of tasks that our psychological capacities regularly fulfill – based on considerations of past selective efficacy. The strategy is to trace the selected functions of our psychological capacities, that we may generate hypotheses concerning the algorithms that currently implement those capacities. This, however, conflicts with point (ii). The lesson of (ii) is that we should positively *expect* that progress in psychology will force us to revise or replace our current categories, at least for those capacities the neurology of which we do not yet understand. To the extent, therefore, that evolutionary psychologists work with categories unconfirmed at the level of neuro-chemistry, they may well be trying to trace the selective history of things that, as presently conceived, do not exist at all.

Phylogenetics and the aptationist program

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Abstract: The aptationist program includes attempts at sorting adaptations from exaptations, and therefore requires knowledge of historical changes in biological character states (traits) and their effects or functions, particularly for nonoptimal aptations. Phylogenetic inference is a key approach for historical aspects of evolutionary hypotheses, particularly testing evolutionary scenarios, and such "tree-thinking" investigation is directly relevant to the aptationist program.

Andrews et al. do not use the term *aptation,* although Gould and Vrba (1982) judiciously explain that

> The general, static phenomenon of being fit should be called aptation, not adaptation. (The set of aptations existing at any one time consists of . . . the subset of adaptations and the subset of exaptations. This also applies to the more inclusive set of aptations existing through time . . .). (p. 6)

Following this terminology, I use the term *aptationist program* to name the tentative identification of different kinds of aptations, including sorting adaptation from exaptation. The term *aptationism* avoids the connotation of a priori preferences implied by adaptationism and exaptationism.

While emphasizing "special design" evidence for adaptation, Andrews et al. also acknowledge the "growing consensus" that phylogenetic analyses are useful to the aptationist program, but they appear to limit the scope of phylogenetics to what they call *the* comparative approach. According to the authors' "standard 1," phylogenetic comparisons aim only at demonstrating correlation between trait variation and environment in numerous related species, and show some limitations (weak evidence for adaptation, irrelevance for unique traits or species, and so forth). They suggest completing this approach by comparing effects of traits in distant lineages (target article, sect. 3.3), and underline the lack of clear view of some historically contingent constraints (sequence of events in a tinkering evolution; sect. 3.1.4.2). The authors apparently overlook the more obvious, direct and central, possible contribution of phylogenetics to the program: testing historical aspects of evolutionary hypotheses.

In fact, equally well fit ("designed") adaptations and exaptations differ, by definition, only by the evolutionary history of the concerned biological traits and effects. Unchanging traits with new effects make exaptations, while function-selected trait changes constitute true adaptations. Aptation resulting from both processes may be equally fit; thus, the history of changes makes all the difference in the general case. The problem boils down to reconstructing a temporal sequence of events: that is, an evolutionary scenario. The phylogenetic tree is by excellence the "time machine" used by contemporaneous comparative biologists for such scenario inference (Carpenter 1989; Coddington 1988; Deleporte 1993; Grandcolas 1997). Among Grandcolas et al.'s (1994) four arguments for phylogeny use (assessing homology versus homoplasy, polarity of change, time lag between changes in different features, and differential cladogenesis), the three former correspond to this approach, documenting temporal succession of relevant changes. This is straightforward for optimally designed traits, which could sometimes be misleadingly optimal exaptations, but is even more relevant for nonoptimal adaptations for which the "optimal design" criterion emphasized by Andrews et al. fails.

I agree with the authors that phylogenetics in itself cannot

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demonstrate adaptation. Particularly, demonstrating fitness is a population biology program, not a phylogenetic one (Grandcolas & D'Haese 2003). But phylogenetics allows us to test the historical dimension of adaptation, which must be a beneficial *innovation;* therefore, although phylogenetic scenario testing will not document trait-associated fitness, it can refute adaptational hypotheses for reasons of historical incompatibility (Coddington 1990). Simply, an adaptation should logically not appear in time *before* the trait it is supposed to improve on, and exaptation must occur *after* the appearance of the trait without the relevant effect. Phylogenetic evolutionary scenario optimization can test for these required polarity and time lag between appearance of trait and delayed effect (Grandcolas et al. 1994). Adaptation and exaptation are evolutionary novelties (apomorphies), which cannot logically be ancestral to their own supposed origins (corresponding plesiomorphies).

Phylogenetic historical inference may also be crucial for demonstrating evolutionary homology (similarity by descent) between occurrences of a supposedly same trait. Problems with the "vertebrate bones" example in Andrews et al. (after Ruben & Bennett 1987) illustrate this point. The authors argue that the calcium phosphate skeleton (CPS) of vertebrates could be adaptive to high metabolism despite its nonoptimal sensitivity to lactic acid compared with the calcium carbonate skeleton (CCS) of many nonvertebrate organisms. Andrews et al. do not document any historical continuity between CCS and CPS; and in fact, close relatives of vertebrates like Hemichordates or Urochordates have no obvious skeleton, and much less high metabolism. The frequency argument ("almost always" in invertebrates) is plainly irrelevant: only phylogenetic topology allows historical inference. Therefore, there seems to be room for complete historical disconnection between CCS and CPS. Under this scenario (which is phylogenetically testable), not only would the hypothesis of metabolic adaptation from CCS to CPS be refuted by historical evidence, but CPS could even be an exaptation, possibly constrained from a plesiomorphic CP metabolism already present before the appearance of vertebrates skeleton and high metabolism. Protection against erecting "just so" evolutionary scenarios through ad hoc choice of convenient taxa in scattered lineages is a major contribution of the phylogenetic program to evolutionary biology (Brooks & McLennan 1991; Coddington 1990).

Andrews et al. note that some highly specific traits may escape detailed comparative investigations. Admittedly, this may be particularly frustrating for some human autapomorphies, possibly doomed to remain unsorted aptations. Alternatives to phylogenetic historical inference (paleontology, archaeology, historical documents; Tattersall 2002) are not always available and often only indirectly adapted to behavioral and cognitive investigations. For such problems, the phylogenetic program suggests the "character states definition and delineation" issue, for example, improving analysis of physiological structures underlying behavior and cognitive processes, and hence possibly turning a unique integrative "trait" into components, some of which, we can hope, show wider taxonomic distribution.

Symptomatically, Andrews et al. (and their ambiguous "skeleton" source paper) present no real or theoretical phylogenies to support their comments. By contrast, papers advocating phylogenetics are stuffed with trees, both in the so-called cladistic approach (Brooks & McLennan 1991; 2002; Grandcolas 1997) and the comparative method approach (Clutton-Brock & Harvey 1984; Harvey & Pagel 1991; Martins 1996). The former makes positive use of phylogenetic historical evidence, with direct relevance to the aptationist program; the latter aims at neutralizing phylogenetic signal ("phylogenetic inertia") to test evolutionary models through "clean" ecological correlation. Although both have limitations, and improved synthesis is desirable, "tree-thinking" methods stand firmly at the core of comparative (hence evolutionary) biology because special design qualifies aptation, whereas only history can efficiently sort exaptation from adaptation.

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Is empirical imagination a constraint on adaptationist theory construction?

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Abstract: Andrews et al. present a form of instrumental adaptationism that is designed to test the hypothesis that a given trait is an adaptation. This epistemological commitment aims to make clear statements about behavioural natural kinds. The instrumental logic is sound, but it is the limits of our empirical imagination that can cause problems for theory construction.

Andrews et al. have proffered a form of instrumentalism that renders adaptationism the experimental hypothesis, and exaptation, constraint, and spandrels the null hypotheses, in a universe of only four sources of design. They provide evidentiary criteria that can be used to determine possible adaptations. We offer an example to demonstrate their useful metric:

Stimulus equivalence (SE) involves the formation of derived relations between a set of stimuli that resembles a mathematical equivalence set. Such sets exhibit the properties of identity, symmetry, and transitivity (Sidman et al. 1982). In the behavioural sciences, the interest is in the spontaneous emergence of these relational properties – in the absence of formal reinforcement or informational feedback – after a minimum number of trained links between the stimuli have been established, typically by employing an arbitrary matching-to-sample procedure. For example, two three-member classes of A1-B1-C1 and A2-B2-C2 might be formed as follows. First A1-B1 and A2-B2 relations would be trained, by means of informational feedback. The first stimulus mentioned in a pair – such as A1 – denotes the sample stimulus, and the second – B1 – constitutes the correct comparison stimulus, following A1, to choose from the array of comparison stimuli (here just B1 and B2). In a series of individual trials, participants learn to select B1 from this array when A1 has been presented, and B2 when A2 is the sample. Then B1-C1 and B2-C2 are similarly trained, the Bs now serving as samples and the Cs as comparisons. Any kind of stimuli can be used in this paradigm, and the relations between them are usually purely arbitrary, to be learned within the experiment, and independent of prior experience.

Formation of an SE class requires satisfying conjointly, in unreinforced tests, the three criteria listed above. *Identity,* – such as selecting A1 when A1 and A2 are presented as comparisons after A1 has served as sample – is normally assumed in humans. Presenting B1 as a sample, with A1 and A2 as comparisons, constitutes a test of *symmetry* as the subject has to pick A1 from an array, inverting the trained relation. Other tests of symmetry would be B2-A2, C1-B1, and C2-B2. Presenting A1 as a sample with C1 and C2 as comparison tests *transitivity,* to achieve which the subject has to choose C1, and similarly for A2-C2. Finally presenting C1 as sample, with A1 and A2 as comparisons, and the subject expected to choose A1, constitutes a combined test of symmetry and transitivity.

Although most laboratory animals can acquire the basic trained relations of arbitrary matching-to-sample, the general consensus within the field is that the ability to form SE classes is peculiar to humans. Consequently some theorise that SE emerges as a by-product of learning to name (Horne & Lowe 1996), others that SE is a necessary precursor to language (Dickins & Dickins 2001). Both camps see a fundamental relationship between symbolic be-

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haviour and SE because symbols are arbitrary representations tied to classes of objects, events, and states of affairs. In this way, a symbol and its relata constitute an SE class. In this commentary we will regard any putative SE *mechanism* as a rudimentary symbol machine. Symbols have uses not only in language, but also in arithmetical processing, mathematical reasoning, and so forth. It is not inconceivable that SE had some cognitive benefit for our species. How might we apply Andrews et al.'s metric to further this conception?

Although SE appears to be human-specific, Tonneau (2001) argues that SE might be a form of functional equivalence (a term used to refer to a group of stimuli which share the same behavioural function, either because they share a common training history, or because of some other kind of transfer of function between them), which is seen in other species. If this is true, it could push our interest further back in phylogenetic time. Alternatively, SE might represent an exaptation of an original functional equivalence mechanism. Comparative data must be used in conjunction with other criteria, such as *special design*, which is the most cogent criterion according to Andrews et al. But special design does not remove the possibility that the trait resulted from an exapted learning mechanism. However, Andrews et al. argue that the property of domain-specificity, if demonstrated, might lend some weight to an adaptationist hypothesis. Developmental specificity indicates a biased outcome for the mechanism involved, and therefore a specific selective story. This is not straightforward for SE because it is empirically difficult to test prelinguistic infants on a matching-to-sample or related paradigm, and there are few ontogenetic studies of this ability. Horne and Lowe (1996) claim that early word learning instils SE, but the absence of prelinguistic data renders this no more than a speculation. But, even if we could overturn this empirical limitation, would we still be able to invoke domain-specificity as a useful criterion?

If an SE *mechanism* is a rudimentary symbol machine, SE might have been coopted to linguistic, mathematical and other symbolic behaviours. The use of the term *coopted* is deliberate – if SE is the bedrock of such behaviours, those elements that differentiate, say, linguistic symbols from general abstract SE classes could be the product of later evolutionary innovations, that is, language-specific mechanisms. *As such, any apparent exaptation of function might not lie within the original mechanism at all, but within the subsequent processing of its output by new mechanisms evolved for highly specific functions.*

In other words, a linguistic symbol, at its most basic, is part of an SE class, and the same is true for a mathematical symbol, and so on. The SE mechanism is still just producing SE classes as "before," but this time in a different domain. And this is critical, for the notion of domain-specificity used here is of a reasonably coarse grain; SE classes can be formed between any kind of stimuli but possibly only under certain conditions. Words are more than rudimentary symbols, having grammatical properties endowed by language-specific mechanisms. However, when we see linguistic behaviour we are also seeing SE behaviour, and it is this that presents us with a problem. The predominance of high-order symbol-crunching mechanisms might make the telling of the developmental story about SE empirically intractable, just as linguistic and mathematical effects might mask SE effects in the lab. This might be only because of the reliance on informational feedback in current empirical scenarios.

We are making a point about exapted learning mechanisms. Andrews et al. argue that a learning mechanism will initially be selected within a particular problem-space. This mechanism can then be exapted to output different functions leading to the mechanism producing either the old and the new function, or only the new. However, looking at the problems facing the SE investigation, we have what is potentially an original learning mechanism, for a relatively broad problem domain, with an output that has subsequently become the input for novel cognitive mechanisms. The function of this SE mechanism has not changed, but its outputs might have been parasitised. Nonetheless, it might well be that the possession of an SE mechanism sets the initial conditions for language evolution and so on. The question of the adaptive status of a putative SE mechanism still remains – a problem that perhaps represents the limitations of our empirical imagination.

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Ontology *is* the problem

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Abstract: Andrews et al. claim that Gould and Lewontin's critique of adaptationism is largely epistemological rather than ontological. In this commentary I argue that, on the contrary, the deepest part of their critique is ontological, raising concerns about the existence of the traits that are the subjects of adaptationist theorising. Andrews et al.'s failure to address this problem undermines their defence of adaptationism.

Andrews et al. understand Gould and Lewontin's (1979) classic critique of adaptationism as largely epistemological rather than ontological. This raises issues of how we can know that a trait is an adaptation or, more specifically, has a given function. In the absence of proper decision criteria for evaluating relevant evidence, a theorist may incorrectly attribute a function to a trait or incorrectly fail to attribute a function to a trait. Andrews et al. make impressive and creditable efforts to specify these criteria.

The trouble, I think, is that the most profound part of Gould and Lewontin's critique really *is* ontological. The deepest difficulty with adaptationism lies in the nature of the traits that are its subject matter. Andrews et al. acknowledge that the definition of a trait is not straightforward, but they make no serious effort to grapple with the difficulty. A trait is generally considered to be an adaptation if it has some effect that is responsible, through natural selection, for its presence in the organism. The effect in question is typically referred to as its *function.* These definitions evidently reflect an idealisation. Any feature will surely have numerous effects, and many or all of these will have some effect on the fitness of the organism and hence on the prevalence of the trait. We should therefore be content to identify those features that have some effect that is of predominant importance in explaining their prevalence. Let us call any feature whatsoever of an organism a trait, and traits that satisfy this last condition, adaptations. Then the real force of Gould and Lewontin's critique is not the epistemological claim that it is difficult to tell whether a trait is an adaptation (though it is), but rather the ontological thesis that most traits are not adaptations.

Of course, as stated, the point is completely uncontroversial. There are infinitely many features of organisms and most of them would not strike even the most rabid Panglossian as likely to be adaptations. Think, for example, of having exactly 250,000 hairs, being smaller than a planet, having a scar above the left eye, or a name beginning with D. Amongst these traits, how do we distinguish the ones that have a good chance of being adaptations and the adaptive significance of which is therefore worth investigating? Andrews et al. note that an adaptation must have effects, but that doesn't obviously eliminate the examples just cited, and it certainly won't do the work needed here. The answer, I suppose, is going to come to intuition, perhaps tutored by proper biological experience. The thrust of Gould and Lewontin's argument, then, is that what may seem a plausible trait to qualify as an adaptation, will very often fail to be one – even to properly tutored intuition. And the reasons for this are widespread and systematic.

One kind of trait that is not an adaptation is illustrated by the example of a spandrel. A spandrel (at least as the example was conceived by Gould and Lewontin) is an epiphenomenon or byprod-

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uct of the properly functional features of a building. Similarly the chin, which might easily be supposed to have had some adaptive function in the transition from apelike and chinless ancestor to modern human is, according to Gould and Lewontin, an epiphenomenon of other changes in facial bone structure and is quite innocent of adaptive significance.

But simple, spandrel-like features point to a more pervasive problem: the problem of organismic integration. I remarked that the core picture of an adapted feature is an idealisation. One example of a trait offered by Andrews et al. is the hand. It plays a part in countless kinds of behaviour, is composed of a large number of distinguishable parts, and is richly connected to other parts of the body, especially the brain. Clearly, the hand will have very many selective effects, many of which will contribute to the fitness of its possessor. Equally clearly, the hand is based on preexisting structures that constrain in important respects its possible modes of operation. It is a complex mixture of exaptation and adaptation. But it is not at all clear why we should expect the process of adaptation to provide us with a means of atomising the whole organ into any determinate set of discrete adaptations. It seems unlikely, for instance, that the little finger is an adaptation, though certainly it plays a part in many of the things humans do with their hands and is, broadly speaking, functional.

What goes for the hand goes much more clearly for the brain and behaviour. The suggestion that the brain is a highly integrated structure is not to be confused with the curious accusation by some extreme adaptationists against their critics that the mind is a blank slate. It is just that, as with the hand, we know that the parts of the brain must be highly integrated, and integrated in such a way that it cannot be assumed that distinguishable parts should have discrete and specific functions (in the very specific sense of function assumed by adaptationists, as opposed to the looser sense in which the little finger, say, is surely functional). This is where justifiable scepticism about such things as the hypothetical waist-to-hip ratio module originates. There is not much reason to suppose that the mind can be atomised into such things at all, and the kind of evidence offered in support of this particular part is quite inadequate to the disclosure of a discrete adaptation. Here, in addition to the difficulties in atomising the traits correctly, as was true of the hand, we have doubts about whether the traits, never mind adaptations, exist. I'm sceptical whether anything less than identification of a neurophysiological structure with the demonstrable function of assessing waist-to-hip structures would overcome this problem.

So, in summary, though Andrews et al. make some sensible moves towards addressing some of the epistemological problems with adaptationism, they have little to contribute to removing the more basic ontological problem. And without doing that, there is little reason to suppose that the adaptationist program has much to discover.

"Just *not* so stories": Exaptations, spandrels, and constraints

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Abstract: It is anthropomorphic to speak of Nature designing adaptations for a specific function, as if with conscious intent. Any effect constitutes an adaptive function if it contributes to survival and to reproduction. Natural selection is blind to what might have been the original function. Mutations arise by purest accident and are selected based on whatever fortuitous effects they might produce.

The target article constitutes a long-overdue response to the critics of the adaptationist program, who have charged both that the prevailing evidentiary standards for claims of adaptation are too lax, and that adaptationism as a research strategy is fundamentally flawed. However, the same critics that have correctly warned evolutionary theorists against creating adaptationist "just so stories," are often guilty of creating arbitrary "just *not* so stories" by uncritically accepting *any* alternative explanation as long as it is an *not* an adaptationist hypothesis, even if it lacks the persuasive force of a plausible causal mechanism (see Figueredo & McCloskey [1993] for a critique of one example of this kind of error; see also Rowe [1993] for a description of similar errors in critiques of behavioral genetics). Although Andrews et al. endorse what Chamberlin (1897) called "the method of multiple working hypotheses," and Platt (1964) called the method of "strong inference," they insist that it must be followed in a completely even-handed way. No theories or hypotheses should be given any preference, and they must all be held to an equivalent level of critical scrutiny. Andrews et al. are completely correct in reminding us that no alternative hypothesis, whether classifying a trait as an adaptation, exaptation, or spandrel, should be treated as the default inference in the absence of supporting evidence.

On the other hand, it should not be conceded that adaptationists are generally lax in their evidentiary standards. Since Darwin, a major activity of evolutionary biologists has been demonstrating that the traits of organisms are in fact adaptations (Mayr 1983). Some traits offer obvious adaptive significance (e.g., eyes), while others offer only subtle clues (e.g., beak width and length). One *must* not, and generally *does* not, accept an explanation for the adaptive value of a trait just because it is plausible and charming (Gould & Lewontin 1979). Instead, there are a variety of methods that evolutionists have used and currently use to test adaptationist hypotheses. These include experiments, such as those with tephritid flies mimicking the spider that preys on them (Greene et al. 1987; Mather & Roitberg 1987); observational studies, such as one looking at the differences in retreat site selection of garter snakes versus the thermal consequences (Huey et al. 1989); and the comparative method, such as one study where the size of different bats' testes were compared in accordance with the sperm competition theory (Hosken 1998). These studies and countless others demonstrate that adaptationism involves more than telling "just so stories." By using such techniques carefully, one is able to show that an adaptation exists or does not exist through sound scientific methodology.

Another troubling point has to do with the seeming anthropomorphism that has crept into the debate about the "real" function of an adaptation. We speak of Nature, personified, "designing" adaptations for a specific function, as if with a conscious intention. Nevertheless, Andrews et al. correctly point out that what distinguishes an adaptive function is that its effect "either enhances or inhibits the replicative success of the genes from which it develops" (sect. 2.2, para. 1). This means that *any* effect constitutes an adaptive function if it contributes to survival and reproduction. No intelligent design is implied in natural selection. Nature is "blind" to what might have been the "original" function of an adaptation. Beneficial genetic mutations arise by blind idiot luck and not providence. They are "selected" by Nature to increase or decrease in the population based on whatever fortuitous effects they might happen to have by purest accident. This is not only true of exaptations, but also of adaptation.

Gould and Vrba (1982), however, restrict the term *adaptive function* to that specific function for which natural selection has shaped the trait in question. Andrews et al. quote them as stipulating that any additional "exapted" effects can be distinguished from the one true adaptive function because natural selection has not "perfected" the trait for the new effect. This is a surprising stipulation coming from such vocal opponents of optimality theory. Whatever happened to the "constraint" argument? Is it possible that the trait cannot be "perfected" for the new effect, because it might interfere with the original effect or function for which it might still be under positive selection? For a variety of reasons, an adaptation might not have been "perfected" by natural

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selection for either its original *or* its subsequently acquired functions.

Nevertheless, if the term *beneficial* means that it confers an advantage in natural selection, then any current beneficial effect is a valid candidate for an adaptive function, because it may have caused the frequency of the gene(s) in question to increase or decrease, whether or not the adaptive trait was secondarily modified. If natural selection occurred for the trait even partially based on the reproductive impact of the new effect, then that effect must be considered one of the current adaptive functions of the trait. If the new effect of an adaptive trait is reproductively relevant, then what Darwin called "nature's continuous scrutiny" must be affected by it because it is completely blind to the trait's original "purpose." The original argument by Williams (1966) regarding the distinction between adaptive functions and epiphenomenal effects, applied to effects which were deemed "beneficial" by some (to improbably high levels of organization) but which were, in fact, irrelevant to natural selection.

Perhaps a final point should also be made regarding the heuristic value of the adaptationist program. Eschewing "naïve falsificationism," Lakatos (1970; 1978), a Neo-Popperian philosopher of science, distinguished a progressive from a degenerating research program as one that "adds empirical content" by making novel predictions while "employing fewer primitives" or ad hoc assumptions. By that more sophisticated standard, the adaptationist research program has done quite well in recent decades, despite premature rumors of its untimely demise. The exaptationist research program, if there is anything even worthy of the name, has yielded very little new knowledge in comparison because of its inability to make novel predictions.

Towards an evolutionary pluralism? The need to establish evidentiary standards and avoid reification of assumptions

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Abstract: The adaptationist and exaptationist programs overlap in their need for a pluralistic approach to understanding evolutionary change, and Andrews et al. effectively illustrate the methodological confounds of these approaches. However, the current critique of adaptationism, especially in the arena of human behavior, rests on the tendency to rapidly reify adaptationist hypotheses prior to broad evidentiary consensus across relevant disciplines.

