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 design 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-