Andrews et al. do a commendable job of outlining the problematic components of the adaptationist paradigm and effectively illustrate how similar issues arise within an exaptationist one. Their call for consensus on evidentiary standards and the inclusion of adaptationist, exaptationist, and other approaches in a pluralistic program deserves repeating often and vociferously. The structure of their article will facilitate its use as a teaching tool in advanced undergraduate and graduate courses. Of particular importance is the authors' stressing of the complexity of attempts to disentangle the numerous adaptations, exaptations, spandrels, and other epigenetic effects that interconnect to produce complex behavior. The emphasis on the role of exapted learning mechanisms (ELMs) and their ability to mislead hypotheses based on tight-fit is a strong contribution. However, there is a problem with the author's treatment of "beneficial effect" as an assessment tool; not because of the reason they introduce, but rather because even if a trait appears to have a beneficial effect, it still must be able to explicitly tie to some measurable increase in reproductive success. The "beneficial effect" scenario is amongst the most misused of the adaptationist approaches for this very reason.

Despite the authors' thorough treatment of the methodological confounds of adaptationism as discussed by Gould and Lewontin (and many others: Futuyama 1986; Kitcher 1985; Tang-Martinez 1997, for example), they miss a main component in the critique of the adaptationist paradigm. The heart of the critique goes beyond the specific adaptationist hypotheses and directly to core assumptions in the adaptationist paradigm.

In keeping with the trend in evolutionary psychology, Andrews et al. place the special design standard as the flagship method for inferring the function of a trait. They emphasize how the special design standard and its related developmental specificity are strong tools, especially when it is difficult to see how an ELM could account for a set of empirical evidence. This illustrates the underlying problem with adaptationist assessment of the evolution of behavioral patterns in humans. Frequently, reified hypotheses are used to construct experiments that produce differences in behavior. These differences are then assumed to represent empirical evidence of functional differences. G. C. Williams (as quoted in the target article, sect. 3.1.6, para. 2) stresses that explanation through adaptation be used only as a last resort after all other explanatory options have been examined (Williams 1966). Part of Gould and Lewontin's (and others') critique is that adaptationists move too quickly in their assertions that all other explanations are untenable.

This use of examples that assume a certain set of "facts" as a baseline to construct explanations (which are, in most cases, viable, testable, hypotheses) is at the core of the modern critique of the adaptationist perspective. This critique is illustrated via two examples used in the article, the waist-to-hip ratio (WHR) and its relationship to mate choice, and the preference of females for symmetrical men. Andrews et al. refer to a series of publications in which there is a debate over whether WHR is an actual component of men's mating preferences – and then go on to say that in their article, "for instructional purposes only," they will assume that it is a real preference (target article, sect. 3.1.3). Frequently, in adaptationist studies, an assumption sets the baseline for what questions are to be asked regardless of a proviso early on as to the possibility that this assumption might not be a true pattern/fact. If there is significant scholarly contention published in peer-reviewed journals, then it cannot be assumed as a starting point that WHR is a "real" evolutionary trait. Here, the assumption is that particular components of male and female differences in body shape are adaptations (i.e., differential reproductive success is conferred by the phenotypic effects of a variable underlying genotype relative to pelvic morphology and fat deposition patterns resulting in the WHR). The first step in asking questions about mate preference and body shape would then be to find out what factors go into body shape and what the degree of variance in body shape across populations is, and to construct an assessment tool to examine the effects of body shape relative to reproductive success for a subset of a population (preferably the population that you would then go on to test for mate choice). Pond (1997) reports that the particular patterns of adipose tissue distribution in human females is probably not an adaptation to energy storage for reproduction, and that therefore it is not clear that the WHR is a measure of potential reproductive success.

In the second example, the authors suggest that the "pattern" of relationship between body symmetry and mate choice is hard to explain by any means other than special design (see Gangestad & Thornhill 1997a). However, components of this "pattern" would not meet the evidentiary standards of many evolutionary biologists. For example, Rhodes et al. (2001) report that men with more symmetrical faces are perceived to be healthier. However, they also report that facial symmetry did not correlate with actual health. Thornhill and Gangestad (1999) report a number of confounding variables, such as an overriding female preference for men who bathe regularly and a preference for T-shirts with no male scent on them, in addition to their highly interesting findings that 13 ovulating college students did prefer the scent of men with reduced Fluctuating Asymmetry (FA). Although there is evidence that FA may play a role in mate choice in human populations (see

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Gangestad & Thornhill 1997a), many of the studies on FA are based on small sample sizes and frequently focus on data collected from undergraduate college students. I do not mean to imply that these studies are not valuable or that they do not provide insight. However, they do not equal a species-wide pattern of behavior that can then be used as a basal datum when constructing hypotheses about human behavior. It is the weight given to some starting point assumptions in the adaptationist perspective that is frequently the underlying "just so story."

I look forward to using Andrews et al.'s article in advanced classes as part of discussions on differing paradigms in evolutionary approaches. I agree that some consensus on evidentiary standards is needed (maybe via a set of interdisciplinary symposia?). The investigation into the evolution of human behavior is an area of rapid change and improvements in methodology. This may be the appropriate time to truly move beyond discrete paradigms into a broader pluralistic approach.

Special design's centuries of success

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Abstract: The fitness maximization standard incorrectly assumes that most adaptations have high heritablility, and it imposes the difficult requirement that correlated phenotypic and environmental contributors to reproduction be controlled for. Despite infrequently recognized problems, the special design standard is the foundation of the spectacular successes of modern medicine. It also suggests that the ancestral environment provides a window into the functioning of the brain.

I will make some technical points, and then offer more general comments. First, the technical points:

The fitness maximization approach for identifying adaptations (target article, sect. 3.1.2) typically interprets a significant positive correlation between the presence (or high or optimal levels) of an assumed-to-be-heritable trait and a fitness proxy (number of children or grandchildren) as signifying that the trait is adaptive. Andrews et al. list three problems with this popular approach; here are two more:

1. The approach assumes that a reasonable sample of a population will vary in the trait, but this assumption is unwarranted. The heritability of most adaptations (especially complex, multigene adaptations like hearts and lungs) is zero, or close to it (see Tooby & Cosmides 1990a; 1990b; and Hagen 2002 for an explanation).

2. Offspring are the end result of the functioning of the entire organism interacting with its environment, so virtually *every* functional attribute of the organism and *every* reproductively relevant aspect of the environment contributes to the fitness proxy. Consequently, even in the very rare cases where a sample of organisms varies in a possibly adaptive trait, numerous possible covariates must be controlled for to determine whether trait variance accounts for reproductive variance.

Whereas the fitness maximization approach focuses on the end of the causal chain linking adaptation to reproductive outcome, the design approach focuses on the beginning of the causal chain; here, the action of natural selection can be discerned much more easily because the phenotype will be specially configured to effectively transform the environment in some reproductively enhancing way – sure evidence for natural selection. By focusing on the end of the causal chain – actual reproductive outcomes – the fitness maximization approach must assume that the environment has not changed in any significant way from the environment of evolutionary adaptedness (EEA); it must hope that sufficient variation exists in the population; it must control for correlated processes that might affect reproduction; and it still provides no information about what the trait in question does.

Despite its successes, the design approach can fail spectacularly. One example: Evidence of design clearly identifies human bipedalism as an adaptation, but the relevant selection pressures are not at all obvious, nor does the evidence-of-design philosophy provide much guidance (though increasingly detailed functional analyses of bipedalism further constrain the possible solutions). Considerable theoretical attention has been devoted to functional design, the first link in the causal chain leading from phenotype structure to reproductive outcome, but subsequent links are usually lumped into the category "reproductive problem" or "selection pressure." To address rare failures, such as understanding the evolution of bipedalism, adaptationists must focus more theoretical attention on the causal chains leading from adaptations to reproduction.

A general observation: Andrews et al.'s fine article may inadvertently have left some readers with the impression that adaptations are difficult to identify and that few have been discovered, especially in humans. In fact, modern medicine is founded on the functional analysis of humans and human pathogens. Thousands of adaptations have been identified at spatial scales ranging from angstroms (e.g., enzyme structure) to meters (e.g., skin). Every bone, organ, tissue, cell-type, and protein is a specialized structure that evolved by natural selection, whose function has been (or will be) elucidated by analyzing the relationship between the trait's structure and its effects on survival and/or reproduction – that is, by analyzing its design.

Evolutionary psychology (EP) simply proposes that neural tissue is organized like every other tissue in the body: as functional units that evolved by natural selection to facilitate or effect reproduction. EP, then, represents a radical rejection not only of classical dualism – that mind and body are incommensurable realms – but also a rejection of an implicit dualism that is the foundation of virtually all sciences of human behavior: that the principles of the brain's organization have little relationship to the principles of the body's organization.

Despite the overwhelming success of the functional, mechanistic approach in physiology, it is sobering to recognize that almost all progress has been made with no explicit recourse to (and virtual ignorance of) evolutionary theory. The simple, almost atheoretical, presumption that body structures serve survival or reproduction has provided a sufficient foundation for the stunning advances in understanding body functions over the past several centuries. Evolutionary theory would seem to be superfluous for understanding body (and therefore brain) functions.

I will focus on the most important of several possible responses to this observation.

The functional organization of the body has been elucidated primarily by the direct examination of morphology: an approach that, at present, is technologically almost impossible for the human brain. With few exceptions, the neural circuits of the brain are currently "invisible." They exist at a scale above the individual neuron, but well below that which can be teased apart with any imaging technology currently available.

Cognitive psychology has developed powerful techniques that provide clear evidence of supra-neuron structure. It must be emphasized, however, how indirect this evidence is. An enormously complex entity – the brain – is stimulated (with images, sounds, sentences, etc.), and its structure is inferred from the corresponding output (e.g., buttons pressed, boxes checked). This is like attempting to understand heart or liver function without being able to conduct a dissection. Further, the hypotheses of cognitive psychologists, unlike those of physiologists, have not been constrained by the assumption that cognitive structures serve survival or reproduction; their hypotheses have usually been inspired by computer science (memory, signal processing), or are often entirely ad hoc.

Progress in cognitive psychology has therefore been slow: The space of hypotheses is too large, and the evidence of function too

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indirect. The theory of evolution by natural selection provides a solution to the first problem. An important implication of this theory is that the functional organization of all organisms will closely reflect their reproductive ecology – their EEA.

If all the reproductively relevant aspects of ancestral environments (i.e., the human EEA) could be specified, all the *potential* innate functions (adaptations) of our bodies and brains could be specified as well. For the brain, the reproductively relevant aspects of the EEA involve the information processing aspects of finding food and mates, detecting and avoiding toxins and predators, interacting with group members, and so on. Whether humans possess any particular psychological adaptation is an empirical question. Fortunately, it is much easier to find something if you have some idea what you are looking for. Studying the past is currently easier than studying brain wiring. The major insight of evolutionary psychology is that if you want to understand the brain, look deeply at the environment of our ancestors as focused through the lens of reproduction.

Adaptationism and inference to the best explanation

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Abstract: Andrews et al. effectively argue that, despite prominent criticism, adaptationism can be a viable research strategy. We agree. In our complementary commentary, we discuss the neglected method of inference to the best explanation and argue that it is a valuable addition to the adaptationist's methodological practice.

More than 20 years ago, Gould (1978) and Lewontin (1979) argued that many adaptationist explanations in sociobiology are "just so" stories of the sort that carry no decent epistemic credentials. This criticism has been passed on to the emerging science of evolutionary psychology and stands as its most general challenge. In their target article, Andrews et al. respond to this challenge by arguing that adaptationism can be a viable research strategy. They discuss appropriate standards of evidence for the correct identification of adaptations and insist that the comparative testing of adaptationist and nonadaptationist alternatives is essential to good science. We strongly agree with them that comparative theory appraisal is a requirement of good science, and in this commentary we complement the contribution of the target article by discussing one important method that will allow the adaptationist to do this.

There are a number of different methods that can be employed to distinguish adaptations from nonadaptations and to test the viability of nonadaptationist accounts. Most of these methods are concerned with testing hypotheses or theories for their predictive success. Prominent in this regard are the hypothetico-deductive method and, specifically within evolutionary psychology, statistical significance testing, both of which have recognized shortcomings (Rorer 1991). Given that the construction of explanatory theories is a major goal of scientific research, it is curious that methodological orthodoxy has given little attention to methods that focus on the explanatory aspect of theory construction. In this commentary we attempt to remedy that deficiency by discussing the neglected method of inference to the best explanation. We claim that this important form of inference is a valuable addition to the methodologist's tool kit that can help assess the evidentiary worth of adaptationist explanations.

Scientists themselves often judge the worth of their theories with explanatory criteria in mind. Such a view of theory evaluation employs a style of reasoning known as *inference to the best explanation.* This phrase captures the basic idea that much of what we know about the world is based on considerations of explanatory worth and it involves the process of judging the best of competing explanatory theories. Recently, Thagard (1989; 1992) has developed an attractive account of inference to the best explanation that involves making judgments of explanatory coherence. Explanatory coherence occurs when propositions hold together because of their explanatory relations. A number of principles combine in a computer program to provide judgements of explanatory coherence. In such judgements, the following criteria are important: explanatory breadth, simplicity, and analogy.

Explanatory breadth, which is the most important criterion, captures the idea that a theory is more explanatorily coherent than its rivals, if it explains a greater range of facts. The notion of simplicity is also important for theory choice, and is captured by the idea that preference should be given to theories that make fewer special assumptions. With the third criterion, analogy, explanations are judged more coherent if they are supported by analogy to theories that scientists already find credible. Overall, Thagard's theory of explanatory coherence (hereafter, TEC) provides an integrated account of multiple criteria that are constitutive of explanatory goodness.

In his analysis of major conceptual revolutions in science, Thagard (1992) argued that Darwin defended his theory of evolution by natural selection not so much in terms of its empirical adequacy as in its explanatory power. In like manner, and more specifically, we suggest that TEC can be employed to help us decide whether adaptation explanations are acceptable. Take, for example, the controversial claim that human language is a biological adaptation. This claim has to compete with alternative theoretical proposals that suggest the evolution of language has a nonselectionist origin. Importantly, TEC enables us to decide which is the best explanatory theory to accept. Not only does it demand that theory appraisal is a comparative affair, it also explicitly operates in context where theory testing by way of predictive success is not a requirement of theory adjudication. Of course, it is well known that claims about the origins of language cannot be settled by the empirical testing of novel predictions because the relevant data cannot be had.

We have employed TEC elsewhere (Durrant & Haig 2001) to argue that in comparison with adaptation explanations, nonselectionist accounts of the origin of language suffer in terms of their overall explanatory coherence. Not only does language not seem to fit the profile of biological characteristics that are byproducts of natural selection, but also, nonselectionist accounts do not explain the full range of relevant empirical phenomena. Further, by having to invoke multiple explanatory accounts to adequately address the different features of language, these nonselectionist accounts violate the criterion of simplicity. Of course, we have nothing like a complete adaptation explanation for language, but that type of explanation is our best currently available theoretical account of its existence.

Holcomb (1996) has also suggested that evolutionary psychologists should evaluate their theories by employing the method of inference to the best explanation. However, we have some reservations about his presentation of inference to the best explanation. Holcomb suggests that a theory that best explains the facts is true. However, because the link between explanation and truth is not direct, we think judgements of the best explanation only provide grounds for a theory's acceptance. Also, we think that Holcomb's suggestion that the demand for (novel) testable predictions normally regulates inference to the best explanation will often be inappropriate. Although predictive success is an important criterion of explanatory goodness, it has been overemphasized in methodological accounts of theory appraisal (Brush 1989; 1994). The theory of explanatory coherence has been shown to have widespread application in assessing the worth of explanatory theories, but it deliberately excludes predictive success as an explanatory criterion. Note, however, that for TEC, explanatory breadth is the appropriate measure of empirical adequacy.

It may prove difficult to establish with any certainty that a given trait is the product (as opposed to the byproduct) of natural

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selection. However, by embracing the range of evidentiary standards outlined by Andrews et al., and adopting a strategy of inference to the best explanation when appraising theories, adaptation explanations can be advanced which go beyond mere "storytelling" and contribute to the growth of knowledge in the behavioral sciences.

Allocating presumptions

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Abstract: A comprehensive evidentiary regime that would encompass adaptations, exaptations, spandrels, and constraints requires *both* a standard to be satisfied and a predesignated default presumption to be maintained before the standard is satisfied. Andrews et al. focus principally on the former component. Some thoughts are here offered on the latter.

In their innovative attempt to bring adaptations, exaptations, spandrels, and constraints under one coherent methodological umbrella, Andrews et al. provide much-needed clarification of these constituent concepts, a highly useful approach for distinguishing among them empirically, and a candid appraisal of both the strengths and weaknesses of various evidentiary standards for identifying adaptations. The article offers, in furtherance of improved methodological rigor, an important and constructive effort both to criticize the critics and to acknowledge and incorporate some of the useful points to be found in at least some of their critiques.

The article is at its strongest when turning back against the proponents of nonadaptationist hypotheses the force of their own claim that clear and defensible evidentiary standards must accompany claims of adaptation; for, if such is true (and it is difficult to argue otherwise), then the same should be true of claims regarding the particular nonadaptation hypotheses these critics advance. There is a pleasing symmetry (not to mention a considerable justice) in demanding that all claims, whether for adaptation, exaptation, spandrel, or constraint, should be subject to stable, appropriate, and identified standards.

The challenge, of course, in creating a comprehensive evidentiary regime that would enable us to distinguish among adaptations, exaptations, spandrels, and constraints is not only in specifying a standard to be satisfied, but also in predesignating the default (but rebuttable) presumption that should be maintained before and until that standard is satisfied. For example (and even leaving to one side the thorny question of what constitutes sufficiency), should the rebuttable presumption be that a given trait is a spandrel, unless there is sufficient evidence that it is instead an adaptation? Or should the presumption be that the trait is an adaptation, unless there is sufficient evidence that it is a spandrel? A number of critics obviously prefer the former approach. Andrews et al. explicitly prefer the latter, arguing that in fact such an approach is "required." That is, the presumption must lie against each of the several nonadaptation inferences until such time as the adaptationist hypotheses are fully rejected. This prompts four observations.

First, even those readers who find this specific allocation of presumption generally appealing, as I do, may nevertheless find it difficult to discern with precision the full complement of logical predicates necessary to render allocating the presumption against these particular nonadaptation inferences so completely inescapable. Is it that the adaptationist account will generally be more parsimonious than an account claiming exaptation, spandrel, or constraint? Is it that a conclusion of adaptation, while "onerous" (following Williams 1996), should or must stand between a less onerous presumption of chance-driven traits and an implied "superonerous" conclusion regarding exaptations, spandrels, and constraints? Is it that some selection, at least, will chronologically precede either exaptation from adaptations, exaptation from byproducts of adaptations (spandrels), or the net results of conflicting constraints? This is a piece of the overall argument that might benefit from further clarification and more explicit development in future work.

Second, Andrews et al. note that inferring that a trait is an adaptation for a proposed function, when it is not, is generally considered to be a greater error than inferring that a trait is not an adaptation, when it is. Taking this as true, then allocating the presumption against inferring any of the several nonadaptations, instead of against inferring adaptations, would seem likely to improve our ability to avoid the second error only at the cost of decreasing our ability to avoid the first. Is this cost worth paying, and if so, why?

Third, does the presumption truly need to be permanently allocated? Andrews et al. note, in another context, that there may be no single list of criteria that must be satisfied to demonstrate that a trait has been specifically designed by selection for a function. Different traits may require satisfaction of different evidentiary criteria. That approach seems eminently sensible to us, despite its lacking administrative simplicity. But if the criteria can be flexible, depending on circumstance, perhaps the allocation of the presumption could or should also be similarly flexible, depending on circumstance. If not, why not?

Fourth, are inferences of exaptation, spandrel, and constraint so identical in pertinent respects that they should or must all bear or benefit from the same evidentiary burden when pitted against an inference of adaptation? And, even if so, what burdens do each of the three of them bear against each other? Should an inference of exaptation from adaptation be preferred over an inference of exaptation from byproduct, in the absence of sufficient evidence, or vice versa? Clarifying the evidentiary standards and presumptions applicable to each dyad would seem to be a useful next step in expanding and strengthening the structure and arguments that Andrews et al. advance here.

Identifying adaptation by dysfunction

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Abstract: Specifying exact selection pressures for identifying adaptations is unnecessary. Novel behaviors are not spandrels since they can only develop because of prior functions. An adaptationist approach has a high prior probability, whereas spandrel hypotheses attempt to prove a negative. The concept of maladaptive spandrel is criticized. The utility of dysfunctional states for identification of adaptations gone wrong is emphasized.

The question is: How to define the evidential standards for identifying an evolved adaptation? A general problem is the target article's demand that understanding the specific selection pressure is necessary to identify an adaptation: "To identify a trait's function is to determine the specific selection pressures (if any) that were at least partially responsible for the evolution of the trait" (sect. 3, para. 1).

For instance, if waist-to-hip ratio (WHR) determines attractiveness across cultures, that could be because it signifies fewer health problems, or youth, or greater reproductive value, or more fertility, or being less likely to be pregnant (and therefore, impregnable), or less likely to have an infectious disease, and so forth. According to Andrews et al., "Using the beneficial effect standard would lead one to the conclusion that the trait was an adaptation for each of these effects" (sect. 3.1.3. para. 1). Any of these could be possible selection pressures, but since all have (funny coinci-

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dence?) the same functional consequence of increasing inclusive fitness, the authors' concern seems to be about historical sequences, rather than inferring a likely adaptation.

The beneficial effect standard is criticized by Andrews et al. because ancestral adaptations may have been exapted to those benefits. Maybe so, but are there exaptations that were never vigorously preshaped by prior selection pressures? Presumably, new uses of old adaptations are exaptations. For example, should recently developed music and calculation be considered as cultural achievements due to an "exapted learning mechanism"? But isn't it striking that damage to the tip of the angular gyrus produces both amusia and acalculia? Presumably, this structure incorporates adaptive functions that we don't understand as yet, but these prior abilities made possible these novel behaviors. Without these evolved processes, neither music nor calculation could have occurred. So how does the exaptation view subvert an adaptationist approach to music, calculations, driving, and so on? Note that it is the joint functional loss that highlights the existence of adaptive preexaptation, because exaptations have effects but not functions. This resembles the argument by unlikely consequence presented by Andrews et al. (see sect. 3.1.6.3, para. 1).

Andrews et al.'s critique of the comparative approach states that it suffers from inferring causation from correlation. However, everything they discuss suffers from this problem, given the lack of ability to experiment on selection over the necessary evolutionary time for adaptations. Therefore, we are always left with naturalistic inferences of various degrees of cogency.

Andrews et al.'s objections to fitness maximization, as an adaptation criterion, are that it requires measuring fitness time, and incorporates the requirement that adaptations maximize fitness with regard to the evolution relevant environment. However certain fitnesses – for example, the fact that we breathe and acquire oxygen – allow reasonable conclusions about adaptive function, without certainty about fitness time, but reasonable security about relevant environment.

In an attempt to provide an example of a spandrel, Andrews et al. state that spandrels evolved because they were genetically linked to selection of favored traits (sect. 5.2, para. 1), continuing, "Many psychological phenomena currently thought of as pathologies, are good candidates as maladaptive spandrels (e.g., schizophrenia)" (sect. 5.2, para. 1). Similarly, they pose an either/or argument as to whether ADHD is an adaptation or a maladaptive spandrel. Klein (1978; 1999) has reviewed the evidential standards for distinguishing disease from deviance. Why not just plain dysfunctional adaptations rather than spandrels? This issue was extensively reviewed in a special section of the *Journal of Abnormal Psychology* (Klein 1999). The history of medicine indicates that illness, dysfunction, and therapeutic interventions allow the discovery of adaptive functions.

Suffering is a perennial human problem. Certain sufferings are due to life contingencies, for example, hunger and thirst on food and water deprivation. In contrast, individuals may begin to feel bad and often manifest bodily changes, suffering from pain, dizziness, rash, malaise, and so on, for no apparent reason. That is why illness was prescientifically defined as an inexplicable involuntary impairment or suffering that could not be attributed to understandable antecedents. *Illness* is a hybrid concept; something has gone wrong involuntarily, and the results are sufficiently major to justify the sick, exempt role. For instance, if peristalsis stops, as in intestinal atony, absorption of nutrients and discarding of wastes cannot be carried out. Lack of peristalsis is a dysfunctional state that highlights intestinal functions.

In medicine, useful practice often precedes theoretical understanding of disease or relevant adaptations. The treatment of scurvy and beriberi led to the discovery of vitamins and enzymatic cofactors; inoculation and vaccination led to immunology; antibiotics led to understanding bacterial biosynthesis; animal breeding and plant hybridization led to formulating natural selection, genetics, and DNA; psychotropic medications led to the current focus on neurotransmitters and synaptic receptorology.

It follows that a major research focus in identifying adaptations should be on the detailed, imaginative, and empirical study of dysfunctions. Delineating processeses that underlie effective treatment of illness, from the point of view of repairing or compensating hypothesized dysfunctions, is a good bet for advancing our knowledge of adaptations.

Presumably, Andrews et al. argue that maladaptations would be selected out more vigorously than maladaptive spandrels. But if a spandrel has no function, it seems positively difficult for a mutation to produce a malfunction; whereas there are many more ways for a function to go wrong than to keep going right.

Evolutionary analyses should include pluralistic and falsifiable hypotheses

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Abstract: Andrews et al. attempt to clarify the standards for determining whether traits are adaptations. The authors argue that tests of adaptationist hypotheses best proceed by assessing the consistency of the traits with the proposed standards. Critical tests of such standards must assess inconsistency – hypotheses must be falsifiable. To fully understand trait evolution, we must consider both adaptive and nonadaptive hypotheses.

Andrews et al. review and critique standards by which to judge traits as adaptations. The authors' aim is to develop a consensus as to the criteria required to demonstrate adaptation. Their article reviews a long and sometimes colorful debate regarding the inclusion and testing of both adaptive and nonadaptive hypotheses for the evolution of traits. The authors make a significant contribution by presenting in detail the standards for identifying adaptation, but their proposed tests of these hypotheses do not adhere to standard scientific methodology, according to which hypotheses must be falsifiable. The authors focus not on falsifying hypotheses, but instead, on finding consistency with hypotheses, and they advocate flexible hypotheses that can be adjusted to accommodate results.

Evolutionary biologists and evolutionary psychologists confront a difficult task regarding trait evolution: It is impossible for researchers to observe directly the evolutionary process. We are left only with the present expression of the trait and with our own impressions. Our impressions have sometimes been short-sighted, failing to identify and test hypotheses that a trait might be a byproduct of an adaptation, or perhaps "random noise" (Buss et al. 1998). Gould and Lewontin (1979) highlighted this shortcoming, suggesting that there are nonadaptive hypotheses that, for some traits, may better explain trait evolution. Adaptation produces complex design and is ultimately responsible for exaptations, whereas nonadaptive forms of evolution can produce traits that outwardly appear adaptive (Buss et al. 1998). Because we cannot go back and watch traits evolve, we cannot be certain that a trait is an adaptation, a byproduct of an adaptation, or random noise. We therefore must rely on presenting several informed hypotheses regarding trait evolution, and these hypotheses must be evaluated by determining whether the expression of the trait is consistent with a hypothesis, or contradicts the hypothesis.

Andrews et al. focus on consistency with hypotheses, but they should concentrate instead on inconsistency with hypotheses. Traditional scientific inquiry requires that we reject all possible alternative hypotheses before we accept a hypothesis. The authors note Williams' (1966) suggestion that we falsify all nonadaptive hypotheses before accepting a hypothesis of adaptation, but then do not further discuss this suggestion. The authors state, for example, that "for morphological (i.e., non-neurological) traits, it is often sufficient to demonstrate that the trait also exhibits complex de-

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sign for the proposed function" (sect. 3.1.6, para. 5) For morphological characters, however, nonadaptive hypotheses also must be considered – specifically, phylogenetic constraint (i.e., genetic constraint *sensu;* Andrews et al., sect. 5.3, para. 1) and allometry. In addition, the hypotheses must be testable and falsifiable. We cannot correctly test a hypothesis of adaptation if the hypothesis is so flexible that we can make nearly any data support the hypothesis. Andrews et al. describe how hypotheses of adaptation might fail even though the trait in question is an adaptation. Hypotheses must be carefully constructed so that they are cleanly falsifiable.

In a study of the effect of sperm competition on sperm morphology in nematode worms, LaMunyon and Ward (1999) found that sperm size varied positively with the risk of sperm competition across several species: The greater the sperm competition risk, the larger the sperm, supporting the hypothesis that sperm size is an adaptive feature in nematodes. Larger sperm appear to be designed for superior competitive ability: Larger sperm crawl faster and adhere better to the substrate where fertilization occurs (LaMunyon & Ward 1998). Support for the hypothesis can be declared, however, only when alternative hypotheses are rejected. Two nonadaptive hypotheses were tested; phylogenetic constraint was rejected because relatedness among species had no effect on sperm size. Allometry did, however, have a significant effect: Larger worms had larger sperm. When the effect of allometry was removed from the data statistically, sperm size still varied as a function of sperm competition risk. The adaptation hypothesis therefore was supported. This example does not demonstrate causation, however. In these worms, it was possible to test causal relationships because they have a brief generation time of only three days. Risk of sperm competition was increased in several populations, and larger sperm evolved over the course of 60 generations, demonstrating a causal effect of risk of sperm competition on sperm size evolution (LaMunyon & Ward 2002).

Most morphological investigations now take such a pluralistic approach, testing both adaptive and nonadaptive hypotheses. Andrews et al. state that "confidence in [nonadaptive] alternative hypotheses for trait design only increases after consideration of all plausible adaptationist hypotheses" (sect. 5.1, para. 3). The reverse also is true. Support for an adaptive explanation for trait design is stronger after considering and discarding nonadaptive hypotheses. When considering the possible mechanisms by which a trait may have evolved, we need to entertain all possible hypotheses. Those that are falsified must be discarded. Such an approach would move us beyond the adaptive versus nonadaptive hypothesis controversy, which tends to obscure understanding of the creative power of evolution. At times, evolution produces traits that are finely tuned to perform some function, and at other times, evolution produces traits that appear only as a result of the ties that bind our genomes into an integrated whole. Adaptationists can take comfort in the fact that constraints and exaptations provide fodder for new adaptations and, conversely, adaptations can drag pleiotropically linked traits into new and exciting, but altogether nonadaptive, forms.

Yes, but it was never just about the science

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Abstract: Andrews et al. present a clear discussion of the various criteria needed to identify adaptations. However, they also imply a history of the debate between adaptationists and their critics that is incomplete. The history implied is one of only genuine scientific disagreement. This neglects the role of nonscientific motives and strawman arguments on behalf of the critics of adaptationists.

The discussion by Andrews et al. of the criteria used to identify adaptations would make this article an excellent contribution to a course on recent evolutionary theory. Even the points I happen to disagree with are made so clearly that they lend themselves to productive discussion. For example, one could ask students to explain why the cell activities involved in behavior are not "constructed from genes or their products" (sect. 2.1, para. 1). One could also ask why *constraints* are anything more than aspects of the environment that serve as selective pressures on new genes. Most important, one could ask if the new jargon introduced by the anti-adaptationists really contributed anything new to evolutionary theory. For example, is Williams' explanation of the snow packing effects of fox feet really fundamentally flawed because he didn't use the terms *spandrel* and *exaptation*?

But what would a student learn from this article about the history of the debate over adaptation? The student would learn that the debate started when Gould and Lewontin (1979) criticized a group of scientists known as adaptationists for being so naïve as to assume that mere "consistency" between a trait's effects and a proposed function should be the standard of evidence used to identify function. The fact that no known adaptationist ever actually took this position is explained away by Andrews et al., who assume that Gould and Lewontin must really have meant that the evidentiary standards used by adaptationists are, in reality, no better than mere consistency. That even this charge is false, is also glossed over by the authors. The student would then be informed that the debate between adaptationists and the followers of Gould and Lewontin persists with "no consensual resolution (though each side appears to think matters have resolved in their favor)" (target article, sect. 1, para. 3). Unless the student remembers that evolutionists and creationists also continue to debate as if the issue is resolved in their favor, they would probably take this to mean that the debate over adaptation currently consists of valid scientific arguments, on both sides, that are in need of the "consensus" provided by the article.

Students would probably find this implicit history consistent, unless they happened to notice one re-occurring citation: Williams (1966). This reference would puzzle students because Andrews et al., and both sides in this rancorous debate, view it as presenting acceptable criteria for identifying adaptations a decade before the debate started. On one hand, the authors point out that adaptationists were "particularly influenced by the writings of George Williams (1966)" and his view that adaptation is an "onerous" concept. On the other hand, Lewontin proclaimed on the book's back cover that it was an "excellently reasoned essay in defense of Darwinian selection as a sufficient theory to explain evolution." If both sides of the debate are in consensus over Williams' criteria for identifying adaptation, what was all the fuss about? The target article implies the explanation given by Rose and Lauder:

> Williams (1966) emphasized that the concept of adaptation is "special and onerous" and should not be applied lightly. *Many did not take his advice,* leading to . . . Stephen Jay Gould speaking at a 1978 meeting of the Royal Society of London. (Rose & Lauder 1996a; emphasis added)

But is this true? Did adaptationists really start assuming all traits were adaptations, or did they, as the target article recommends, use adaptation as a hypothesis to be tested? If the former is the case, then Gould and Lewontin are indeed to be thanked for their contribution to adaptationist thinking. If, however, the latter is true, then Gould's and Lewontin's attacks become strawman arguments motivated by nonscientific concerns. The student could use Andrews et al.'s article to partially answer this question by noticing that all of the tests used by adaptationists are far better than mere consistency. What the student would be unable to evaluate, because it is so glaringly absent in the article, is the role of nonscientific ideological motives in the attacks by the anti-adaptationists.

As has been well documented in a number of recent books (see Alcock 2001; Pinker 2002; Segerstråle 2000) anti-adaptationists feared that the adaptationist approach somehow threatened their ideological positions, particularly those related to Marxism and feminism. In some cases, anti-adaptationists held the mistaken no-

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tion that adaptationists were arguing for genetic determinism, and hence thought the existence of certain adaptations would mean that their attempts at social reform were doomed to failure. In other cases, anti-adaptationists committed the naturalistic fallacy and thought that adaptationists were excusing certain undesirable patterns of behavior when they claimed those behaviors were adaptations.

I assume Andrews et al. are well aware of the nonscientific dimension to the history of the debate over adaptation, and I suspect that their decision to exclude this from their article was a conscious attempt to mend fences, refocus the debate on scientific issues, and build a consensus from which the next generation of scientists can advance knowledge. I find these goals laudable, and I am glad that Andrews et al. have written their fine article. I have only two reasons for bringing up the nonscientific side of the debate over adaptation. First, it is unfair to the adaptationists who were the targets of attacks to give those attacks more legitimacy than they warrant. Second, ignoring the inaccuracies of those attacks only makes such unfounded attacks more likely to continue to hamper evolutionary science in the future.

Is this article a good discussion of the different scientific criteria used to identify adaptation? Yes, but the debate over adaptation that has raged for the past 30 years has never been just about the science.

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When is a trait an adaptation?

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Abstract: The authors outline research strategies that may identify the possible adaptive value of a trait. But this does not solve the problem of how to decide which characteristics of living organisms require an adaptive explanation. I suggest that knowledge of the ontogenetic and phylogenetic construction of a trait facilitates the identification of features that may have been acted on by natural selection.

The gauntlet has been thrown down to the critics of adaptationism: What are the criteria by which a trait, or a component of a trait, can be identified and catalogued as an exaptation? The authors make the case that the adaptationist approach has been more successful in developing a set of criteria that can serve for empirically ascertaining the adaptive value of a trait. Central to the adaptationist arsenal is the criterion of special design (Williams 1966). That is, a trait exhibits such proficiency, efficiency, and economy in achieving a functional outcome, that it is unlikely to have the form that it does unless it has been acted on by natural selection. More often than not, however, we know neither the problem that needed solving, nor whether the trait in question is an adaptation designed to solve that particular problem. Therefore, we cannot know a priori the task for which the standards of proficiency, efficiency, and economy are designed to meet (Lauder 1996).

Besides placing emphasis on the argument from design, Williams (1966) also pointed out that adaptation is an onerous concept that should be used only when all alternative explanations have failed. In part, this admonition solves the dilemma. As the workings of a trait become understood, we are in a better position to see if certain fitness-enhancing consequences consistently arise, and whether the construction of the trait is neutral with regard to those fitness enhancements. In following this approach, I would suggest that the decision as to whether a particular trait requires an adaptive explanation should arise from an analysis of the phylogeny, ontogeny, organization, and comparative variation of the trait in question. Once an adaptive explanation is deemed necessary, then the various techniques outlined by the authors can be used to ascertain the function of the purported adaptation. Let me illustrate the first step with an example.

In muroid rodents, play fighting in the juvenile phase involves the behavioral patterns typical of adult precopulatory behavior (Pellis 1993). The question is what, if any, features of the content of play fighting require an adaptive explanation? For most species thus far studied, the play fighting of the juvenile phase closely resembles the pattern of sexual behavior seen in adults, in terms of the frequency of use of the different tactics of contact (attack) and avoidance of such contact (defense). Such one-to-one mapping of play fighting to sexual behavior suggests that what needs explanation is species differences in sex, not play, with play fighting being the precocial expression of sexual behavior (Pellis & Pellis 1998). This explanation fails to account for some of the variation in the content of play fighting present in some species. For example, in rats, even though all the behavioral tactics typical of precopulatory encounters are used in their play fighting, the relative frequency of use is not the same. In play fighting, the most frequently used tactics are those that are rarely used in sex. Furthermore, the most frequent tactics undergo age-related changes in use that cannot simply be attributed to changes in the maturation of the sexual behavioral system or of sensorimotor capabilities. Indeed, there appear to be neural and hormonal mechanisms that are specific to these particular changes in the content of play fighting (Pellis 2002; Pellis et al. 1992). That is, whereas the developmental sequence of changes in play fighting of most species can be accounted for parsimoniously as a byproduct of the maturation of the species-specific pattern of sex, that of the rat cannot. Following the approach that I think can be derived from Williams, an analysis of play fighting that has taken into account the phylogeny (Pellis & Iwaniuk 1999a), ontogeny (Pellis & Pellis 1990; 1997), organization and mechanisms (Foroud & Pellis 2002; Pellis 2002), and cross-species variation (Pellis & Pellis 1998), has identified a pattern of the trait that may need an adaptive explanation. The next step in the analysis is to determine what kind of adaptive function this modified pattern of development may serve.

Examination of the use of the behavioral content of play fighting in adulthood has revealed that rats, but not other species of rodents, incorporate such play in nonsexual encounters. Furthermore, the contexts and patterns of modification of those play patterns in adulthood (Pellis 2002) are consistent with the broader comparative literature that suggests that some species have coopted play fighting in adulthood as a tool for social assessment and manipulation (Pellis & Iwaniuk 1999b; 2000). If so, then a plausible hypothesis is that the modified pattern of play fighting in juvenile rats is designed to provide physical or cognitive training in the use of play fighting in adulthood. This adaptive hypothesis can then be tested by determining whether juvenile play fighting achieves the standards of proficiency, efficiency, and economy suitable for such training. Some data indicate that the juvenile play fighting of rats may do so (Foroud & Pellis 2002; Pellis et al.1999). Comparative methods can also be used to test whether the modifications in juvenile play fighting present in rats are consistently present in other species that have functional uses for play fighting in adulthood.

To me, the approach illustrated above seems to be in keeping with the spirit of Williams' message concerning the overuse of adaptive explanations. Andrews et al. actually use Williams' cautionary note in defense against some of the charges of the critics. Yet, they then go on to support the strict neoDarwinian approach in which it is assumed "that whatever an animal does must be adaptive" (Alcock 1988, p. 7). This seems incompatible with Williams' more cautious approach, yet the authors do not then proceed to show how these two extreme views of adaptation can be rendered compatible. Indeed, if Williams' approach had become predominant from the 1970s onwards, rather than the approach exemplified by Alcock, one wonders whether the critics of adaptationism would have needed to, or have been able to, put forward their criticisms.

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The importance of comparative and phylogenetic analyses in the study of adaptation

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http://primate.uchicago.edu/dario.htm

Abstract: Homology can provide strong evidence against exapted learning mechanism (ELM) explanations for psychological and behavioral traits. Homologous traits are constructed by commonly inherited developmental mechanisms. As such, demonstration of homology for a trait argues for its construction by an inherited rather than an exapted developmental process. We conclude that comparative evidence can play an important evidentiary role within evolutionary psychology.

Andrews et al. raise an important objection to the argument from design as applied to psychological and behavioral adaptations: that evidence for special design may arise as a byproduct of learning mechanisms that evolved for other purposes. The possibility that an exapted learning mechanism (ELM) may produce outputs that mimic naturally selected special design argues for the importance of additional lines of empirical evidence for adaptation. We argue here that demonstration of homology can provide strong evidence against ELM explanations when used in conjunction with evidence for complex functionality.

Homology is defined as equivalence or correspondence of organismic parts due to common ancestry (e.g., Sluys 1996). Homologies in behavior and its cognitive and neurobiological substrates can be assessed with the comparative approach, much like homologies in other traits (Atz 1970; Wenzel 1992). Andrews et al. argue that the comparative approach provides only weak evidence for adaptation. However, they discuss the use of the comparative approach only to investigate the convergent evolution of traits (i.e., homoplasies), and neglect entirely the use of this approach to investigate the phylogenetic history of traits (i.e., homologies). We argue that although phylogenetic continuities reveal little about functional design, they allow inferences about the nature of development that can refute ELM alternative explanations.

ELMs produce phenotypes that are the developmental outcomes of novel environments interacting with adaptations designed for other purposes. As Andrews et al. state, "if a particular behavioral or cognitive trait is the output of an ELM, it will have developed in response to modern environmental input" (target article, sect. 3.1.6.2). A refutation of the ELM hypothesis therefore requires demonstration that the phenotype in question is the product of an inherited developmental process rather than an ad hoc one. Likewise, the historical definition of adaptation embraced by Andrews et al. entails that adaptations must be constructed by inherited developmental processes that link the expression of adaptive phenotypes in current organisms to selection for such phenotypes in their ancestors.

Homology is the product of common developmental processes inherited across taxa (e.g., Wagner 1989). Since inherited developmental processes argue against ELM explanations, evidence that human traits are homologous to traits expressed among nonhuman species indicates that such traits are unlikely to be developmental byproducts of modern human environments. To provide compelling evidence for adaptation, however, homologous traits must play the same functional roles in human and nonhuman species. Homology for a human brain structure with a distinctly human function would suggest exaptation rather than adaptation. Thus, comparative phylogenetic analyses of traits must be complemented by functional analyses.

Andrews et al. argue that the comparative approach is problematic when making inferences about adaptation within a single species, such as humans. Other evolutionary psychologists have downplayed the importance of phylogenetic analyses for the study of human psychological and behavioral adaptations (e.g., Daly & Wilson 1995; Tooby & Cosmides 1989). Accordingly, comparative research with nonhuman primates has seldom informed work on the evolution of human psychology and behavior. Research on other taxonomic groups is sometimes used by evolutionary psychologists to generate hypotheses, but it is not viewed as a potential source of empirical evidence about adaptation.

The evidentiary value of homology for the investigation of human psychological and behavioral adaptations will depend on how frequently such adaptations show meaningful homologies with adaptations in nonhuman species. This is an empirical question that cannot be answered a priori, nor simply dismissed. Although the comparative/phylogenetic approach may be of limited use for potentially species-specific human traits such as language, it could be very useful for the investigation of psychological adaptations for mating, parenting, attachment, cooperation, aggression, fear and defense, and other complex behavioral and motivational systems that are unlikely to arise de novo in any single species. As one example, consider the similarities of both neurobiological and functional aspects of fear conditioning in human and nonhuman vertebrates (e.g., Ohman & Mineka 2001). Such similarities strongly suggest that the basic components of human fear conditioning are not products of an ELM. As another example, consider the psychological and behavioral adaptations for attachment to a caregiver in human children (Bowlby 1969). The development of attachment and the functional design of this system are very similar in human and nonhuman primates. Interestingly, a human-like attachment system is almost ubiquitous among the Old World monkeys and the apes, that is, the nonhuman primates that are phylogenetically closest to humans, and absent or rare among the prosimians and the New World monkeys, that is, the nonhuman primates that are phylogenetically more distant from humans (Maestripieri, in press). This suggests that the attachment system is not the product of the modern human environment but instead is an adaptation, the history of which can be tracked in the evolution of the Primate order. Although there may be slight differences among species in some neurotransmitters underlying the regulation of attachment processes (e.g., in the relative role of oxytocin vs. endogenous opioids), or in the precise behavioral expressions of attachment, the attachment system as a whole shows evidence of homology and thus, construction by an inherited developmental process.

In sum, we suggest that research on nonhuman species, and in particular, on nonhuman primates, has an important role to play in human evolutionary psychology. The use of phylogenetic continuity to support the hypothesis of adaptation may seem counterintuitive, given that phylogenetic inertia and selection are often presented as competing explanations for the nature of phenotypes. Darwin (1859), in fact, often used nonadaptive homologies as evidence for evolution against the thesis of special creation. Such examples, however, do not refute the possibility that many functional traits are preserved across taxa precisely because of their adaptive consequences. As Andrews et al. state, "much of the genome will be highly conserved because it results in advantageous phenotypic effects" (sect. 2.3). A corollary of this statement is that many adaptations will probably be homologous across species. In short, there is no conceptual argument that demonstrates the incompatibility of homology and adaptation, and, in fact, recent thought in theoretical biology suggests that the two concepts are intimately related (e.g., Wagner & Altenberg 1996). Thus, phylogenetic evidence should be part of any comprehensive strategy for the empirical demonstration of psychological adaptations.

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It's adaptations all the way down

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Abstract: Although antiadaptationist authors encourage us to consider alternatives to adaptationist positions, the alternatives offered do not necessarily relieve us of the burdens of adaptationist explanations. Even if something is an exaptation, it may be derived from an adaptation. If it is a byproduct, it is a byproduct of an adaptation. Even the ELM, the hypothetical exapted learning mechanism, is an evolved learning mechanism, though used outside its natural domain.

One of the ironies of the adaptationist debate is that an anti-adaptationist assertion may lead one directly, if unwillingly, to an adaptationist position. Proponents of the exaptationist program discourage the conclusion that any particular aspect of an organism is an adaptation, and encourage us to consider instead that we are seeing only an exaptation or a byproduct of an adaptation. Gould and Vrba recognize that from a primary exaptation, one can get a secondary adaptation (Gould & Vrba 1982), without pointing out that the primary exaptation itself is derived from a primary adaptation. A byproduct of an adaptation, by definition, exists because of an adaptation and is therefore also a piece of the adaptationist picture. In the psychological domain, exapted learning mechanisms, too, exist because of the process of natural selection. They are adaptations.

Proposing that something is an exaptation does not excuse one from the adaptationist's burden. Exaptations have adaptations in their history. Consider the software engineer designing a program for a given purpose. Programs are constructed by pirating available components that perform a sufficiently appropriate function. Fresh code is written only to modify the borrowed code and to fill in gaps. Just because the programmer borrows (exapts) code, does not mean he or she has not created a program that is precisely designed for a particular function. Jury-rigged as it is, the new program was designed to complete its particular purpose, like a new adaptation built out of existing functional components. Furthermore, it is built out of code that was also designed for a specific function. There exists an adaptation-exaptation cycle: An adaptation that worked well (say, the wing designed for heat retention) may become an exaptation (e.g., the same wing used for flight). Then, if any mutation increases in frequency because it increases fitness, it has become an adaptation again (the wing designed for flight). At any stage in this process, adaptation by natural selection is an important causal factor in the existence of the wing. Many proposed exaptations would require an adaptationist argument if completely described: A complete description would identify the original adaptation from which the trait was exapted.

Another anti-adaptationist proposal is that a feature of an organism may be a byproduct rather than an adaptation itself. However, if something is a byproduct, then it is a byproduct of an adaptation. Even if the aspect being considered (e.g., the spandrel or the chin) is not functional, it is a product of adaptation by natural selection, and it has come into being because of the evolution of its supporting adaptation. Again, a complete characterization of the feature would identify that adaptation, demonstrate that it was an adaptation, and identify the selection pressures that led to its evolution. The anti-adaptationist is again led to an adaptationist claim.

The authors of the target article invite us to consider an exapted learning mechanism (ELM) as a possible psychological exaptation. One may suppose that invoking this exaptation excuses one from an adaptationist position, but it does not. Because we are living in a strange modern world, many of the psychological processes we use every day are used to interface with the modern environment, not the environment in which they evolved. We use our evolved learning mechanisms to memorize the phone number of our favorite restaurant, read a map, or learn Microsoft Word. Even these learning mechanisms are adaptations. The design and development of learning mechanisms is one of the tremendous advances of natural selection, since the amount of available DNA (only 30,000 genes) cannot possibly code for all possible environments and contingencies. However, learning is by no means singular, and some learning mechanisms are malleable and multipurpose by design. Various learning mechanisms are designed for a variety of tasks and a range of domain specificity. Some of the most powerful learning mechanisms may be those associated with language learning. Other learning mechanisms (e.g., those that support more associationistic learning, those underlying learned motor patterns) are designed to be more open, and may be more easily functionally "exapted." They are all adaptations.

Does this demand the conclusion that every aspect of an organism is a current or former adaptation? No, it is necessary to consider whether the aspect in question is a meaningful way of dividing up the phenotype. As Symons reminds us, "By identifying adaptations one carves the phenotype at its natural, functional joints" (Symons 1992). The example that Gould and Lewontin gave us of an exaptation, the spandrel in San Marco's cathedral, is not an adaptation because it is not a meaningful unit. It is an improper way of carving up the cathedral, not a functional feature that is being used for something other than its intended function. It shows no complexity of design which might suggest that its maker intended it for any purpose at all. The trick is not to separate the adaptations from the exaptations, but to identify the functional units. (Gould and Lewontin mock those who may have asked about the function of the chin. One remarkable difference between chins and eyeballs is their relative complexity.) Certainly, the forces and mechanisms in evolution that Gould and colleagues ask us to consider (the random fixation of alleles, allometry, pleiotropy, and other ontologically forced correlations) are important and significant, but they cannot explain the functional design we see.

Andrews et al. outline the standards that might be adopted by anyone taking an adaptationist position. The onerous burden of taking an adaptationist position is not side-stepped by some of the proposed anti-adaptationist suggestions. If one is describing an exaptation or a byproduct, a complete description will include an adaptationist story and would benefit from adopting the suggested standards. We rely on an adaptationist approach in biology in general, and in psychology in particular, because of the extreme complexity of design that we endeavor to understand. Gould and Lewontin ask us to believe that "constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change as it occurs" (Gould & Lewontin 1979, p. 581). Whether they are more interesting is, I suppose, a matter of taste; but that they are primary factors in creating the complexity that we see in biology and psychology, is unlikely.

The evidentiary standard of special design is a little bit like heaven

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Abstract: Adaptationist explanations for well-known phenomena are of limited value to psychological science. To be truly useful, evolutionary psychological research programs must produce novel discoveries about contemporary cognitive and behavioral processes. The concept of special design is especially useful. Even if special design cannot be convincingly demonstrated, rigorous attempts to meet this evidentiary standard can produce novel scientific contributions.

It's easy to be a critic, and hard work to be a good one. Criticisms of adaptationism are a dime a dozen, but many critics just wave

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vaguely at other concepts that may offer alternative explanations. When adaptationist logic is applied to the psychological sciences (in the field of evolutionary psychology), the same sorts of criticisms often arise. That's not very useful. Useful scientific critiques don't just stipulate that there might be alternative explanations. They specify actual alternative explanations, defend them with evidence, and promote deeper scientific understanding of evolution and its consequences.

It's also easy to be an adaptationist, and hard work to be a good one. Adaptationist explanations for psychological phenomena are a dime a dozen. But useful research programs in evolutionary psychology do more than just generate adaptationist explanations for psychological phenomena. They consider plausible alternative explanations, address them with evidence, and promote deeper scientific understanding of evolution and its consequences.

That's not easy to do. For reasons both logical and psychological, it is difficult to convince a skeptical audience about the veracity of any one explanation for the origin of a psychological phenomenon; and it's even more difficult to convince them about the veracity of any one evolutionary explanation (Conway & Schaller 2002).

There's another problem, too, that evolutionary psychologists face when trying to convince others about the value of their enterprise. The problem stems from the fact that evolutionary psychology bridges two different scientific cultures. Evolutionary psychological explanations must impress two different audiences with different objectives.

On the one hand, there's the audience of evolutionary biologists, a set of scientists whose first order of business is to inquire into the evolutionary processes that influence the features of populations. These folks may get very excited by debates about adaptations, exaptations, and spandrels. They are, after all, professionally interested in the past.

On the other hand, there's the audience of psychologists, a set of scientists whose first order of business is to inquire into the cognitive processes that influence the actions of individuals. These folks may be unimpressed by adaptationist explanations for readily apparent psychological phenomena. ("Okay, so we're likely to help relatives more than strangers? I already knew that. And older men tend to like younger women? I knew that too. So what?") Nor are many psychologists excited by debates about different kinds of evolutionary origins. Psychologists aren't professionally interested in the past; they are professionally interested in the present, so that they can better predict the future.

This is why adaptationist explanations for psychological phenomena meet with different objections from different kinds of scientists. Some evolutionists may object because alternative evolutionary explanations can't be ruled out (and so an adaptationist explanation might simply be wrong). Psychologists object – or don't care at all – because these explanations are simply explanations. If an evolutionary explanation (no matter how true) generates no novel predictions about the way the mind works, then the typical psychologist shrugs, "So what?"

Of course, evolutionary psychological research programs can lead to more than mere explanation. This is often overlooked by critics, and – more unfortunately – by many enthusiasts as well. Far too many folks are far too happy to merely invent evolutionary explanations for psychological phenomena that we already know to occur. Some of these explanations may be right. But so what? Explanations about the past contribute meaningfully to the objectives of psychological science only when these explanations lead to novel discoveries about the way the mind works right here, right now.

This is where the concept of special design comes in especially handy. When one speculates that a specific psychological process emerged as an adaptation that facilitated some specific functional outcome, one opens the door to a bunch of additional implications – implications about subtle cues that may trigger the operation of that process, and about nonobvious constraints operating on that process. These implications are translatable into hypotheses that can be tested and, if supported, may reveal brand-new discoveries about the here-and-now.

For example, in the realm of helping behavior, the logic of inclusive fitness leads not only to the obvious hypothesis that we help kin more than nonkin, but also to more interesting hypotheses specifying additional variables that moderate this effect (Burnstein et al. 1994).

Within the realm of interpersonal relationships, adaptationist logic leads to some obvious hypotheses, but also to additional hypotheses specifying subtle deviations from the obvious. As men get older they prefer women who are comparatively younger, yes, but teenage boys prefer older women; and this interesting exception to the rule is predicted from the same logic as the rule itself (Kenrick et al. 1996). Then there's the hypothesis that women not only prefer the smell of symmetrical men, but that they show this preference especially when they're ovulating (Gangestad & Thornhill 1998). No one encounters those findings and says "So what, I knew that already."

Psychological inquiry into human prejudice processes also benefits from adaptationist principles. Rigorous application of these principles has yielded a number of novel hypotheses and consequent discoveries about the specific features in others that elicit prejudicial responses, the specific forms that these prejudices take, and the specific domains and contexts in which these prejudices are most likely to occur (Kurzban & Leary 2001; Neuberg et al. 2000; Schaller 2003).

These and other highly specified findings are not so easily explained by alternative explanations that imply more generalized consequences. But that's not the main reason they are compelling to a psychological audience. For these folks, these findings are compelling specifically because they tell us something that we didn't already know.

These considerations make me think that the evidentiary standard of special design is a little bit like heaven. As an atheist, I figure that no matter how hard folks work to get to heaven, they won't make it. But that's okay; I'm glad they're trying if it motivates them to be better people. I'm also skeptical that evolutionary psychologists can convincingly rule out nonadaptationist explanations for human psychological phenomena. No matter how hard one tries to meet that onerous standard of special design, some critics just won't be convinced. But that's okay. By trying hard to meet that standard, we are more likely to generate novel predictions, discover new phenomena, and make useful contributions to science.

Where are all the genes?

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Abstract: Andrews et al. argue for adaptationism in cognitive research. However, the problem of evolvability brings into question the number of genes required for the evolution of cognitive mechanisms. Are there enough? Also, greater consideration should be given to alternative vicarious selection processes, which may produce cognitive mechanisms. Finally, identifying constraints with optimality arguments is more difficult than the authors think.

Andrews et al. develop perhaps the best case yet for an adaptationist research strategy in psychology. But their adherence to optimality thinking (via special design), together with the gene-centered view of Williams (1966) and Dawkins (1982/1983), runs into a theoretical problem: Where are all the genes required to fine-tune phenotypic traits to proficient levels of fitness? This question might be dismissed as a straw-man argument against a version of strong adaptationism. The authors, however, offer a version of adaptationism that recognizes factors (e.g., genetic constraints, developmental constraints, spandrels) in addition to natural se-

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lection, which may shape many phenotypic traits. In their view, a mixture of adaptive and nonadaptive evolutionary processes likely explains the evolution of cognitive mechanisms. I argue that the number-of-genes problem may nevertheless undermine the scientifically viability of this weaker adaptationist research strategy.

The best evidence for a phenotypic adaptation is special design, which requires specificity and proficiency of a trait, according to Andrews et al. In evolutionary psychology, specificity requires evidence that a cognitive trait is relevant to certain problems but not others. Proficiency requires evidence that the trait is on an evolutionary path to optimality, though there may be constraints that keep it from achieving optimality. For an adaptionist research strategy in evolutionary psychology to be viable, *specificity* implies that a relatively large proportion of cognitive mechanisms exhibit evidence of special design; otherwise domain-specific mechanisms could be attributable to other evolutionary processes. Proficiency implies that some unknown number of genes are available for natural selection to tune traits for proficiency (i.e., towards optimal design).

The notions of evolvability and modularity (e.g., Schank & Wimsatt 2000; Wagner & Altenberg 1996) are critical to an adaptionist research strategy because pleitropic interactions among genes constrain the evolution of adaptations: A change in one gene may have fitness consequences for many characters via pleiotropy and many if not most changes will be deleterious (Lewontin 1978). Modularity is therefore critical to phenotypic evolvability because modular adaptations are those distinguished by relatively few pleiotropic interactions among modules, thereby allowing natural selection to operate quasi-independently on each module (Schank & Wimsatt 2000). This strongly suggests that if cognitive mechanisms have domain specificity and exhibit proficiency, there must be a large number of genes to provide the quantitative genetic variation needed for natural selection to produce proficient cognitive mechanisms. Thus, Andrews et al. make the tacit ontological assumption that there are a large number of genes for domain specific cognitive mechanisms to be quasi-independently tuned by natural selection. These genes cannot be shared to a substantial degree because the problem of pleiotropy would begin to demodularize cognitive mechanisms.

Evolvability, modularity, and adaptationism suggest that there must be a large number of genes available for adaptive evolution, but how many genes are required and how many genes are there? The human genome project has revealed that human genomes have considerably fewer genes than previously thought, ranging from 30,000 to 90,000 depending on the criteria used to identify genes (Claverie 2001). This range does not tell us how many genes are required to evolve domain-specific cognitive mechanisms in humans. But these estimates should be worrisome for adaptationists, especially if there are supposed to be a large number of domain-specific cognitive mechanisms. Even more worrisome is the expectation that numbers of genes across mammal species is likely to be very similar (Claverie 2001; Mouse Genome Sequencing Consortium 2002). Evolvability and modularity would appear to require more genes in humans to explain presumably more domain-specific cognitive mechanisms (e.g., domain-specific mechanisms of language). Also looming is Kauffman's (1993) problem of complexity catastrophes when selection processes are required to maintain a large number of modular adaptations (Schank & Wimsatt 2000).

If there are not enough genes for evolution by natural selection of many – if not most – domain-specific cognitive mechanisms, does this reduce the importance of evolutionary thinking in psychology? I do not think so. Andrews et al. do not give sufficient consideration to exapted learning mechanisms (ELMs). Donald Campbell (1990) proposed that the evolution of cognition, language, and culture might substantially occur by vicarious selection and transmission mechanisms (VSTMs), which would include ELMs. What might be learned and transmitted within and between generations? Heuristic rules that make us smart in specific problem contexts (Gigerenzer et al. 1999). Such rules might look like they are gene-based and special design adaptations because they are domain specific, suboptimal but proficient (Gigerenzer et al. 1999). However, they need not be. VSTMs must nevertheless have overall positive fitness consequences, but particular heuristic rules need not. I think a more viable and long-term research strategy involves identifying VSTMs and their products (e.g., heuristic rules; Gigerenzer et al. 1999).

Finally, I have little confidence that optimality reasoning can tell us much, especially regarding cognitive mechanisms. This is partly because we are limited beings whose cognitive mechanisms are more often characterized by satisficing than optimizing (Gigerenzer et al. 1999; Simon 1969). I also have little confidence that optimality reasoning can generally reveal limitations. Consider Andrews et al.'s example of handicapping in chess. They imagine a scenario in which the handicapped player does not reveal the handicap (e.g., not castling). Optimality reasoning, they believe, can reveal the handicap. This is unlikely. A master-level player who was handicapped by not being able to castle would likely play for a position in which it was reasonable not to castle (e.g., play for a closed center); or, the inferior play of the weaker opponent might never reveal any suboptimal positional or tactical moves of the master forced by the handicap. In either case, the handicap is not revealed to the weaker opponent. Indeed, depending on how the game unfolds, the weaker player may conclude that his opponent was not allowed to move his king's rook or perhaps his king. Why should we think that optimality reasoning would be any more successful in revealing constraints for systems that are more complex than the game of chess?

From exploration to justification: The importance of "special design" evidence

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Abstract: The authors present a balanced critique of the adaptation/exaptation debate and specify some of the hard evidentiary criteria that are needed to advance our understanding of human evolution. Investigators must build more "special design" criteria into their theorizing and research. By documenting that certain traits meet these rigorous criteria, the evolutionary sciences will ultimately rest on a firmer theoretical foundation.

In very many ways, it is unfortunate that Stephen J. Gould did not live long enough to read and comment on this important target article. He might have agreed with many of the cogent points raised by Andrews et al., who present a fair, open, and balanced critique of the complex and subtle issues that define the adaptation/exaptation debate. The central messages of the target article – that demonstrating adaptations is an onerous process, that the function of traits must be understood and tested in relation to competing alternative theories, that different traits may require different evidentiary criteria, and that testing hypotheses about constraints, exaptations, spandrels, and adaptations entails thinking in terms of an adaptationist approach – should be incorporated into the theorizing and research of *all* scientists who are interested in evolutionary issues.

Very few, if any, traits have been fully tested for "special design" properties. Nevertheless, some evolutionary scientists have been slower than others to build special design criteria into their thinking and research. This is certainly true in some areas of evolutionary psychology (one exception being the research on developmental instability and short-term mating conducted by Gangestad, Thornhill, and their colleagues). As Gould and others have lamented, one is often struck by the casual way in which some evolutionary scholars claim or make strong inferences that certain

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traits are primary or secondary adaptations in the absence of sufficient supportive evidence. Many evolutionary scientists have been more comfortable erring on the side of misclassifying certain traits as adaptations (making Type I statistical errors) than misclassifying traits that might truly be adaptations as not being so (making Type II errors). "Overclassification" errors are common in new disciplines striving to gain an identity and establish intellectual footholds in emerging scientific fields, especially when new disciplines are in the context of *exploration.* Now that a larger base of descriptive data has been gathered on different features of human evolution, *all* evolutionary scientists must move into a *justification* phase (see Meehl 1978). In doing so, special design principles must be tested to substantiate or discredit current assumptions about whether certain traits might be adaptations.

This will not be an easy task. The footprints of adaptations are likely to be more difficult to identify, follow, and examine for many behavioral and psychological traits than for most morphological ones. To complicate matters, some of the behavioral and psychological traits of greatest interest to evolutionary scientists may have mixed design, making their detection and testing all the more challenging. Many morphological traits (e.g., the eye) evolved in response to stable environmental features (e.g., properties of illumination, shading, contours) that were fairly consistent throughout evolutionary history. Many behavioral and psychological traits, on the other hand, may have evolved in response to changing or shifting environments in which countervailing selection pressures shaped certain traits (e.g., female orgasm).

When discussing psychological and behavioral traits, Andrews et al. allude to the importance of identifying "the underlying decision-rules and information processing algorithms encoded into the structure of the nervous system either through genetics, learning, or some other process" (sect. 2.1). Understanding the nature and operation of specific decision-rules/algorithms and providing evidence for their special design will be a major task in the coming years. Though this is not highlighted in the target article, evolutionary scientists need to pay greater attention to how evidence for special design can and should be demonstrated at the level of cognitive functioning. The development of PET and fMRI technologies has begun to expand our knowledge of how and where certain types of information are processed within the brain, but additional information processing models and methods should be used to test for special design properties.

Recent advances in social cognition involving controlled versus automatic information processing (see Wegner & Bargh 1998), and connectionist modeling (see Smith 1998), are cases in point. Under certain conditions, the special design of some decision-rules might be evident from when and how readily certain evolutionary-relevant stimuli "prime" certain types of thoughts, emotions, behaviors, or modes of automatic information processing. For example, it might be possible to document that certain stimuli are very easy to prime, very difficult to countercondition, and very difficult to "terminate" when individuals enter automatic processing modes. Once activated, these decision-rules might bias or systematically alter the way in which certain types of social information are attended to, interpreted, stored, retrieved, and remembered in unique, patterned ways. The trick, of course, will be to identify and discount the possible impact of different exapted learning explanations. Evidence for special design might also be inferred from the manner in which certain types of information are organized within and between associative networks, in certain schematic representations, in specific exemplars, and perhaps in distributed representations. Evolutionary scientists need to think more deeply about how the footprints of special design might be inferred from how the social mind is structured and operates, given specific evolutionary-relevant inputs.

Andrews et al. wisely counsel evolutionary scientists to use multiple evidentiary standards to identify adaptations. To marshal highly compelling evidence that certain traits are adaptations, however, it will be necessary not only to adopt multiple, rigorous evidentiary standards (e.g., coevolutionary optimization modeling, special design), but also to apply and test these standards in varied cultures. Critics of evolutionary approaches to human behavior will remain skeptical of even strong special design evidence unless it can be documented in more traditional cultures and societies. If evidence for the special design of certain traits is found only in Westernized cultures or societies, the adaptation status of these traits will be legitimately questioned (cf. Yu & Shepard 1998).

I hope this target article will facilitate a conceptual shift in many areas of evolutionary science – a shift away from the mere description and exploration of *possible* adapted traits toward a more complete testing and understanding of traits that might *truly be* adaptations. When the dust settles, the application of special design criteria may very well reveal that human beings possess a much smaller set of adaptations than some scholars have presumed. Those traits that do survive the onerous burden of special design will, however, put the evolutionary sciences on a much firmer theoretical foundation.

The fuzzy zone between exaptation and phenotypic adaptation

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Abstract: The target article adopts an adaptationist research strategy that, while logically coherent, suffers from various limitations, including problems in reconstructing past selective environments, ambiguity in how narrowly to define adaptive problems or selection pressures, and an overemphasis on specialization in evolved psychological mechanisms. To remedy these problems, I support a more flexible approach involving phenotypic adaptation and cultural evolution.

Andrews et al. tackle an important and complex problem. They note that in speaking of "behaviors and cognitive processes" as traits, they are "implicitly referring to the underlying decision-rules and information processing algorithms encoded into the structure of the nervous system either through genetics, learning, or some other process" (sect. 2.1). This is a strategy that is general enough to fit a variety of approaches to the study of behavioral adaptation, from evolutionary psychology to behavioral ecology to cultural evolutionism (Laland & Brown 2002; Smith 2000). Note that it leaves open the possibility that the design process for a given behavioral adaptation is something other than genetic evolution by natural selection. But when Andrews et al. get down to work, they seem to quickly rule out any process of adaptive design other than genetic evolution of particular traits to solve particular adaptive problems.

Andrews et al. closely follow the approach to adaptationist analysis propounded by leading theorists in evolutionary psychology (i.e., Symons, Tooby & Cosmides, and Thornhill). While this position has some virtues, it also suffers from limitations and ambiguities. In particular, several distinct problems arise when researchers attempt to carry out the "reverse engineering" approach advocated by this school of evolutionary psychology:

1. The problem of reconstructing past environments/selective pressures;
2. The problem of how broadly or narrowly to define the adaptive problem or selection pressure;
3. The related problem of how specialized an evolved psychological mechanism must be to qualify as an adaptation.

Much has been written regarding (1), often under the rubric of the "environment of evolutionary adaptedness" (EEA). The problem here is not just that the human EEA covers a vast period of time, or that it encompasses a vast range of natural environments and corresponding socioecological forms (even restricting our-

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selves to the Pleistocene). There is the additional problem that environments and selection pressures that are no longer extant – "the Pleistocene world of nomadic foragers" (Symons 1989) evoked at several points by Andrews et al. – cannot be directly studied. As a result, arguments linking the demonstration of adaptation or exaptation to such contexts are inherently limited to plausibility arguments rather than direct empirical tests. Where is the empirical evidence that a "sweet tooth" was adaptive in the "calorically limited ancestral environment," that ancient social contracts vulnerable to free riders were countered by evolved "cheater-detection modules," or that men of the EEA gained fitness advantages in choosing mates with high waist-hip ratios? There is a large gulf between the rigorously collected and analyzed survey data or lab experiments of evolutionary psychology, and the just-so stories about the EEA that provide the "adaptive" component of "adaptive design" arguments.

Problems (2) and (3) are rather more complex (Smith 1998; Smith et al. 2001). The standard evolutionary psychology approach to revealing adaptive design is to construct an argument linking (a) ancestral selection pressures that pose (b) a specific adaptive problem with (c) a specialized cognitive module evolved for solving just that adaptive problem. The specialized module in turn implies: (d) a specific set of genes coding for its underlying neurological circuits. In principle, the argument is sound and provides a satisfying causal structure linking adaptations to selective pressures in a tight lock-and-key manner reminiscent of the releasing stimuli and fixed-action patterns of classical ethology. In practice, however, we can only guess at (a) and (b), and rarely have any evidence at all for (d). Cognitive psychologists themselves are bitterly divided about the degree to which (c) holds in higher-level forms of human cognition.

In addition, there is the problem of how to analyze an evolved mechanism (cognitive and otherwise) that generates facultative responses to a variety of "adaptive problems," including ones that are relatively novel. Andrews et al. tackle this question by proposing that we distinguish cases of adaptation from exaptation. In essence, if we can build a case for the specificity of linked selective pressure, adaptive problem, and cognitive mechanism (elements [a]–[c] above), then we have a bona fide adaptation; but if the cognitive mechanism or adaptive problem is insufficiently specific, even if the effects of patterned behavior produced by this mechanism are adaptive, then we have an exaptation – in the case of learning, an exapted learning mechanism (ELM). But the distinction between these two options in any specific case is ambiguous at best, and a semantic issue at worst (Smith 1998). Andrews et al. discuss this issue, using the example of driving a car and optical flow, but ultimately waffle by concluding (see target article, Note 3) that it all depends on how the researcher "carves up" behavior. My point is that Andrews et al., and standard evolutionary psychology theory, are analytically hampered by their glorious vision of a set of tightly defined adaptive problems, cognitive modules, and one-mechanism-at-a-time adaptive responses. This may work fine for certain behavioral phenomena, but is inadequate for analyzing less tightly coupled systems.

One alternative to this "demonstrate special design, or else it's just an ELM" approach is to analyze adaptive behavioral variation as forms of *phenotypic adaptation* that in any specific instance may draw on a variety of cognitive mechanisms and other adaptive processes (including cultural transmission and evolution). This is admittedly less precise but very often far more realistic. Abundant evidence suggests that humans are particularly well designed for engaging in processes of phenotypic adaptation, using what in behavioral biology are termed *conditional strategies,* or in psychological language might be labeled *broad-purpose learning mechanisms.* Humans also adapt to a considerable extent via processes of cumulative cultural evolution – a phenomenon on which Andrews et al. are conspicuously silent.

These various attributes of human behavioral adaptation presumably reflect a hominid evolutionary history characterized by severe environmental fluctuation (Potts 1998), and colonization of an unprecedented variety of habitats (Foley 1996) via generation of novel technological and institutional responses. It is critical to remember that this behavioral diversity has been generated and maintained within a single evolving species, was essentially complete even before the origin and spread of agriculture (Kelly 1995), and was highly adaptive as measured by both environmental fit and reproductive outcomes. This suggests that human behavioral adaptive mechanisms are not limited to the highly specific and inflexible mechanisms discussed by Andrews et al. – the "stone-age minds" maladapted to post-Pleistocene conditions so often portrayed in the evolutionary psychology literature.

In sum, the research program advocated by Andrews et al. (and mainstream evolutionary psychology) looks far better in the abstract – as philosophy – than in practice – as a guide to either empirical research or theory building. By adopting a more realistic research strategy, evolutionary psychology could contribute a great deal to understanding behavioral adaptations and exaptations, but only in conjunction with other traditions such as behavioral ecology (Winterhalder & Smith 2000) and cultural evolution theory (Henrich & McElreath 2003).

Adaptationism and molecular biology: An example based on ADHD

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Abstract: Rather than starting with traits and speculating whether selective forces drove evolution in past environments, we propose starting with a candidate gene associated with a trait and testing first for patterns of selection at the DNA level. This can provide limitations on the number of traits to be evaluated subsequently by adaptationism as described by Andrews et al.

In a small example about Attention Deficit Hyperactivity Disorder (ADHD), Andrews et al. evaluated the hypothesis of Jensen et al. (1997) that "the presence of ADHD traits in *some* children" represents placement on the "response-ready" rather than the "problem-solving" end of a dimension of behavior that may have been beneficial in past environments but detrimental in current environments. Andrews et al. concluded from this: "Because ADHD appears to lack special design for response readiness, the evidence seems to be more consistent with the hypothesis that ADHD is a maladaptive spandrel that persists despite selection, not because of it" (sect. 5.2).

As specialists in the area of ADHD, we respectfully offer some technical objections, including (1) disagreement with the assertions that "symptoms or consequences of ADHD have been found to hold an advantage" (Goldstein & Barkley 1998) and that ADHD is a disorder characterized by "a group of individuals, all of whom share the same failure of adaptation" (i.e., a deficit in behavioral inhibition) (Barkley 2001) – which seems to suffer from the common error of inclusion (i.e., assuming that all individuals with a heterogeneous disorder exhibit a characteristic of the group); and (2) disagreement with the acceptance of the null hypothesis about adaptation, which may suffer from the use of multiple tests.

We have used a molecular biological approach (Swanson et al. 1998a; 1998b) that may (1) avoid the many (see Sergeant et al. 1999) and often petty (see Swanson et al. 1998c) disagreements about a complex clinical literature, and (2) limit the number of alternatives to be considered in a psychological approach. We are aware of views that complex behaviors may involve so many genes (Plomin et al. 1994) and require analyses of genotypes so expensive as to make our approach impractical. But these views are changing (see Pennisi 2002), and here we present a concrete example.

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We started with a candidate gene, the dopamine receptor D4 (DRD4) gene (Swanson et al. 2000a). This gene is extremely polymorphic in the human population as a result of an "imperfect" 48 base-pair variable number of tandem repeat (VNTR) in exon 3 that codes for the third cytoplasmic loop in a DA receptor that has regional localization in brain regions (e.g., anterior cingulate gyrus) involved in control of attention and movement (see Posner & Raichle 1994). Two to eleven repeats (R) have been identified, but the most common alleles in the worldwide human population are the 4R (~68%) and 7R (~15%) variants. We found the 7R allele to be increased in ADHD samples (LaHoste et al. 1996; Swanson et al. 1998c), and many other investigators replicated this finding (see Collier et al. 2000 and Faraone et al. 2001). Next, we used genotype as an independent variable. In a study of ADHD children (Swanson et al. 2000b) we found that the 7R-present subgroup did not exhibit some characteristic signs of cognitive deficit (slow and variable responding) that were manifested by the 7R-absent subgroup, and in a reaction time study of normal adults, we found that the 7R allele may confer an advantage in conflict resolution (Fossella et al. 2002). Subsequently, we focused on variation in a nonclinical sample of 600 chromosomes by sequencing the exon 3 VNTR (Ding et al. 2002) and used established statistical methods from evolutionary biology to test the hypothesis of selection at the DNA level based on nucleotide motif, allele frequency, linkage disequilibrium, and patterns of variation predicted by the "Out of Africa" theory. Based on this, we proposed that the 4R allele was the ancestral DNA sequence and that the 7R allele originated about 50,000 years ago as a rare mutational event (requiring multiple recombinations, gene conversions, and single nucleotide mutations to be derived from the 4R sequence), yet rose to high levels attributable to positive Darwinian selection. With this in hand, we then sequenced DNA from a clinical sample to investigate why an allele with the "fingerprints" of selection is overrepresented in individuals with ADHD, which led to the suggestion that the 4R and 7R alleles probabilities are the result of "balanced selection" (Grady et al. 2002).

Given evidence of selection at the DNA (nucleotide) level, speculation about the traits (and the association with ADHD) can be limited and tested in the context of the type of program proposed by Andrews et al. One could speculate that individuals with ADHD and the 7R genotype had personality traits such as novelty seeking that drove migration out of Africa and enriched the 7R allele in groups that populated the Americas (Chen et al. 1999). Another possibility, based on Darwin's (1874) hypothesis that selection will be the result of "any advantage which certain individuals have over others of the same sex and species solely in respect of reproduction," is that individuals with ADHD and the 7R genotype may have manifested traits affecting sexual selection and mating behavior that resulted in increases in the 7R allele depending on the cultural milieu (Ding et al. 2002). Specific types of cultural selection in males favoring nurturing fathers ("dads") or non-nurturing fathers ("cads") could account for the higher prevalence of the 7R allele in some ethnic groups than in others (Harpending & Cochran 2002), and determining the allele frequencies of DRD4 7R in cultures known to exhibit variation in particular behaviors could be used to test this.

To follow this molecular biological approach and limit the number of traits to be evaluated in a psychological approach, we propose the following steps: (1) identify a candidate gene associated with a trait (or a condition such as ADHD); (2) evaluate the DNA nucleotide sequence of the gene to see if any allele has the "fingerprint" of selection; (3) identify the protein change that was produced by the sequence change from the ancestral coalescent DNA sequence; (4) determine the functional significance of the structural difference; and then (5) propose and test hypotheses about a restricted set of plausible traits that may be influenced by these differences in DNA variants and might have contributed to selection.

Adaptation *for*, exaptation *as*

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Abstract: The expression *exapted as* is offered as a substitute for the target article's *exaptation for* and *exaptation to* on the grounds that *exapted as* is less likely to foster the pernicious intuition that natural selection designs for future consequences.

I am grateful for Andrews et al.'s clarifications concerning adaptionism, particularly for their point that the recognition of exaptations is secondary to and dependent on the recognition of adaptations. I also endorse their conclusion that Darwinian explanatory stories should more frequently contain fortuitous consequences as steps in the evolution of traits. Our own preliminary theory of the evolution of babies' cries was a theory of that type, invoking the fortuitous consequences of the evolution of the speech apparatus in babies as a determinate of the form of babies' cries and adults' sensitivities to them (Dessureau et al. 1998; Thompson et al. 1996; 1998; see also, Falcon et al. 2002).

Because I think Andrews et al.'s article will have wide influence, I hope these authors will reconsider – perhaps even recant – their use of the expressions *exapted to* and *exapted for* in favor of the alternative *exapted as.* Different expressions afford different patterns of thinking. I fear that the expressions *exapted to* and *exapted for* will make much mischief in the years to come by fostering the idea that exapted traits are produced on account of their future utility.

Natural selection is a scientific metaphor or "model" (Thompson 2000; Thompson & Derr 1995; Williams 1966). It is used to explain how organisms, as they have descended through time, have come to more or less match to the demands of the circumstances in which they have lived. The model is akin to the process by which breeders eventually create organisms matched to their needs by breeding some members of a herd, flock, or stand of organisms instead of others in the same herd, flock, or stand. In the model, breeders choose organisms for their properties – high-butterfat cows over low, good-flying pigeons over bad, sweet-tasting corn over bland. These choices determine the breeding future of the individuals chosen or not chosen. In nature, the survival and breeding of organisms is taken to occur for the same reason: because something selected them on the basis of their properties.

Without both its parts, the formulation "Organism O has been selected for Property P" is dangerously incomplete. In the context of natural selection, it is meaningless to say what organisms we selected if we do not say what properties we selected them *for.* By itself, an individual-by-individual enumeration of the organisms that the breeder permitted to breed would tell us nothing much about how the selection regimen was going to change the flock. Furthermore, in an evolutionary context, to say that we selected organisms for P is useless if we fail to specify which sorts of organisms we obtained by that selection regimen. Selection claims display a sort of referential opacity. An organism that is selected for P may display a variety of other properties that the breeder (or nature) might not have selected, if he or she had the choice, because they had fortuitous consequences on the fitness of his/her stock (cf. Williams 1966). Understanding evolution as a historical process requires our knowing what sorts of other properties "came along" when we were engaged in our selection for P.

The philosopher of biology Elliot R. Sober (1984) has given much careful thought to this problem. He writes:

> [T]he idea of selection for and against characteristic . . . [may be understood in terms of] a toy my niece once enjoyed playing with before it was confiscated to serve the higher purposes of philosophy. [The toy is a transparent plastic cylinder with three horizontal layers.] Each horizontal layer contains holes of the same size. The holes on each level are larger than those on the level below. The balls also vary in size. If the balls are at the top, shaking the toy distributes them to their various levels. This is a selection machine. Balls are selected for their smallness.

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> The smaller a ball is, the more successful it is at descending. Balls of the same size happen to have the same color. The smallest balls, and only they, are green. So the selection process selects the green balls, because they are the smallest.
>
> There are *two* concepts of selection that we must pry apart. There is *selection of objects* and there is *selection for properties.* The smallest balls are the objects that are selected; it is equally true that the green balls are the objects that are selected. However, the concept of selecting for properties is less liberal. There is selection for smallness, but there is no selection for being green.
>
> "Selection of" pertains to the *effects* of a selection process, whereas "selection for" describes its *causes.* To say that there is selection for a given property means that having that property *causes* success in survival and reproduction. But to say that a given sort of object was selected is merely to say that the result of the selection process was to increase the representation of that kind of object.
>
> When the green balls reach the bottom more frequently than the blue ones, we think that there must have been a reason why green balls were selected; so they must have had some property that was selected for. But the property in question was not their color. There was *selection of* green objects, but no *selection for* greenness. I offer the following slogan to summarize this logical point: *"selection of" does not imply "selection for."* (Sober 1984, pp. 99–100)

In a later passage, Sober insists that we extend that convention to the expression *adaptation for:*

> [T]he concept of adaptation needs to be understood in terms of the idea of *selection for properties;* the idea of *selection of objects* will not suffice . . . If a neutral trait is pleiotropically linked to an advantageous one, it may emerge because of a process of natural selection. It was selected, but this doesn't mean that it is an adaptation. The reason is that although it was selected, there was no selection *for* that trait.
>
> The main idea here is to contrast adaptations with fortuitous benefits. After [stegosaur] dorsal fins became prevalent in the species, they may have performed any number of functions. Perhaps they served as cooling systems. Perhaps they helped stegosaurs attract mates. But if these additional benefits did not play a causal role in the emergence of the trait, it would be a mistake to describe the fins as adaptations for temperature control or mating (Sober 1984, p. 197).

Here Sober is making exactly the same distinction between adaptations and fortuitous effects as the target article authors are making between exaptations and adaptations when they write, in section 2.2.1:

> [Adaptations] are traits that have been constructed by a process of phenotypic modification by natural selection for a particular gene-propagating effect . . . [A]n *exaptation* is a pre-existing trait. . . that acquires a new beneficial effect without being modified by selection.

Sober is determined to limit the selection-for-Property-P attribution to those Ps that are causally efficacious in determining the greater reproduction of the organisms that bear them. The target authors, however, seem to blur that distinction by coupling the prepositions *to* and *for* with both adaptation and exaptation. Thus, in their terminology, a trait is exapted *to* (approximately 27 times) or *for* (approximately 7 times) its effects, even though the authors acknowledge that it is neither selected *by* them nor *for* them.

I have spent nearly a lifetime trying to expunge my students' intuitions that natural selection somehow manages to sniff out the future and generate traits that will be suitable to it. I fear that the moment we accept either *exapted for* or *exapted to* as standard usage, my students will begin to demand to know how it is that natural selection is prescient in designing exaptations. I urge that, following Sober, we reserve the use of *adapt for* to the "relation between a trait and its selecting consequences," and then use *exapt as* to refer to "the relation between a trait and its fortuitous nonselecting consequences." In so doing, we would be following the verbal practice implicit in such ordinary-language sentences as, "I bought the tool for turning screws, but when I got it home, I found I could use it as a chisel."

Thus, if speaking of the stegosaur and believing that the fins on its spine are selected by their capacity to ward off the bites of predators, but also believing that these fins had the fortuitous beneficial effect of disseminating body heat, we would write that the stegosaur's fins are adaptations *for* protection that are subsequently exapted *as* heat disseminators. This exaptation might later lead to selection *for* increased surface area in the fins or *for* their vascularization, and these further changes would be adaptations *for* heat dissemination.

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Why specific design is not the mark of the adaptational

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Abstract: Andrews et al.'s analysis suffers from a series of conceptual confusions they inherit from Gould's work. Their proposal that adaptations can be distinguished from exaptations essentially by specific design criteria fails because exaptations are often maintained and secondarily adapted by natural selection and therefore, over evolutionary time, can come to have similar levels of design specificity to adaptations.

Andrews et al. attempt to construct a scientific methodology that distinguishes adaptations from exaptations (cf. Buss et al. 1998). They essentially arrive at the classic view that the mark of the adaptational is design-likeness, albeit limited by constraints and antithetical forces. This approach is inadequate, and perpetuates a set of conceptual confusions originating in Gould's (1991a; Gould & Vrba 1982) analysis and perpetuated by Andrews et al. For example, Andrews et al. accept Gould's misleading dichotomy between adaptational *functions* and exaptational *effects,* but it is absurd to suggest that, for example, birds' feathers exapted for enabling birds to fly do not today have the function of enabling flight. Function is an explanatory concept; when an effect explains via natural selection the current presence of the very trait of which it is an effect, then the effect is a function irrespective of whether it is an adaptation or exaptation. Natural selection is an explanatory principle that reaches beyond original selection to encompass maintenance of traits in a population; thus, exaptations can be naturally selected and can have functions (Wakefield 1999). Gould and Vrba's claim, approvingly quoted by Andrews et al., that "adaptations have functions; exaptations have effects" (Gould & Vrba 1982, p. 6), is therefore misleading in suggesting that an exaptation's effects cannot explain the exaptation's current presence via natural selection. Andrews et al.'s definition of function as "the effect that causes the trait to evolve" (sect. 2.2.1) is then appropriately broadened to "the effect that causes the trait to evolve or be maintained by selective pressure."

Even the notion that adaptation is properly limited to original selection is questionable. If adaptations are traits with functions, then what Gould calls exaptations are often in fact adaptations. Gould justifies his definition of *adaptation* by the etymological claim that the term's Latin roots (*aptus ad,* fitted for) indicate reshaping something to fit something else: "[A]n adaptation is, literally, something fit (aptus) by active construction for (ad) its usage" (Gould 1991a, p. 45). However, according to the Oxford Latin Dictionary, although the rarely used verb *adapto* does suggest active modification, the locution *aptus ad* can indicate that something is fitted for a new use in virtue of its previous nature. For example, a person's nature can be *aptus ad* committing a betrayal, and a particular location in Gaul can be *aptus ad* engaging the enemy in battle. The same distinction exists in English. Whereas the verb *to adapt* indicates modification, the state of *being well*

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adapted to encompasses cases where one's previous nature fits an environment. Etymology thus suggests what is clear on conceptual and theoretical/explanatory grounds, that there is no justification for classifying only original selection as adaptation. Gould's exaptationist "argument" is neither ontological nor epistemological, but rather, a series of semantic manipulations.

If exaptations can be maintained by natural selection, the distinction between adaptations (effects that caused the original selection of a trait) and naturally selected exaptations (further effects that caused the later maintenance of the trait) becomes strictly a historical distinction with little theoretical interest. The distinction has no bearing on whether natural selection explains a trait's current presence, and it has no necessary implications regarding a trait's design specificity. Thus, historical evidence (direct or indirect, e.g., via comparative data) is necessary to disentangle adaptations and exaptations. For example, knowing that unossified brain sutures occur in young birds, suggests they did not originally develop to serve their current human purpose (for which there is certainly selective pressure) of allowing as large a head as possible to emerge through a birth canal of limited diameter.

Design specificity cannot replace such historical arguments. Andrews et al. themselves point to some of the problems in passing (sect. 4) but do not fully explore the devastating consequences of their observations for their attempt to disentangle adaptations and exaptations epistemologically. On the one hand, adaptations are jury-rigged out of pre-existing structures not perfectly designed for their new functions and significantly constrained in a variety of ways, so design-specificity is limited and not optimized even for adaptations. On the other hand, over evolutionary time, exaptations are maintained by selective forces only if they are as design-specific as available alternatives. Moreover, their specificity is honed by secondary adaptations that occur in mechanisms with which they interact. So, even a pure exapted structure eventually becomes part of a system that looks highly design-specific. Indeed, *over evolutionary time, one would expect the average degree of apparent design-specificity of naturally selected adaptations and natural-selectively maintained and honed exaptations to approach approximately the same level in a large range of cases.* Thus, the design-specificity criterion would not be useful for selecting between hypotheses.

This is why it is often surprising when one finds out that traits are exaptations (e.g., birds' feathers that allow them to fly, human babies' unossified brain sutures that allow their large heads to fit through the birth canal). Such traits can appear so well fitted to their exapted functions that it seems it can't be by chance. And it's not by chance; it's by natural selection. On the average, only the best-fitted exapted traits get maintained by natural selection; the rest are jettisoned, superseded, or reshaped. Darwin noted that, although unossified brain sutures clearly came into existence for other reasons, they are now indispensible to human fitness, implying selective pressure. Surely enabling movement of the child's head through the birth canal is now a function of unossified brain sutures in humans with power to partially explain why such sutures are maintained in the human species.

Whether exaptations are always or only sometimes naturally selected depends on how definitional ambiguities are resolved. Gould (1991a) says exaptations are "features that now enhance fitness, but were not built by natural selection for their current purpose" (p. 46), implying selective force, but admittedly often implies otherwise. In any event, natural selection clearly must be invoked in the prime morphological examples of exaptation presented by Gould and others, which Andrews et al. claim offer the best case for their design-specificity approach to identifying adaptations. Thus, Gould's hope in proposing the adaptation/exaptation distinction of decreasing the dominance of natural selection as the prime explanatory mechanism in evolutionary theory goes unfulfilled in these central cases.

Cognitive and behavioral traits present a difficult challenge for Andrews et al.'s design-specificity criterion for distinguishing adaptation from exaptation because, if learned, they often mimic design specificity. Andrews et al. offer a series of useful approaches for distinguishing learned traits from naturally selected traits (e.g., sects. 3.1.6.1–3.1.6.3). However, their repeated suggestion that ruling out learning explanations supports adaptationist versus exaptationist explanations is incorrect. The reason is simple: Whenever developmental mechanisms rather than learning explains a behavioral trait, there is no a priori reason to favor an adaptationist over exaptationist explanation for the current existence of the developmental mechanism. Andrews et al. seem to assume that, because learning seems highly design specific, the only plausible alternative is adaptation. If so, their assumption is a further manifestation of the fallacious notion that adaptation is a priori likely to be more design specific than exaptation.

A straw man on a dead horse: Studying adaptation then and now

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Abstract: Although Gould and Lewontin's (1979) paper stimulated an extraordinary response, the current study of adaptation is – and should be – more than a defense against their criticisms. Adaptations are studied by biologists in new and exciting ways, including experimental manipulations of populations in the field and laboratory, comparative analyses of taxa with known evolutionary relationships, and quantitative genetics. These techniques go beyond ascertaining whether or not a trait is an adaptation.

Although Gould and Lewontin's (1979) paper stimulated an extraordinary response from biologists, philosophers of science, and others, it is important to view the study of adaptation as more than simply a defense against the criticisms leveled in "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." Whether examined in humans, chimpanzees, or oysters, adaptations can be studied productively in a variety of exciting ways, and most evolutionary biologists do not currently structure their research around Gould and Lewontin's ideas. Here I outline some of the current methods for understanding the function of traits, and suggest where Andrews et al. may be missing some opportunities by focusing on a response to Gould and Lewontin.

As Rose and Lauder (1996a) point out in a recent volume on adaptation, by the late 1970s, the old style adaptationism attacked by Gould and Lewontin was experiencing a decline for many reasons, including the advances in molecular biology that made clear the complexities of genetic variation, and an increased understanding of the action of selection at multiple levels, such as selfish DNA sequences. We do not examine traits the same way we did in the 1960s or 1970s, not because we have been cautioned against doing so by enemies of optimality, but because the facts do not support such an endeavor. An even more recent chapter on adaptation (Reznick & Travis 2001) does not even mention the Spandrels paper. Modern evolutionary biology does not simply ask whether a trait is an adaptation or not. Instead, we attempt to understand the action of selection – as well as other forces – by examining the potentially adaptive nature of traits.

What are some of the current ways for studying adaptation? Experimental analyses in both the field and the laboratory have greatly enhanced our understanding of the effects of natural selection on behavior. For example, varying predation levels (by other fish) on guppies in the streams of Trinidad have resulted in rapid changes in traits ranging from senescence rates to the degree of ornamentation and mate preference (Houde 1997; Reznick & Travis 2001). Lower predation sites are associated with males that have more gaudy orange coloration, and females from these sites prefer the elaborately ornamented males (Houde 1997). Experimental introduction of fish from low predation to

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high predation areas resulted in a reversal of the preference behavior of females within a surprisingly small number of generations; such studies have often shown us the amazingly short time required for evolution to occur (Reznick et al. 1997). Students of human evolution sometimes seem to arm-wave about the time frame required for evolutionary change, but it is important to realize that information about the rate of evolution exists and can be useful in trying to understand which traits are likely to be transitory noise and which are potential adaptations.

Improvements in the use of phylogenetic and comparative analyses have also allowed greater insight into the adaptive nature of traits within and among lineages. Although Andrews et al. acknowledge the utility of the comparative approach, it is worth noting that this method now includes techniques for accounting for different degrees of evolutionary relationships (Martins et al. 2002). A recent exciting study of multiple mating in insects revealed that taxa in which females routinely mate with more than one male tend to be more speciose, suggesting that sexual conflict arising from the different costs and benefits of multiple mating to each sex also leads to differentiation (Arnqvist et al. 2000). Note, too, that the fact that humans have no other extant congeners is irrelevant for addressing some interesting questions about the function of traits shared with other taxa.

Ecological genetic techniques, particularly quantitative genetics, have also enabled biologists to examine the effects of selection in natural populations (Roff 1997). Quantitative genetics allows the study of traits that show continuous variation, such as height, frequency of reproduction, or the tendency to obesity, and obviates mapping a discrete gene or genes onto the trait in question. Such studies do not require a large number of generations, making them particularly advantageous for long-lived organisms.

The methods described above lend themselves to use with human behaviors with varying degrees of ease. Certainly, multiple generation experiments on human populations are not an option, so one of the most powerful tools of science, a manipulative experiment, is almost always ruled out. Perhaps the largest stumbling block is the difficulty of measuring fitness in humans, and knowing what environment is the relevant one, as Andrews et al. state. However, the problem about measuring fitness that they mention – "This is a problem because selection is a statistical process" (target article, sect. 3.1.2) – is not clear to me. Selection is statistical in that it is measured in individuals relative to other individuals, but this is the case whether one studies people or petunias, and both theoreticians and empirical researchers have discussed appropriate ways to measure fitness. I do not see why those studying human behavior should give up on the possibility of measuring the fitness consequences of traits suggested to be adaptations.

Finally, I am not sure that solely discovering whether traits are exaptations, or currently adaptive, is of much value in understanding evolution. Again, few evolutionary biologists working in nonhuman systems concern themselves with this issue, despite Gould and Vrba's hopes. A literature search of the ISI Web of Science using *exaptation* as a keyword showed only 72 citations since 1975; in contrast, the word *adaptation* yielded 59,719. Such a measure is obviously crude, but the point is that by attempting to counteract a now outdated criticism of a field, Andrews et al. run the danger of committing either of the metaphorical blunders alluded to in the title of this commentary.

Authors' Response

Adaptationism, exaptationism, and evolutionary behavioral science

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Abstract: In our target article, we discussed the standards of evidence that could be used to identify adaptations, and argued that building an empirical case that certain features of a trait are best explained by exaptation, spandrel, or constraint requires the consideration, testing, and rejection of adaptationist hypotheses. We are grateful to the 31 commentators for their thoughtful insights. They raised important issues, including the meaning of "exaptation"; whether Gould and Lewontin's critique of adaptationism was primarily epistemological or ontological; the necessity, sufficiency, or utility of design evidence, phylogenetic analyses, homology, and molecular genetics in distinguishing exaptations from adaptations; whether adaptationists accept adaptationist hypotheses too quickly; and the real utility of adaptationism to human behavioral science. We organize our response along the major points of the target article, in some situations defending our original claims and in others modifying them. While debate on these issues will undoubtedly continue, we are cautiously optimistic that the main points of the target article (as modified by our response) will help move the debate in a positive direction.

We are grateful to the authors of the 31 thoughtful commentaries on our target article. Several challenge core components of our argument. Some offer illustrations that bolster our points. Yet others offer additional or alternative perspectives on inference in evolutionary science. All highlight issues important to progress within evolutionary behavioral science.

The argument of our target article can be summarized under five major points: (1) We laid forth several definitions and basic conceptual issues concerning adaptation, exaptation, spandrel, constraint, and the methodological focus of adaptationism; (2) we summarized the basic epistemological concerns raised about adaptationism; (3) we argued that the special design criterion for identifying adaptation is an acceptable standard, whereas mere consistency is inadequate, and we discussed a number of criteria that may help rule out alternatives to specific adaptationist hypotheses; (4) we discussed four tools useful in sifting through competing hypotheses about trait design: comparative analyses, optimization analyses, design analyses (information about the trait's features in relation to its effects), and information about how the trait develops in relation to its effects; (5) we argued that building an empirical case that certain features of a trait are best explained by exaptation, spandrel, or constraint requires a demonstration that they are not better explained by adaptationist hypotheses and that, therefore, the testing of alternatives which Gould and Lewontin request implicitly requires the testing of adaptationist hypotheses.

We organize our response around how the commentaries address these five major points. Issues raised about the last two points overlap, hence, we combine their discussion in section R4. In general, we defend our argument against

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criticisms. But the commentators have led us to reconsider several of its aspects; our understanding of the process of carrying out an exaptationist program has been enhanced, deepened, and modified by the current insights. Although we have attempted to discuss all major concerns, by necessity some excellent points made by individual commentators go unaddressed.

R1. Definitional and basic conceptual issues

Adaptationism is a research strategy that seeks to identify adaptations and the specific selective forces that drove their evolution historically. A trait is an adaptation for a particular benefit if the benefit was historically responsible for the shaping of the trait. The benefit(s) responsible for the shaping of a trait are the trait's functions. A trait may acquire other benefits not responsible for its evolution. A trait is an exaptation to a benefit that arose after the trait's evolution. A constraint opposes the modifying influence of a selective force on a phenotype.

A number of commentators object to our handling of particular definitional stipulations. **Browne** observes that exaptation does not imply function and does not explain trait evolution. We agree, though we reject any suggestion that we claimed otherwise (see target article, sect. 2.2.1). In the light of the fact that exaptation is not an explanatory concept, **Thompson** urges us to reconsider our use of the expressions *exapted to* and *exapted for* in favor of the alternative *exapted as.* Biologists speak of *selection for* a particular effect in reference to a benefit *causing* a trait's evolution. The expressions *exapted to* and *exapted for* an effect may similarly imply causation, despite our clear intentions not to do so. We agree that poorly chosen terminology could "make mischief for years to come by fostering the idea that exapted traits are produced on account of their future utility" and, in fact, we discussed this very point when writing the target article. We preferred the term *exapted to* over Gould and Vrba's (1982) *exapted for* precisely because the former may have implied selection less strongly (though we managed to use the latter several times inadvertently, nonetheless). Thompson's suggestion to use the phrase *exapted as* has the right intentions. It entails, however, the need to specify the type of device a structure is "exapted as," rather than simply the fortuitous benefit that arose (e.g., "exapted as flight facilitators" vs. "exapted to flight"). In our view, the phrase *exapted to* can appropriately imply acquisition of a new benefit.

Wakefield argues against the fundamental distinction between benefits that drove a trait's evolution and benefits that a trait acquired after its evolution. Because the latter benefits contribute to the maintenance of a trait, both kinds of benefits invoke selective pressures. Hence, according to Wakefield, both adaptations *and* exaptations have functions (cf. **Browne**, **Thompson**). This point is part of a larger argument about the ability of special design evidence to discriminate adaptations from exaptations, which we address below.

Crawford and **Smith** argue or imply that the concept of exaptation is a fuzzy one. Does the ability to use a hand for manipulating a computer mouse reflect the function of the hand? Or is it a fortuitous effect of the hand? Crawford recommends that we answer such questions by thinking about how the original worked. If a beneficial effect is achieved through the physiological or psychological processes that evolved to carry our similar but not identical tasks, it is an adaptive effect. If not, it is a fortuitous effect. Hence, being able to manipulate computer mice and open refrigerator doors are adaptive effects of the hand, whereas digesting a non-nutritional item such as Diet Coca Cola is a fortuitous effect of the digestive tract. An extension of Smith's point that humans adapt through cumulative cultural evolution is that they effectively create new environments for which their adaptations have, in Crawford's terminology, both adaptive and fortuitous effects. As noted in the target article (sects. 2.2.2 and 3.1.5), one major way that traits are exapted to new effects is through organisms' creating environments for themselves that beneficially exploit their preexisting traits; humans are particular good at (and perhaps have been selected for) doing so. The important point with respect to epistemology is that the tight fit between a feature and the task to which it has recently been put (e.g., through niche- and cultural-construction) sometimes means that it will be difficult to discern the function and hence the selective pressures that led to the trait. We don't disagree, then, with Smith's view that the task of identifying adaptations, functions, and the selective forces that gave rise to them is not easy. In the case of some (perhaps many) psychological traits, it may not be possible. (We do disagree with his conclusion that, because of these difficulties, the adaptationist approach is not effective as a guide to research and theory building; for contrasting opinions and illustrations, see **Hagen**, **Rutherford**, **Schaller**, and **Simpson**.)

Brown makes the case that an understanding of adaptive evolution must feature developmental mechanisms and plasticity. We agree. The recent work on evolvable developmental plans is exciting. The means by which flexible developmental plans are maintained, however, is not obvious. As noted by West-Eberhard (1998), individual selection may often favor more specialized developmental plans at the cost of evolvability. Our point that "those taxa that happen to maintain more versatile, more evolvable developmental plans may be more effective at entering and exploiting new niches" (sect. 2.4) was not that "only *some* taxa maintain versatile and inherently evolvable development" (Brown); rather, it was that clade selection may be a significant factor accounting for the widespread conservatism of flexible developmental plans (West-Eberhard 1998).

Rutherford argues that many "alternatives" to adaptation – byproduct, exaptation, or exapted learning mechanism – imply adaptations, and therefore their full understanding will be a story involving adaptations. We generally agree, but note that nothing we said in the target article suggests otherwise (on exapted learning mechanisms and their role as adaptations, see sect. 3.1.5). (But see also **Barrett & Henzi** on alternatives to explaining phenomena other than adaptation, exaptation, or byproduct [e.g., disease], and **Atran** on complexity not tied to specific adaptive pressures.) Our focus was on epistemological issues facing a researcher asking whether a particular trait *X* is an adaptation for a particular effect *Y.* One alternative explanation may be that the trait's fit with a particular effect is the outcome of an exapted learning mechanism not specialized for that particular trait and its effect. A complete understanding of the selective pressures accounting for that alternative requires an understanding of the learning mechanism's function. In sifting through alternatives, however, one can find that a trait is the outcome of a learning mechanism not specialized

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for producing *Y* and, therefore reject the target adaptationist hypothesis without coming to fully understand the function of the learning mechanism.

Figueredo & Berry remind us that Nature is not an intelligent agent who *designs* adaptations with specific functions, such that each adaptation has one "real" function that Nature had in mind. Fortuity plays a role in adaptation as well as exaptation, as adaptation relies on the chance introduction of mutations that have favorable effects. Moreover, any and all benefits that contributed to the replicative success of genes affecting a feature can be thought of as "functions" of a trait. In our view, the term *design* nonetheless has utility in the epistemological realm. As emphasized in the target article, selection *need not* result in good design for a particular effect, but *only* selection can be responsible for, in Gould's terms, "eminently workable design" (Gould 1997d, p. 57).

Zuk maintains that the goal of modern adaptationism is more than simply identifying adaptations; it aims to understand the consequences of selection more broadly. Our focus on the issues of debate between adaptationists and Gould and Lewontin led us to construe adaptationism in a particular way and miss some important new ways of studying adaptation. For example, selection operates at multiple levels and, hence, some important consequences of selection must be understood in terms of selection at the genetic level. We agree that some of the most exciting work in evolutionary biology concerns phenomena such as genomic imprinting (**Brown**) and genetic conflicts of interest between the sexes (Zuk). We accept, then, that our characterization of adaptationism was influenced by the fact that we focused on the debates involving Gould and Lewontin, and hope that Zuk's commentary serves as a partial remedy to the bias. Her reminder that adaptationism is alive and well (indeed, thriving) in evolutionary biology is also a welcome one, but we think it a mistake to regard the issues addressed in the target article as "outdated." Zuk acknowledges the "stumbling block" of measuring fitness in evolutionarily relevant environments to the study of human adaptation, but underestimates, in our view, the implication that a study of adaptive design – a focus of the article – is therefore of primary significance. Debate about how one should understand the selective history underlying human psychological adaptation continues, often revolves around standards of evidence, and regularly invokes the concepts of constraints, spandrels, and exaptations (see, for example, the recent volume by Rose & Rose [2000]; see also **Dannemiller**, **Dupré**).

R2. The epistomological focus

Gould and Lewontin's criticisms of adaptationism have been largely epistemological in nature, and not ontological. In particular, they make two criticisms: (a) adaptationists often use inappropriate evidentiary standards for accepting adaptationist hypotheses; and (b) adaptationists often fail to consider alternative hypotheses to adaptation.

Objection 1: Gould and Lewontin's deepest criticisms of adaptationism concern ontological problems, not epistemological ones. Although acknowledging the importance of Gould and Lewontin's epistemological arguments and granting us some success in addressing them, **Dupré** argues that a major and separate *ontological* problem with adaptationism identified by Gould and Lewontin remains unresolved: Adaptationists atomize the organism into distinct parts, each of which is then assumed to be optimally designed for a specific function. In fact, however, organisms are integrated phenotypes, and it is not possible merely to "carve" the organism into component parts, interpreted in isolation from the rest of the organism. Selection cannot operate on individual features in isolation. Because of ubiquitous pleiotropy and patterns of correlated growth, the phenotypic space through which selection can move the evolution of an organism is not the entire *n*-dimensional space defined by all variation in all *n* measurable features. Many of the basic "traits" that adaptationists speak of, let alone the adaptations, don't exist.

Reply 1: The epistemological standards of evidence are relevant to this issue. As acknowledged in the target article, a full answer to the question "What is a trait?" is not readily explicated. Gould and Lewontin (1979) did raise the issue but offered little in the way of guidance. After noting, "For lack of space, we must omit an extended discussion of the vital issue 'What is a trait?'" (p. 585), they cited a single illustration of how one may be misled by inappropriate atomization (the well-known example of viewing the chin as a "thing" as opposed to a result of the interaction between two growth fields). **Dupré**'s commentary similarly does little to explicate a firm resolution to this problem. Neither he nor Gould and Lewontin advise against speaking of traits at all. (Obviously, Gould himself often wrote of individual traits as products of evolution.) Given our current understanding of the problem, Dupré suggests that the answer to the question of which traits have some chance of being adaptations will "come to intuition, perhaps tutored by proper biological experience."

In our view, the problem of what constitutes a trait is not completely disconnected from the epistemological problem of how one identifies adaptation. The larger epistemological problem facing adaptationism is not "What are adaptations?" but "How do we come to understand the outcomes of adaptation?" (**Zuk**). The problem of describing the effects of adaptation on any level other than that of the whole, integrated organism is an issue within that larger epistemological context. Knowing that a trait can qualify as an adaptation is not merely a matter of tutored intuition. One knows that a trait could qualify as an adaptation when one has evidence for the special design of the trait for a particular function.

Put otherwise, an adaptationist claim that a particular feature has been honed by selection to serve a particular function typically entails two subclaims: first, that selection was able to operate on that feature with sufficiently low costs arising from pleiotropic consequences for other traits; second, that the benefits responsible for its evolution correspond to those of the claimed function. The first of these subclaims (which may imply that the feature can be treated as a product of selection in [relative] isolation from the rest of the phenotype) is that which **Dupré** argues cannot be assumed casually. He implies that satisfactory compliance with standards of evidence for special design does not eliminate the fundamental problem associated with that claim. In fact, however, the claim is not a primitive assumption immune to empirical evaluation. Special design evidence can address it. In particular, evidence for the special design of the feature for the putative function is evidence *not only* of the claim that the function drove the evolution of the fea-

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ture; it is evidence that the feature was not so highly integrated into a network of other features by pleiotropy that it could not be modified by selection. If the chin should indeed be understood not as a feature designed by selection for a particular function but, rather, as the outcome of the interaction of two growth fields, then any rigorous application of standards of evidence for special design should not yield support for a claim that the chin is an adaptation specially designed to perform a particular function.

The argument is akin to the argument for the empirical meaning of the existential quantifiers within Ramsey sentences (e.g., Lewis 1984; Maxwell 1970). **Dupré**, in effect, argues that the features that adaptationists claim to be products of selection have little if any real empirical meaning. The Ramsey sentence is a means by which logical empiricists expressed a theory in a way that gave theoretical terms indirect empirical meaning while eliminating any surplus meaning of those terms. In a Ramsey sentence that expresses theoretical claims about, say, atoms, one states, first, that there exist such entities (represented by arbitrary symbols), and then goes on to state precisely what these entities are purported to do and what empirical derivations follow. Evidence that corroborates the empirical derivations is evidence not only for the theoretical claims about what atoms do, it is potentially compelling evidence for the existence of entities that do what atoms are purported to do (despite no direct observation of them). So too, evidence that satisfies appropriate standards of evidence for special design – should these standards be sufficiently rigorous – is evidence that the feature claimed to have been selected for a particular function is a meaningful one.

The Ramsey sentence is intended to capture the empirical consequences and meaning of a theory with no surplus meaning, by replacing all theoretical terms with arbitrary symbols. Of course, it is impractical for scientists to use symbols as theoretical terms in practice, though it may be advisable to use terms that have minimal surplus meaning above what is embodied in a theory. For that reason, we personally prefer to refer to adaptations for specific psychological functions as "psychological adaptations" or "specializations," rather than as "cognitive modules" (**Smith**) or "psychological mechanisms"; the terms "module" or "mechanism" may have surplus meaning that is not required by theory to account for functional specialization underlying behavior (e.g., Fodorian modularity or correspondence with a discrete neurophysiological structure).

Reply 2: Equipped with appropriate standards of evidence, adaptationism has succeeded despite tutored intuition as the primary guide. As **Hagen** expresses very nicely, the very adaptationist approach that **Dupré** claims has little to discover, has had enormous success in the study of human biology and medicine. Our understanding of virtually any organ system and its components owes itself to a functional analysis of the system (see also **Rutherford**).

Dupré's concern appears to be more specifically with the atomization of psychological traits, however, as the primary physical substrate responsible for behavior – the brain – is not a collection of individual features capable of being selected upon in isolation from each other. (See also Finlay et al. 2001.) Rather, "we know that the parts of the brain must be highly integrated, and integrated in such a way that it cannot be assumed that distinguishable parts should have discrete and specific functions" (Dupré). Individual preferences or dispositions or algorithms (e.g., preferences for waist-to-hip ratios) should not be viewed as traits, let alone adaptations, absent "identification of a neurophysiological structure with the demonstrable function" for these particular preferences or assessments. In the face of the ontological problem, "there is little reason to suspect that adaptationism has much to discover" about behavior. **Davies** echoes, "To the extent . . . that evolutionary psychologists work with categories unconfirmed at the level of neurochemistry, they may well be trying to trace the selective history of things that, as presently conceived, do not exist at all." (For related comments on the unknown nature of cognitive modules, see **Smith**.)

Based on such concerns, one might presume that the adaptationist approach has discovered little about animal behavior. Yet that's not so; it has led to remarkable discoveries in the study of nonhuman animals by treating particular preferences, behavioral dispositions, and so on, as entities capable of being fashioned for particular functions, and in absence of an understanding of their neurophysiological bases. One recent illustration is provided by collared flycatchers on the island of Gotland. The extra-pair paternity rate is approximately 15% in this population. Males who sport large forehead patches (a secondary sexual character) account for a disproportionate number of the extrapair fertilizations, partly due to female preference (Sheldon & Ellegren 1999). Moreover, observational and experimental evidence shows that females whose social mates have relatively small forehead patches are particularly likely to engage in extrapair copulations (Michl et al. 2002; Sheldon et al. 1999). As males with large forehead patches tend to have more successful offspring (compared with their half-siblings; Sheldon et al. 1997), this pattern of female preference for and seeking of extrapair mates makes sense as a means of increasing the genetic fitness of offspring. Males with large forehead patches actually invest less in offspring in their nest than those with smaller forehead patches, except when mating late in the season, a time at which most females already have had their broods and the opportunities for extrapair fertilizations are relatively scarce (Qvarnström 1999). Females do not prefer males with large patches as social mates in the early season (purportedly because what they gain in genetic benefits is offset by loss of paternal investment), but do in the late season (when this trade-off is relatively absent; Qvarnström et al. 2000). And, finally, the offspring of males with large forehead patches tend to be male – the sex that most benefits from having such a sire (Ellegren et al. 1996).

If particular flycatcher behaviors are not adaptive in the specific sense assumed by adaptationists, the fact that this constellation of behaviors have the demonstrable effects that they do is the sort of "strange coincidence" that scientists avoid admitting (Salmon 1984). It seems reasonable to conclude that female and male collared flycatchers possess suites of adaptations – preferences for extrapair mates, conditional motives for seeking extrapair mates, preferences for social mates conditional on time of the mating season, conditional allocation of effort to paternal investment, means of affecting the sex ratio of offspring – for functions of obtaining genetic benefits for offspring, and so on. At the very least, we can say that the adaptationist approach that atomizes the psychological features of collared flycatchers has led to remarkable discoveries about their behavior. And, again, this is but one small illustration of a larger point (see **Figueredo & Berry** on the progressive nature of the adap-

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tationist program; for examples of human psychological research, see **Schaller**.)

Reply 3: The alternative strategy of insisting that all traits be identified at a neurophysiological level is not obviously superior. Naturally, the psychological features responsible for adaptive behavior in these birds have physiological substrates in the birds' brains, and selection on those substrates must have had at least minor (though unknown) pleiotropic effects on other behaviors. **Davies** and **Dupré** imply that one need identify these substrates before proceeding. No doubt, study of the brains of collared flycatchers could potentially lead to interesting insights about how functionality is achieved and, furthermore, may revise our understanding about the structure of flycatcher behavior (Davies; on humans, see Duchaine et al. 2001). We disagree, however, with the assumption that one must first identify meaningful targets of selection at the neurophysiological level and then proceed to understand their function.

Neurophysiological examination will tell little about the functionality of behavior in absence of a good understanding of how individuals respond to and act on their environments. The value of the adaptationist approach for psychology is that it leads to hypotheses about the adaptive structure of behavior in relation to environments, and hence fosters our understanding of environment-behavior relations in a way that studying brain structure per se simply cannot (see **Hagen**, **Schaller**, **Simpson**). It is doubtful that researchers would come to our current understanding of collared flycatcher mating preferences, contingent allocation of parental effort, and so on, by first looking at bird brains to find the traits that exist – or, indeed, through any nonadaptationist-minded approach. Similarly, it is highly unlikely that one would have discovered that women's preferences for the scent of symmetrical men varies across the menstrual cycle by examining women's brains. The trait was only discovered after Gangestad and Thornhill (1998; Thornhill & Gangestad 1999) conjectured that, if past selection operated in a particular way (based on sexual selection theory and optimality thinking), it may have shaped women's preferences to vary contingently as a function of cycle-based fertility status – that is applied adaptationist thinking. Hence, **Davies** is flatly wrong when saying,

> With respect to psychological traits, we must have already accomplished, to a significant extent, the central task of psychology to commence with the question concerning past selective efficacy. In the case concerning scent preferences and the menstrual cycle, we would have no idea what to look for in the historical record if we had not first discovered the function of this trait within our psychology.

So, too, is **Atran** when saying, "at best, strong adaptationist arguments retrodict old discoveries."

Objection 2: Gould and Lewontin's objections have been largely motivated by nonscientific concerns. **Palmer**'s commentary argues that the debate was never just about science; criticisms of adaptationism, he claims, were motivated by sociopolitical positions and concerns (see also **Crawford**).

Reply: The nonscientific issues are irrelevant to judging the validity of the arguments. **Palmer** assumes rightly that we are well aware of these issues and that we avoided their discussion intentionally. In effect, the motives that led an author to propose an argument are irrelevant to judging whether the argument has validity. In Reichenbach's (1938) terminology, the former occur within the *context of discovery,* whereas the latter occurs within the *context of justification.* Bringing issues within the context of discovery ("Darwin was part of the land-owning class during the rise of capitalism") to resolve those within the latter ("His theory therefore must have overemphasized the importance of winning competitions") is to commit an ad hominem or genetic fallacy. As noted by Alcock (1998), Gould himself used the rhetorical device of turning a popular audience against intellectual adversaries by questioning their motives, knowledge, or diligence on multiple occasions, thereby (and understandably) irritating those he attacked. We have little doubt that some of Gould and Lewontin's claims about adaptationists were very unfair to them (Palmer). But, naturally, his doing so doesn't mean that *his* critics' ad hominem arguments have any greater force.

This is not to say that extrascientific motives or beliefs don't affect the way individuals conduct their science – of course they do. Moreover, once an issue has been decided on the basis of relevant evidence and a particular individual is found to be wrong, one can naturally ask the psychosociological question of why the particular individual was misled (e.g., extrascientific motives, lack of knowledge, poor training, bad luck, etc.), to which issues within the context of discovery are perfectly relevant. Ultimately, those interested in the history or sociology of science will offer their views on these matters (again, see Alcock 1998 for one account). But they were not directly pertinent to the issues discussed in our target article. We were not so much interested in mending fences as in focusing on the scientific matters of the debate.

R3. The special design standard and ruling out alternatives to adaptation

We discuss the standards of evidence that could be used to identify adaptations, and when and how they may be appropriately used. We argue that the standard of special design is better than mere consistency. And while we argue that one cannot identify the function of an adaptation without some evidence of specificity and proficiency, we argue against developing a prespecified list of criteria that, if satisfied, constitutes evidence of adaptation. Ultimately, building an empirical case that certain features of a trait are best explained by selection for a particular function requires demonstrating that they cannot be better accounted for by alternative hypotheses. Satisfying a prespecified list of criteria can interfere with this task

Objection 1: Special design evidence cannot differentiate adaptations from exaptations. **Wakefield** claims that the classic view that adaptations alone possess design-likeness arises from conceptual confusions inherited from Gould and Vrba's (1982) discussion of exaptations, which we purportedly perpetuate. Specifically, Wakefield argues that: (a) because natural selection maintains and modifies exaptations, they can have functions, which thereby explain them; (b) over evolutionary time, selection operates on adaptations that interact with exaptations, and hence, exaptations become enmeshed in systems of features that exhibit specificity of function; (c) given this fact, as well as the recognition that adaptations cannot be expected to be perfectly designed themselves, there is little reason to suspect that, on the average, adaptations will exhibit design-likeness any greater than exaptations, and therefore special design fails as a means to

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distinguish them; (d) ultimately, then, the distinction between effects that led to the original evolution of a trait and further effects that led to its maintenance is a historical one with little theoretical importance; special design does not stand in for historical analysis. Relatedly, **Deleporte** claims that special design signifies "aptation"; only phylogenetic analysis can distinguish adaptation from exaptation.

Reply 1: There is an interesting conceptual distinction between positive selection for alleles recruited into a population by selection, and negative selection against alternative alleles, which maintains a trait. **Wakefield** is of course correct in stating that the beneficial effects of exaptations act to *maintain* a trait in a population (see also Gould 2002). He implies, however, that there is no interesting distinction between selective pressures responsible for the recruitment of *new* alleles (previously represented at negligible levels in a population) into a population, and selection against alternative alleles (mutations) responsible for maintenance of a trait. In fact, evolutionary biologists commonly distinguish between selection for modifying and selection for maintaining traits such as sexual reproduction (Hickey 1993; Lenski 1999), polymorphisms and reproductive altruism in eusocial organisms (Harvell 1994; O'Donnell 1998), and cooperation (Axelrod & Hamilton 1981). One reason for making this distinction is particularly relevant to the distinction between adaptation and exaptation: Whereas positive selection for new alleles can potentially alter the configuration of a trait dramatically over evolutionary time, negative selection against deleterious mutations (trait maintenance) does not; it merely ensures continued expression of the trait's "design," shaped through positive selection. As negative selection cannot be responsible for remolding of a trait, it does not *explain* the process where-by traits achieve their configuration. By convention (see Williams [1966] for a brief history), the term "function" applies to the beneficial effect that explains *the alteration of a trait through positive selection,* a usage that Gould and Vrba (1982) merely adopted. Wakefield may believe that there exist good etymological arguments (by our view, largely irrelevant to scientific distinctions) for overturning convention and applying the term "function" to exaptation as well (see also **Browne** commenting on Millikan's proposal that the beneficial effects of certain traits recruited into larger systems of traits be referred to as proper derived functions). But he should not insist that there be *no* terminological means (e.g., the terms "function" vs. "beneficial effect") for distinguishing between selection responsible for molding a trait and selection against mutations that maintains trait expression. The distinction is real and substantively important.

One reason for its importance is particularly relevant to the epistemological concerns of the target article: Recruitment of alleles responsible for major trait reshaping takes place over expanses of evolutionary time. When one observes special design evidence that a trait has been *shaped* (not merely maintained) by selection to perform a particular function (e.g., by satisfying criteria of special design discussed in the target article), one can infer that *the beneficial effect represented by the "function" and accounting for positive selection, persisted at a sufficiently intense level and/or prolonged period to drive trait evolution.* Observing that a trait has a particular beneficial effect (maintaining the trait currently), absent evidence of special design for a "function" of achieving the beneficial effect does *not* permit such an inference. Traits can potentially become "exaptations" in single generations. They become "adaptations" only over evolutionarily meaningful periods of consistent selection for them. Finding evidence for positive selective forces that shaped a trait hence permits inferences about *historical selection pressures* in a way that finding evidence for selection currently maintaining a trait does not.

Wakefield believes that Gould and Vrba were misguided in thinking that there is any worth in distinguishing between the positive selection leading to trait alteration and the selective pressures that maintain a trait due to fortuitous beneficial effects, but in our view Wakefield's failure to appreciate important distinctions leads to muddled reasoning. Hence, he observes, "it is absurd to suggest that, for example, birds' feathers exapted for enabling birds to fly do not today have the function of enabling flight." We agree with this statement, but disagree with the implied accusation that Gould and Vrba's treatment suggests otherwise. The structures of wing and tail feathers of many birds have not merely been maintained since the time feathers were exapted to flight; they have been reshaped by a process of *adaptation* which favored structures that facilitated flight (see sect. 2.2.2 of the target article). This process of secondary adaptation, which Gould and Vrba clearly distinguished from primary exaptation, involves positive selection for a *function,* not a fortuitous beneficial effect. In the instance of bird feathers, it has generated design *for the function of flight.* When feathers were a primary exaptation, they presumably did not possess such design. Indeed, soft, plumaceous feather structures close to the body surface have purportedly not been shaped similarly for flight and do not demonstrate special design for it. By muddling the distinction between primary exaptation and secondary adaptation, Wakefield incorrectly implies that exaptation is responsible for feathers having the function of flight. (Naturally, if one ignores this distinction, one must conclude that nearly all functionality derives from exaptation, for nearly all traits were shaped from prior adaptations or byproducts. But that misses the point of making the distinction. See Gould 2002, pp. 1229–36.)

Reply 2: ***Wakefield****'s claim that exapted traits exhibit the same degree of good design for their effects as adaptations appeals to processes of adaptation.* Purely (and, therefore, initially) exapted traits almost certainly do not exhibit either developmental or design specificity for the exapted effect. If so, it is only by extraordinary coincidence, for, after all, they probably possess at least equally good (and in most cases, superior) design for the effect(s) responsible for their positive evolution (i.e., their function[s]). **Crawford** makes this point (and a number of interesting extensions of it) very effectively. Yet Wakefield concludes, *"over evolutionary time, one would expect the average degree of apparent design-specificity of selected adaptations and selectively maintained exaptations to be approximately the same"* (emphasis in original). The argument leading to this conclusion is a curious one. To explain how the design-specificity of exaptations arises, Wakefield invokes processes accounting not only for the maintenance of exaptations (negative selection against alternatives), but also for positive selection for adaptation: "Their specificity is honed by *secondary adaptations* that occur in mechanisms with which they interact. So, even a pure exapted structure eventually becomes *part of a system* that looks highly design-specific" (our emphasis). Wakefield seems to assume that exaptation (and the resulting selective pressures that maintain a trait)

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accounts for special design here. But of course it doesn't; rather, adaptation (positive selection for a function resulting in altered trait structure) does. (Indeed, the exaptation itself doesn't possess special design; only the larger system, retooled for the new function, exhibits it. See **Browne**.) Wakefield's conclusion that one process of adaptation (secondary modification) will, over evolutionary time, generate the average apparent design-specificity as a result of other processes of adaptation is not one with which we would disagree. But his argument is irrelevant to whether processes *other than adaptation* account for design-specificity.

Wakefield is quite correct in noting that an exapted trait itself need not undergo adaptation to become part of a system that demonstrates special design. But we, following Gould and Vrba, discussed this point: "Some traits are complex, meaning that subcomponents can be discriminated and interact in ways to produce effects. . . . Technically, complex features are probably mixtures of exaptations and secondary adaptations" (sect. 2.2.1; see also Gould & Vrba 1982, pp. 11–12). The fact that unaltered features can become part of complex traits (or larger systems) that have special design is a complication that may have interesting implications worth pursuit (see, for instance, **Browne** on derived proper functions). But again, it does *not* have the implication that selection merely *maintaining* an exaptation can generate special design.

Reply 3: There exist empirical examples illustrating the usefulness of applying criteria of special design to identify exaptations, even when these traits are embedded within larger systems that possess design. In sharp contrast to **Wakefield**, **Browne** argues the opposite point: that exaptation does not imply function and does not explain trait evolution. Using criteria of special design, one can often detect exaptation, even (or perhaps particularly) when the exaptation is part of a larger network of adaptive traits. The beneficial effect of the black heron's wing derived from its ability to shade water illustrates this point. Positive selection on the heron's neural system to use the wing for shading involves adaptation. The features of the wing itself, however, do not exhibit special design for shading and, hence, based on special design considerations we would not conclude that the wing itself has been *adapted* for shading. The beneficial effect involves exaptation. (Below, we discuss the relevance of phylogenetic analyses to inferences of exaptation.) Browne's example of the cheetah's tail is another illustration of the same point.

Objection 2: The study of adaptations faces the problem that past environments and selective pressures cannot be directly studied, and hence, we can only guess about the nature of past selective pressures. **Smith** notes that the environments in which humans purportedly evolved – "the Pleistocene world of nomadic foragers" – no longer exists and, therefore, cannot be observed. In absence of direct observation, claims about various traits being adaptations or exaptations are "inherently limited to plausibility arguments" rather than based on sound *empirical* foundations.

Reply 1: Unobservable entities can have empirical meaning. **Smith** appears to suggest that unobservable entities can have no empirical meaning. In philosophy, that extreme positivistic view was rejected nearly 70 years ago. Applied more generally, the view would argue that not only adaptationist arguments but also all of particle physics is "inherently limited to plausibility arguments." Atoms, positrons, electrons, and neutrons, let alone smaller particles, have never been observed. Theoretical statements about these entities attain empirical meaning through the observations that they explain. Such "indirect" evidence can provide a very powerful empirical basis for the existence of theoretical entities. Hence, Perrin's (1913) indirect estimation of Avogadro's number based on 13 different methods (e.g., Brownian motion, the thickness of soap bubbles) convinced most physicists in his day that atoms truly do exist (see Salmon 1984). "Unobservable" should not be confused with "nonempirical."

Reply 2: Adaptationist arguments reliant on indirect evidence can be powerful. The argument that an appreciation of design can provide powerful though indirect evidence for the nature of selection pressures that effectively operated on an organism (even if no longer present) was not constructed by evolutionary psychologists; it dates at least to Williams (1966). Simple examples suffice to illustrate its validity. Bird wings are powerful evidence of selection pressures for flight in the ancestral environments of modern birds in which wings evolved. Would direct observation of the conditions in which wings evolved provide any greater certainty for the claim that such selection pressures existed? If we observed a species of flying birds living in a newly constructed environment in which flight were no longer favored, would we be led to doubt that selection favored flight ancestrally?

No doubt, unconvincing arguments and "just-so" stories can be found in the literature. But the strength of the methodology should not be judged on the basis of poor applications of it. We attempted to identify criteria that, if applied, will lead to correct inferences about selection. While **Smith** and others may find these criteria inadequate, their dismissal requires more than the inaccurate claim that, because ancestral conditions cannot be directly observed, any claims about them have no empirical meaning.

Additional point 1: **Brase** nicely illustrates how criteria such as proficiency, economy, and reliable production can be inadequate to distinguish a particular adaptationist claim from an alternative with work on natural frequencies. Both hypotheses agree that natural frequencies are computationally easier. The special-purpose design argument is that they also constitute a privileged representational format. Brase discusses how work on biased outcomes of developmental learning mechanisms and the application of refined criteria of specificity contribute to resolution. More generally, he emphasizes a general point of our article that both he and **Haig & Durrant** made very explicit: Acceptance that a trait is an adaptation for a particular function must be made as "an inference to the best available explanation, given all the evidence (preferably using multiple, independent, and converging lines of evidence)." He adds the interesting observation that, because relevant evidence may come from multiple traditional disciplines (or subdisciplines), achievement in adaptationist science is hindered by the narrowing of interests and knowledge within traditional academic divisions.

Additional point 2: The design of signals. One point that we did not make but that has been made in the literature is that sexually selected signals are adaptations, yet are often wasteful and therefore appear to violate the criteria of efficiency and economy (Miller 2000). Adaptationists attempting to discern these signals nonetheless do look to certain forms of specificity and proficiency, particularly in the light of the adaptations in receivers that act on them. Such signals demonstrate specificity, if they do in fact affect the behavior

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of receivers in specific ways and appear to have no other beneficial effects. Furthermore, they may be proficient at signaling certain qualities (e.g., genetic benefits for offspring) when viewed through the lens of optimality models within which their selection is interpreted (e.g., Getty 2002).

R4. Tools useful for testing competing hypotheses and applications to alternatives

We note four tools that are useful in sifting through competing hypotheses about trait design: comparative analyses, optimization analyses, information about the trait's design in relation to what it does, and information about how the trait develops in relation to what it does.

Building an empirical case that certain features of a trait are best explained by exaptation, spandrel, or constraint requires a demonstration that they are not better explained by adaptationist hypotheses. We argue that the testing of alternatives that Gould and Lewontin request implicitly requires the testing of adaptationist hypotheses.

Objection 1: The target article endorses a rebuttable presumption in favor of adaptationist hypotheses. In the target article, we argued that the same tools that are useful in testing adaptationist hypotheses (comparative analyses, optimization models, information about the trait's design in relation to its effects, and information about the trait's development in relation to its effects) are also useful in testing alternative hypotheses such as exaptation, spandrel, and constraint. The reason we gave for this claim was that building an empirical case that certain features of a trait are best explained by hypotheses of exaptation, spandrel, or constraint, requires a demonstration that they are not better explained by adaptationist hypotheses. **Haig & Durrant** refer to this as *comparative theory appraisal,* but in this context we prefer to call it *comparative hypothesis appraisal* because adaptation, exaptation, spandrel, and constraint are all different hypotheses for trait design under a single theory – evolutionary theory.

Jones misreads us in claiming that we are arguing for a rebuttable presumption in favor of adaptationist hypotheses. We stated that commitment to the scientific enterprise requires agnosticism in the absence of evidence (sects. 5.1 and 6), and this was clear to at least some of the commentators (e.g., **Figueredo & Berry**). We also stated that the utility of adaptationist methodology in testing evolutionary hypotheses for trait design does not lie in any ontological commitment to the idea that traits are adaptations (sects. 5.1 and 6), and we should not be interpreted as advocating even the rebuttable presumption that traits are adaptations. The utility of adaptationist tools lies in the fact that they are not only necessary to appraise adaptationist hypotheses, but they are also necessary to appraise alternative hypotheses. To paraphrase **Haig & Durrant**, the use of adaptationist methodology is often necessary for the purpose of comparatively appraising competing hypotheses for trait design.

Objection 2: We advocate a standard of mere consistency rather than one that focuses on falsifiability. **LaMunyon & Shackelford** argue that we apply a standard of evidence to adaptationist hypotheses that is one of mere consistency. We do not set forth a methodology for constructing hypotheses so that they are "cleanly falsifiable." (See also **Pellis**.)

Reply: We did not advocate a standard of evidence of mere consistency. We disagree with the claim that we advocate the use of a nonfalsifiable standard of "consistency" for accepting adaptationist hypotheses for trait design. But before addressing it, we first take issue with **LaMunyon & Shackelford**'s statement that a consistency standard does not allow falsifiability. Under a consistency standard, a hypothesis is falsifiable if aspects of the trait's design, development, or phylogenetic history could be inconsistent with the target hypothesis. The problem with consistency is that it is usually insufficient grounds for accepting a hypothesis. Evidence of inconsistency lowers the probability that the target hypothesis is true relative to alternatives, but evidence of consistency often does not increase its probability relative to all the alternative hypotheses. For example, a beneficial effect standard would be consistent with adaptation, but it would not lower the probability that exaptation was true (see sect. 3.2).

In fact, a major thrust of our article was to argue that a consistency standard is inadequate. In effect, we argued that one should not accept a particular hypothesis until all alternative hypotheses are shown to be very unlikely to account for a trait. In discussing special design evidence, then, we explicitly described how evidence about the development of a trait, environmental mismatch, alternative means of achieving tight fit (e.g., ELMs), or phylogeny can be useful in ruling out alternatives. We are perplexed by how **LaMunyon & Shackelford** came away from our article thinking that the standards we endorsed allowed that an adaptationist hypothesis could be "so flexible that we can make nearly any data support the hypothesis."

LaMunyon & Shackelford describe work in which sperm size in nematode worms was shown to be associated with sperm competition risk. As this relationship need not reflect adaptation to sperm competition, phylogenetic constraint and allometry were subsequently ruled out as complete explanations. Furthermore, experimental manipulation of sperm competition led to the evolution of larger sperm. This research nicely illustrates how sequential investigation can sift through alternative hypotheses. We fail to understand, however, how it illustrates inadequacies in our standards. The standards we describe under sections 3.1–3.4 of the target article would not lead to the acceptance of the hypothesis that sperm size is affected by sperm competition based on correlations between sperm competition risk, sperm size, and sperm motility/adhesion.

We do note, however, that tests that cleanly and undeniably "falsify" hypotheses are sometimes – perhaps often – not possible. Tests of specific hypotheses are typically tests of a specific hypothesis of primary interest, auxiliary hypotheses, and assumptions about conditions of the test (e.g., Lakatos 1970), and hence, do not "cleanly" expose the hypothesis of primary interest (see **Figueredo & Berry** on "naïve falsificationism"). In the work described by **LaMunyon & Shackelford**, for instance, had control for the body size-sperm size relationship removed any association between sperm competition and sperm size, the adaptationist hypothesis would not have been cleanly *falsified,* as the test makes the auxiliary assumption that any correlation between body size and sperm size is *not* due to variation in sperm competition. For example, Clutton-Brock and colleagues (e.g., Clutton-Brock 1982) found that an association between body size and antler size in deer was at least partly due to differences in sexual selection, and hence were not merely the result of constrained "correlations of growth" (Gould & Lewontin 1979).

Pellis describes a research program that uses data on

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design, ontogeny, phylogeny, underlying mechanisms, and cross-species comparisons to infer a pattern of play-fighting in muroid rodent juveniles. We agree that this program is "in keeping with the spirit of Williams' message concerning the overuse of adaptive explanations" (Pellis) and, furthermore, illustrates our point that, "there may be no uniform list of criteria that must be satisfied to demonstrate that a trait has been specifically designed by selection for a function. Different traits may require satisfaction of different criteria" (target article, sect. 3.1.6). We fail to see, however, how we endorsed weaker standards and the view "that whatever an animal does must be adaptive."

Objection 3: Even with a good evidentiary standard, adaptationists sometimes move too quickly in accepting adaptationist hypotheses. **Fuentes** does not challenge our criterion for acceptance, but he argues that adaptationists nevertheless sometimes move too quickly in accepting adaptationist hypotheses. He argues that two examples we discussed in the target article – men's preference for lower than average waist-to-hip ratios, and women's preference for symmetrical men – demonstrate this point.

Reply 1: Even the best scientists occasionally miss plausible alternative hypotheses. We don't argue with the broad point; even the best scientists do occasionally miss plausible alternative hypotheses. The reason for this may be, as **Dickins & Dickins** suggest, that individual scientists have limited imaginations. A good example is **Barrett & Henzi**'s discussion of the different possible explanations for the long interbirth interval of !Kung San women. However, the two examples that **Fuentes** offers, in our view, do not illustrate this point. We truly did use the waist-to-hip ratio example "for instructional purposes only" (because of its specific features), and did not claim that adaptation had yet been convincingly demonstrated. We furthermore did not argue that work on women's preference for symmetrical men had yet demonstrated, beyond reasonable doubt, adaptation for acquiring genetic benefits for offspring; indeed, we explicitly noted that "even more work may be required to satisfy the onerous standard of special design and convincingly demonstrate the precise functions of the preference shifts" (sect. 3.1.6.3). At the same time, we did offer the example of women's preference for symmetrical men precisely because we could think of no alternative hypothesis that could explain the data. Our caution in avoiding any claim that the standard of special design had been met was in part because we recognized that our imaginations are limited and we may have missed a plausible alternative. Fuentes, despite his criticism, and despite the fact that we agree that further testing is desirable, offered no alternative hypothesis himself. In any event, we do think that it is important to distinguish between a claim that a particular hypothesis can be inferred to be correct from the explication (in as precise terms as possible) of a particular hypothesis as a guide to tests. The latter is desirable, even when evidence falls far short of justifying the former.

Reply 2: The problem of accepting hypotheses too quickly is not unique to adaptationists. **Davies** and **Schank** both argue that adaptationist thinking has little to offer psychology. But claims that various behaviors and affective states are maladaptive run rampant throughout psychology (e.g., severe depression, suicide, ADHD, and so on). These claims are largely unsubstantiated because psychologists' ignorance of anything more than the simplest form of adaptationist thinking has led to a systematic failure to generate plausible, sophisticated adaptationist hypotheses for many psychological phenomena. Psychology needs adaptationist thinking precisely because its practitioners are genuinely interested in determining what is and what is not adaptive, often for humane reasons.

Sometimes even evolutionary researchers accept nonadaptationist hypotheses too quickly. Gould himself has been guilty of this (Alcock 1998). Another example, provided by **Barrett & Henzi**, illustrates a similar point. They accept the claims of Sperber and Girotto (2002; in press) that the Wason selection task (WST) is not capable of scientifically exploring hypotheses about the existence of cheating detection mechanisms in the brain and that further uses of the task should be discouraged. Sperber and Girotto (2002) provide evidence that comprehension mechanisms can account for the existing known content effects in the WST. Barrett & Henzi imply that Sperber and Girotto's account of content effects in the WST is nonevolutionary, but Sperber et al. (1995) state that comprehension mechanisms must have an evolutionary origin too. In any event, in our view, Sperber and Girotto's claims go beyond the evidence that they have produced. To satisfactorily support their claim, they must show that it is simply impossible to ever devise a WST that manipulates content that does not tap a comprehension mechanism. Sperber and Girotto's evidence does not go so far; at best, they have shown that many of the content effects observed in the WST can be explained by a comprehension mechanism.

Reply 3: Special design is not a particular type of evidence, it is a criterion for accepting adaptationist hypotheses. We think another reason that adaptationists occasionally accept adaptationist hypotheses too quickly has to do with confusions regarding the term "special design." No other scientific field that we know of has a specific name for an evidentiary criterion for accepting a particular type of hypothesis. In other fields, most scientists just know that they have to show that all alternative hypotheses have difficulty accounting for the data before accepting any particular hypothesis. The use of a specific name can lead to misunderstandings if it is not chosen carefully. The term "special design" itself suggests a focus on design evidence (i.e., how the trait's features relate to its effects), and this interpretation has been exacerbated by the development of evidentiary shortcuts purporting to list design characteristics of adaptations (e.g., complexity, efficiency, economy, precision, etc.). In the target article, we argue that design evidence is a necessary part of building an empirical case for adaptation. Without some evidence of specificity and proficiency, we argued that it will often be impossible to determine what the trait is an adaptation for. But "special design" is a criterion for acceptance and should not be construed to mean that the scientist should rely solely on design evidence. As we pointed out in the target article, sometimes the exclusive reliance on design evidence can lead the scientist to erroneously accept adaptationist hypotheses. The standard of "special design" cannot be met without design evidence, but it requires that all plausible alternative hypotheses have difficulty in explaining the data before scientists can accept a particular adaptationist hypothesis as an explanation for a trait. Meeting the standard of special design may require the scientist to gather additional sorts of evidence (e.g., developmental or comparative evidence).

Objection 4: As adaptation and exaptation are distinguished in terms of historical timing, comparative analyses

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(e.g., cladistic analyses) are (a) sufficient and/or (b) necessary to discriminate adaptation and exaptation from each other. Several commentators argue that, because adaptation and exaptation are distinguishable in terms of historical timing of a benefit and the evolution of a trait, comparative analyses provide important evidence for discriminating exaptation from adaptation. Recent developments in cladistic analysis (e.g., the use of independent contrasts) allow for the estimation of relative timing, thereby offering a crucial tool. **Blackburn** argued that a sufficient criterion for demonstrating exaptation is whether the phenotypic structure that allows for the effect evolved prior to the acquisition of the beneficial effect. However, other commentators (**Dannemiller**, **Deleporte**) went further and argued that phylogenetic analyses were *necessary* for distinguishing between adaptation and exaptation.

Reply 1: Cladistic analysis is not sufficient, in and of itself, to establish that adaptation has not occurred. While we argue that adaptationist tools are necessary for appraising both adaptationist and nonadaptationist hypotheses, some adaptationist tools can build stronger cases for some hypotheses than for others. Such asymmetries exist because different hypotheses do not fully overlap with each other with respect to the criteria required to accept them. For example, we agree that phylogenetic history can be useful in demonstrating exaptation by determining whether the phenotypic structure that allows for the effect evolved prior to the acquisition of the beneficial effect. We alluded to this criterion in section 5.5 when we stated, "in some instances, it may be possible to make an inference of exaptation by examining the phylogenetic history of the trait, as in the case of birds' feathers evolving from reptiles' scales for a thermal insulation effect and subsequently becoming exapted to flight." But this reference was somewhat obscure and certainly inadequate. We are grateful to these commentators for remedying this deficiency. As Blackburn notes, such evidence is *sufficient* to demonstrate that exaptation has occurred. However, as he also notes, if the effect is acquired prior to the evolution of the structure, or they occur simultaneously (i.e., the historical criterion for demonstrating exaptation is not satisfied), this is only weak evidence of adaptation. First, a phylogenetic analysis is often limited by the completeness of the cladogram used in the analysis (**Blackburn**). If structure and effect occur at the same point in the phylogenetic tree, it may be because the cladogram is incomplete (i.e., exaptation is still a possibility even if its probability of being true is reduced). Second, phylogenetic analyses often cannot efficiently sort out the order of evolutionary processes that occur in between speciation events – the temporal separation between the origin of a structure and subsequent exaptation to a new effect could be collapsed into a single point on a phylogenetic tree if they occur between speciation events. Finally, evidence of adaptation also requires some evidence that the phenotype was modified by selection for the effect (i.e., that the phenotype did not evolve by chance).

This example also illustrates the point made above: *If a methodological tool is really useful in testing adaptationist hypotheses, it will also tend to be useful in testing alternative hypotheses.* We argued that the search for evidence of special design is useful in demonstrating exaptation and spandrel, and the search for evidence of optimal design is useful in demonstrating constraint. However, while we argued that comparative studies are useful tools in the adaptationist toolbox, we did not provide an example of how comparative studies could be used to test alternatives such as exaptation. **Blackburn**, **Dannemiller**, and **Deleporte** showed how this is possible, and Blackburn's Figure 1 nicely summarizes how phylogenetic analyses can be used to help build empirical cases for adaptation, exaptation, and spandrel.

Nonetheless, although phylogenetic analysis can build a strong case that exaptation has occurred, it cannot, by itself, establish that adaptation for a particular beneficial effect has *not* occurred. Through fortuity, a trait may acquire a new beneficial effect. The new beneficial effect, however, may lead to modifications in the trait, sometimes leading to significant reshaping, such that the trait's design is to be understood as (secondary) *adaptation* for the new effect. The classic example of bird feathers provides a nice illustration. We know, from the relative timing of the first appearance of feathers and ability to fly, that feathers were exapted to flight. Some feathers have undergone substantial redesign that can only be understood as *adaptation* for flight. The phylogenetic analysis cannot provide the critical information; only a consideration of design can. As emphasized in the target article, a trait can be a complex mixture of adaptation, exaptation, spandrel, and constraint, and it is, in principle, possible to distinguish them empirically (sect. 5.5). Gould (2002) makes the same point in his recent treatise and gives several examples in which one can identify both the exapted parts of a trait and the secondarily adapted parts.

Reply 2: Cladistic analysis is not necessary to establish that adaptation has occurred. Some commentators argued that phylogenetic analyses were not only sufficient but also *necessary* for distinguishing between adaptation and exaptation. According to **Dannemiller**, "It is analyses based on historical and cladistic criteria that, Gould argued, would ultimately be necessary to separate adaptations from exaptations." Similarly, **Deleporte** argued that "special design qualifies aptation, but only history can efficiently sort exaptation from adaptation."

Under this characterization, special design is insufficient to demonstrate adaptation – additionally, one must show that the structure does not originate prior to the acquisition of the beneficial effect on the phylogenetic tree. None of the commentators who explicitly or implicitly challenged the idea that special design is sufficient to demonstrate adaptation gave any logical argument for why our analysis in the target article was wrong. **Deleporte** merely asserts (without justifying) that phylogenetic analyses are necessary to distinguish between adaptation and exaptation. **Dannemiller** bases his position on the following quote from Gould's final treatise:

> The relative timings for the origin of a form and for the inception of its current function – as inferred either from the branching points of a cladistic analysis, or from direct knowledge of historical sequences – provide the main criteria for distinction of exaptation from adaptation. (Gould 2002, p. 1235)

However, we think Dannemiller incorrectly interprets this passage. First, the quote is ambiguous on the necessity of phylogenetic analyses and could just as easily be interpreted as saying that they are *useful* or *sufficient* to demonstrate exaptation. Second, even in this treatise, Gould has always cited with favor, and without any hint of reservation, Williams' (1966) analysis of adaptationism (Gould 2002; Gould & Vrba 1982), which is the classic defense of the special design standard. Third, it is quite telling that Gould has over the years accepted design evidence *by itself* (i.e., *not*

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in conjunction with other criteria such as the phylogenetic cooccurrence of structure and function) as sufficient to demonstrate adaptation as well as to provide criteria for what would constitute evidence of adaptation (e.g., Gould 1977 [essay 12]; 1980 [essay 3]; 1983 [essays 1–3]; 1985 [essays 1 and 2]; 1991b [essays 14 and 17]). Finally, Gould has specifically recognized that evidence of "complex adaptive design" is sufficient to demonstrate adaptation (Gould 1997d, p. 57). If Gould thought that evidence of complex adaptive design was sufficient to demonstrate adaptation, he could not have believed that phylogenetic analyses were *necessary* for distinguishing adaptation and exaptation.

At the same time, it should be noted that our standard for the acceptance of adaptationist hypotheses is more stringent than Gould's. As indicated in the target article, we argue that sometimes exapted learning mechanisms (ELMs) can generate cognitive traits that eventually come to exhibit "complex adaptive design." The special design criterion that we advocate would not allow the scientist to accept a particular adaptationist hypothesis until one has shown that all alternative hypotheses (including ELM hypotheses) have difficulty in accounting for the features of the trait.

Objection 5: Optimality reasoning cannot tell us much, particularly regarding cognitive mechanisms. **Schank** claims that humans are limited beings whose cognitive mechanisms are more often characterized by satisficing than optimizing. Therefore, optimality analyses will tell us little about human cognition.

Reply: One of us recalls John Maynard Smith responding to precisely this point made at a Ciba Foundation symposium on characterizing psychological adaptations (Ciba Foundation 1997). We must not conflate two different ways in which we might use the term *optimality.* As described in the target article, optimality modeling asks what outcome selection would produce under constraints. Adaptation does not come free, and hence, all adaptations evolve despite their costs. Maynard Smith noted that selection relentlessly favors the *best* (optimal *under constraints*) design available. Selection does not "satisfice" – merely favor what is "good enough" or "necessary" for survival and reproduction (see also Williams [1966] on this form of reasoning). The optimal cognitive design available under constraints, however, need not be the one that maximizes the number of right answers or takes into account all available information; the additional costs of a computationally expensive procedure may outweigh its marginal benefits over a less accurate but cheaper procedure. Though not using formal optimality analyses, Shepard (1992) nicely illustrates this form of reasoning when asking why we have three receptor types for color perception (in addition to the ability to assess overall lightness-darkness). This is the minimum number needed to achieve color constancy under natural lighting conditions. To perceive true color (spectral frequencies of object reflectance) under these conditions, we would need at least three additional receptor types. Given small marginal returns to perceiving true color over achieving color constancy, however, the "optimal" receptor number may well be the number we have. In our view, optimality analyses may prove to be very useful to understanding *why* our cognitive capacities are "limited" and *why* we utilize "satisficing" procedures.

Relatedly, **Schank** argues that optimality analyses will offer little insight into constraints. Just as a chess player can hide an imposed constraint ("no castling") through judicious play, so selection can hide constraints. Most analogies break down somewhere, however, and Schank has extended this one beyond its appropriate relevance, in our view. As **Figueredo & Berry** note, selection does not design with deliberate foresight. Unlike the chess player, then, selection will tend to favor the best design available under constraints, even if that design fully reveals the constraints under which it was operating.

Objection 6: The program we outline does not serve as an effective guide to research or theory on human behavioral adaptation. **Smith**, a leading human behavioral ecologist, argues that the research program that seeks to understand adaptation in terms of design "looks far better in the abstract – as philosophy – than in practice – as a guide to either empirical research or theory building," and recommends an alternative research program that seeks to understand phenotypic plasticity in terms of what behavioral biologists refer to as "conditional strategies," or psychologists might label "broad-purpose learning mechanisms." Perhaps similarly, **Schank** recommends a program of research that focuses on "vicarious selection and transmission mechanisms" accounting for learning and transmission between generations. **Atran** offers a different but related argument: that "strong adaptationist" attempts to explain organic design in terms of specific adaptations should be combined with a "weak adaptationist" approach that acknowledges that some functional complexity "results largely from more general physical, chemical or biological processes governing complex systems."

Reply 1: Conditional strategies and broad-purpose learning processes should be distinguished. **Smith**'s conclusion conflates two very different phenomena. Within behavioral ecology, a *conditional strategy* is an adaptive expression of different tactics depending on cues that, in the environments in which the strategy would have evolved, moderate tactics' net benefits. The reproductive strategies of collared flycatchers discussed earlier provide an illustration. Males with large forehead patches tend to invest in offspring less than other males, except late in the breeding season. Trade-offs between mating effort and parental investment were presumably important in the shaping of tactic choice. Large-patched males have greater access to females as extrapair mates and purportedly invest to a larger extent in extrapair mating effort than other males. Late in the season, however, most females have already bred, such that there are few extrapair mating opportunities. At that time, it may pay large-patched males to invest in offspring as much as other males. Female choice, then, is similarly affected by season. Females prefer large-patched males as extrapair partners. They show no preference for them as social partners throughout most of the season; presumably, whatever benefits they gain in offspring genetic fitness is offset by lower paternal investment. Late in the season, when choosing a large-patched male does not entail trading off paternal investment, however, females *do* prefer them as social mates. A number of other aspects of collared flycatcher mating behavior also evidence a remarkable degree of conditionality and context-dependency (e.g., female interest in extrapair males depends on the size of the forehead patch of her social mate).

Smith's commentary suggests that these and other conditional strategies studied by behavioral ecologists are the outcome of "broad-purpose learning mechanisms." Ironically, however, that is almost certainly what these conditional strategies cannot be. To show that they could be, one

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would have to both demonstrate that collared flycatchers possess a "broad-purpose learning mechanism" that performs similarly across different domains of behavior, and also specify the constellation of inputs to that system that ontogenetically shape behavior to be conditional on precisely the conditions on which collared flycatcher behavior is conditional. To show, further, that this mechanism is adaptive across domains, one would have to also demonstrate that the constellations of inputs typically encountered by these birds result in behaviors that, across domains, are adaptive. That these requirements can be met seems very unlikely. Hence, most behavioral ecologists accept that selection has shaped the remarkable facultative nature of such mating strategies to be *uncoupled* from the facultative nature of a host of behaviors in other domains (e.g., foraging, predator avoidance, investment in kin, investment in social alliances, etc.).

Indeed, modeling examples show that the *inability* of selection to uncouple performance across domains imposes a constraint that limits adaptation to specific problems (e.g., Kirkpatrick and Barton's [1997] assumption that female mate choice based on sexual signals entails costs in ability to perform other tasks well, such as foraging or predator avoidance [e.g., through pleiotropic effects of perceptual mechanisms], not surprisingly results in the expectation that performance on all tasks will be compromised by the constraints; see Houle & Kondrashov 2002). Collared flycatcher mating and parenting strategies do indeed exhibit "phenotypic plasticity," but it is plasticity patterned through processes *specific to* mating and parenting strategies. Special-purpose adaptation need not be understood through the metaphor of "the releasing stimuli and fixed-action-patterns of classical ethology" (**Smith**). (This point also addresses the related claim by **Brown** that "flexibility is designed and not due to random chance"; we consider the "decision rules" of contingent strategies [which may involve flexible development] to be adaptations that generally exhibit "specificity and proficiency" for a function – albeit through variable expression.)

Of course, humans do learn. As stressed in the target article, learning itself is accomplished through adaptations (see also **Brown**, **Dickins & Dickins**, **Rutherford**). Based on empirical data and theory, evolutionary psychologists argue that learning is influenced by domain-specific functional specializations; language learning, the learning of food aversions, the learning of snake phobias, and the learning of cultural information each obey regularities not shared by the other learning phenomena. Learning in these domains need not be a result of fully separate mechanisms (**Smith**), and some evolutionary psychologists may have been wrong to imply so. Nonetheless, learning appears to be influenced by inputs specifically adapted to particular domains. Furthermore, Smith is absolutely correct in emphasizing the "cognitive niche" that humans occupy. Without doubt, the success of humans has centrally depended on their ability to acquire and transmit cultural information. Evolutionary psychologists (e.g., Boyer 1998; 2000; Tomasello 2000) have sought to understand the nature of human adaptations upon which cultural learning is founded, though this understanding is far from complete (see also Flinn 1997). As noted earlier, the fact that learning and cognitive processes can be exapted to many novel tasks (even if similar to ones in which they evolved to perform) may increase the difficulty of inferring their function. (See **Simpson** on the potential utility of recent advances in information processing theory and methods for testing special design claims.) Moreover, as Dickins & Dickins rightly point out, obtaining evidence that might help one assess a claimed function (such as developmental specificity) is sometimes intractable. The target article did not claim that the adaptations and their functions will be readily discerned; its focus was on methodologies for doing so.

Reply 2: Physical and biological properties are potentially important sources of complexity. A theme underplayed in the target article but prominent in Gould's writings is one that traces to the arguments of D'Arcy Thompson (1917) presented in his book *On Growth and Form:* That much organic complexity is actually the result of physical and chemical forces and not a reflection of functional specialization (see, for instance, Gould 2002, pp. 1182–214). The most important modern work in this tradition is Stuart Kauffman's (1993) *The Origin of Order,* in which he argues that complex dynamic systems have intrinsic properties that generate "order for free," properties that are to be understood independently of the precise historical forces that shaped the organism. **Atran**'s argument that aspects of human cognitive architecture may be understood partly in terms of "more general physical or biological processes," the appreciation of which does not require knowledge of the particular historical environments to which humans have been exposed, appears to fall along this general line of reasoning. Much complexity in human cognitive architecture, so goes the claim, may not have been shaped to solve particular adaptive problems. (See also **Schank**, who argues that the human genome does not possess the number of genes sufficient to support a multitude of cognitive specializations, a claim that, in our view, cannot be fully evaluated in a nonspecific form.)

We note, first, that **Atran**'s version of "strong adaptationism" is not the form of adaptationism we described. Whereas we proposed adaptationism as a methodological approach to understanding organic complexity, Atran's strong version is rooted in an ontological assumption that functional specialization underlies complexity. Williams' (1966) classic exposition of arguments of design did not include "complexity" in his list of attributes that informally contribute to a conclusion that a "presumed function is served with sufficient precision, economy, efficiency, etc. to rule out pure chance as an explanation" (p. 10). Though he did note, "Adaptation is [sometimes] assumed . . . not on the basis of a demonstrable appropriateness of the means to an end but on the indirect evidence of complexity and constancy" (p. 10), evidence of complexity alone he described as "motivation" for research into function, not a sufficient basis for inferring function. Atran's commentary is a useful reminder that organic complexity is not, by itself, evidence for functional specialization.

In the specific case of language, the argument that syntactic recursion reflects unspecialized complexity strikes us as not a particularly well-explicated one (e.g., in what sense is recursion "a physically optimal sort of interface . . . between two physically suboptimal . . . systems" [**Atran**], and how does this theory explain the precise features of language?). **Haig & Durrant** offer the general argument that criteria of "explanatory coherence" be applied to the evaluation of alternatives (most importantly, *explanatory breadth,* the ability to explain a greater range of facts), which strikes us as very useful, and claim that alternatives

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to the nonselectionist accounts for the origin of language "suffer in terms of their explanatory coherence" (see Durrant & Haig's highly relevant 2001 paper, which we did not cite in our target article because it was published after ours was submitted; see also Holcomb 1996). Additionally, evidence for positive selection of genes involved in language bolsters the argument for adaptation (see **Swanson**, **Moyzis**, **Fossella**, **Fan & Posner** [henceforth **Swanson et al.**] and below). Of course, it is quite possible (indeed, likely) that preexisting features were exapted to specific benefits involved in language and other symbolic processes, with subsequent selection for features specialized for language. **Dickins & Dickins** present the interesting hypothesis that stimulus equivalence was one such adaptive feature. That a complex feature not specialized for function of the sort proposed by Atran was so exapted is a hypothesis in need of additional explication and bolstering.

Additional point 1: Comparative evidence of homology is useful in eliminating ELM hypotheses. **Roney & Maestripieri** propose that comparative evidence of homology in a psychological trait, when used in conjunction with design evidence, is useful for eliminating ELM hypotheses. They argue that the demonstration of homology shows that the organism has inherited a biological predisposition for producing the trait. Moreover, while they agree with us (as do **Blackburn**, **Dannemiller**, and **Deleporte**) that comparative analyses are useless for analyzing uniquely human traits, they argue that many human psychological traits could be homologous to those in other primate species, such that evidence of homology could play a much larger role in human evolutionary psychology than is currently appreciated. We think this is a very interesting idea precisely because homology intuitively seems to suggest biological predisposition. It could be a very useful piece of evidence in sifting through competing hypotheses for psychological design. At the same time, we think the idea may need some development and suggest caution in its application.

One potential problem that we see with homology in a psychological trait is that its relation to biological predisposition may be tenuous. A learning mechanism that produces exapted effects could, in principle, be preserved during speciation such that homologous psychological mechanisms in sister species are exapted to the same effect (see species 3 and 4 of Figure 1A in **Blackburn**'s commentary). As a hypothetical example, consider the human capacity for reading. People can learn to read quite well (demonstrating proficiency), and they develop neurological structures in the brain that come to exhibit specificity for this task. Most researchers regard the capacity for reading as the byproduct of some unspecified ELM because reading is a recent phenomenon, and there is no developmental predisposition for it (Pinker 1997a). However, imagine that human beings diverge into two or more species, each retaining the capacity to read. A Martian scientist utilizing the criterion of homology, in conjunction with evidence of specificity and proficiency, would erroneously conclude that each species had psychological adaptations for reading.

Moreover, it is not clear that the failure to find evidence of homology has any bearing at all on whether a trait is an adaptation or the product of an ELM. For these reasons, evidence of homology does not appear to be any better than consistency with biological predisposition, as the example just given suggests.

Additional point 2: The relevance of molecular genetics. **Swanson et al.** argue that evidence from molecular genetics, showing that genes associated with particular traits have undergone positive selection, constitutes an additional source of information pertinent to testing adaptationist hypotheses. They illustrate this point with exciting lines of research on ADHD. They propose that there is a subtype of ADHD patients with the DRD4 7R allele that bears the signs of positive selection. In particular, this allele differs radically from the other common alleles at this locus by more than six recombinations or mutations, and so is not a simple variant of these other alleles (Ding et al. 2002). Moreover, this allele is younger than the other common alleles, which suggests that some force has modified it (i.e., selection). Further, the DRD4 7R allele subgroup of ADHD subjects appears to show no deficits in neurological testing, whereas their ADHD counterparts lacking this allele do show deficits. Swanson et al. hypothesize that the 7R-present allele may contribute to a trait of high novelty seeking in some individuals, the function of which could be to fill new, available niches through migration. Though the molecular genetic data are compelling evidence for selection, this particular hypothesis is not to be accepted on the present evidence in light of our criteria, as alternatives to their proposed function are possible (e.g., the 7R allele may have other, unknown advantageous effects [via pleiotropy] accounting for its success *despite* its association with ADHD). Swanson et al. have developed a prima facie case for the 7R allele contributing to an adaptation *for a particular beneficial effect,* acceptance of which will depend on whether the hypothesis, after undergoing rigorous testing, satisfies the onerous demands of the special design criterion.

Additional point 3: The relevance of maladaptation. **Klein** offers the very useful observation that knowledge about maladaptation can inform the nature of adaptation, and rightly points out that the history of medicine is replete with such examples. One way in which psychological adaptations can and have been studied is through the phenomenon of dissociation. For example, Stone et al. (2002) found that a patient with specific brain damage performed worse on social contract reasoning problems than reasoning problems concerning precaution, despite the problems' equal difficulty, according to controls. This evidence suggests that these two forms of reasoning do not share at least one component, hence offering potential insight into underlying cognitive architecture. (For other examples, see Klein et al. 2002a; 2002b.)

Additional point 4: The study of traditional societies. **Atran** and **Fuentes** noted the need to study traditional societies and not merely "standard populations" (such as university students). We did not explicitly discuss this point but, clearly, such studies are useful and, in some cases, essential to an understanding of psychological adaptations. Study of traditional societies is not an additional tool for studying adaptation in the sense that studies of development, optimality, molecular genetics, or maladaptation are; studies using any of these approaches can, in principle, be done in traditional settings.

R5. The utility of the adaptationist framework to an understanding of behavior

The focus of our article was on the epistemological issues concerning how one identifies an adaptation and tests al-

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ternatives to specific adaptationist hypotheses. Though the utility of the approach for understanding human behavior was presumed, we did not address in detail the specific ways in which answering questions of adaptation, exaptation, byproduct, or constraint contribute to empirical research or theoretical development in behavioral science. A number of authors comment on the utility (or lack thereof) of an adaptationist approach. **Davies** in particular challenges the claim that "the study of psychology requires or even benefits much from standards of evidence that enable us to distinguish adaptations from nonadaptation." (See responses to related points by **Smith** and **Dupré** above).

Several commentaries counter this claim and argue the manner in which an adaptationist perspective can contribute to psychology. **Schaller** notes that psychologists will say, "so what?" to evolutionary explanations if they generate no novel predictions about the way the mind works. When, however, "one speculates that a specific psychological process emerged as an adaptation that facilitated some specific functional outcome, one opens the door to a bunch of additional implications . . ." that are "translatable into hypotheses that can be tested and, if supported, may reveal brand-new discoveries about the here-and-now." He nicely illustrates this point with several examples. **Hagen** emphasizes the "spectacular successes" achieved through application of a special design standard in modern medicine but acknowledges that these have largely come without any help from evolutionary theory. In the study of human cognition, however, evolutionary theory may be particularly helpful in generating ideas about what to look for – that "a window into the functioning of the brain" results when "we look deeply at the environment of our ancestors as focused through the lens of reproduction." Faster progress in cognitive science may be possible using an evolutionarily informed approach, in that "it is much easier to find something if you have some idea of what you are looking for." **Simpson** sees the potential for greater contribution to psychology by evolutionary science with a conceptual shift "away from the mere description and exploration of possible adapted traits toward a more complete testing and understanding of traits that might truly be adaptations."

R6. Summary

With great confidence, we suspect that not all commentators will be satisfied with our responses. We fully expect that debate on these matters will continue. Some will be resolved by further discussion. Others will be decided by progress, or lack thereof, achieved by specific forms of adaptationist thinking. From our perspective, however, our dialogue with commentators has been a productive one; we hope that it will ultimately contribute to progress in evolutionary behavioral and psychological science. Our own thinking has been altered or challenged by this exchange in a number of ways. For instance, we underemphasized the potential utility of phylogenetic analyses. And, though we stressed, "there may be no uniform list of criteria that must be satisfied to demonstrate that a trait has been specifically designed by selection for a function" (sect. 3.1.6), we did not consider several criteria and tools that may be useful in conjunction with those we did discuss: evolutionary genetic analysis, the study of maladaptation, and, with caution, comparative analyses pertinent to ELMs. Because of the variety of criteria other than design considerations that may be useful, it may be misleading to term the standard we espouse the "special design standard"; the relevance of criteria we and others discuss can be generally understood in terms of inference to the best explanation.

Commentators are clearly divided in their predictions about whether the adaptationist program in human behavioral science has much to offer, with less sanguine views generally (though not universally) based on ontological rather than epistemological concerns. Though our target article focused on epistemological issues, we recognize that adaptationist methodology will be more or less useful depending on how the world happens to work. We remain cautiously optimistic that the adaptationist approach, appropriately applied, will yield tremendous gains in knowledge about human behavior – strides that this approach can uniquely achieve.

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The letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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