Evolutionary Psychology: An Exchange

To the Editors:

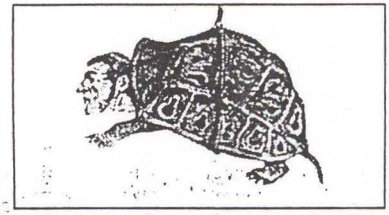
Evolutionary psychology is the attempt to understand our mental faculties in light of the evolutionary processes that shaped them. Stephen Jay Gould [*NYR*, June 12 and June 26] calls its ideas and their proponents "foolish," "fatuous," "pathetic," "egregiously simplistic," and some twenty-five synonyms for "fanatical." Such language is not just discourteous; it is misguided, for the ideas of evolutionary psychology are not as stupid as Gould makes them out to be. Indeed, they are nothing like what Gould makes them out to be.

Evolutionary psychology often investigates the adaptive functions of cognitive and emotional systems—how natural selection "engineered" them to solve the kinds of problems faced by our ancestors in their struggle to survive and reproduce. The rationale follows from two premises Gould himself states nicely:

> (1) "I...do not deny either the existence and central importance of adaptation, or the production of adaptation by natural selection. Yes, eyes are for seeing and feet are for moving. And, yes again, I know of no scientific mechanism other than natural selection with the proven power to build structures for such eminently workable design."
>
> (2) "The human brain is the most complicated device for reasoning and calculating...ever evolved on earth."

Quite so. First, adaptive design must be a product of natural selection. Complex organs like eyes have many precise parts in exacting arrangements, and the odds are astronomically stacked against their having arisen fortuitously from random genetic drift or as a byproduct of something else. Second, the brain, like the eyes and the feet, shows signs of good design. The adaptive problems it solves, such as perceiving depth and color, grasping, walking, reasoning, communicating, avoiding hazards, recognizing people and their mental states, and juggling competing demands in real time are among the most challenging engineering tasks ever stated, far beyond the capacity of foreseeable computers and robots. Put the premises together—complex design comes from natural selection, and the brain shows signs of complex design—and we conclude that much of the brain should be explained by natural selection.

So where's the controversy? Gould claims his targets invoke selection to explain *everything*. They don't. Everyone agrees that aspects of the living world without adaptive complexity—numbers of species, nonfunctional features, trends in the fossil record—often need different kinds of explanations, from genetic drift to wayward asteroids. So



yes, we all should be, and are, pluralists. But we should not be *indiscriminate* pluralists. Gould blurs his own distinction when he writes,

> We live in a world of enormous complexity in organic design and diversity—a world where some features of organisms evolved by an algorithmic form of natural selection, some by an equally algorithmic theory of unselected neutrality, some by the vagaries of history's contingency, and some as byproducts of other processes. Why should such a complex and various world yield to one narrowly construed cause?

It shouldn't, of course, but then most researchers aren't trying to explain the entire "complex and various world." Many of them *are* trying to explain "complexity in organic design"—the remarkable natural engineering behind the ability of creatures to fly, swim, move, see, and think. Now, complex design *should* yield to one "narrowly construed cause"—Gould knows of no scientific mechanism other than natural selection with the proven power to build it, remember? Those blinkered, narrow, rigid, miserly, uncompromising ultrapanselectionists whom Gould attacks are simply explaining complex design in terms of its only known cause.

In the case of the human brain, Gould accuses evolutionary psychologists of ignoring an alternative:

> Natural selection made the human brain big, but most of our mental properties and potentials may be spandrels—that is, nonadaptive side consequences of building a device with such structural complexity.

Evolutionary psychologists are not ignorant of this hypothesis. They have considered it and found it to be unhelpful.

First, it is rooted in a false dichotomy between "conventional natural selection working in the engineering mode" and "spandrels," the nonadaptive byproducts that are "sources for later and fruitful reuse" and which "may later be co-opted" for useful purposes. What is missing from these phrases is the subject of the verb. Reuse *by whom*? Co-opted *by what*? Most snails have a spandrel formed by the space around their shell axis; what allows some species to use it to brood their eggs? Are they generally more clever and dextrous? No; their anatomy and nervous systems have been altered in an adaptive way to take advantage of the spandrel. So the reuser and co-opter are none other than: natural selection. Not only do co-opted spandrels implicate selection, but selection implicates spandrels. We evolved from organisms without eyes, feet, and other complex organs. The organs must have originated in precursors that were spandrels for some ancestral organism. The distinction in which spandrels work "in addition (and sometimes even opposed to)" natural selection is spurious.

Unlike snails, of course, we humans *are* clever enough to co-opt our spandrels in our lifetimes, as when we use our noses to hold up eyeglasses. But how did our brains get clever enough to do that? This is exactly what a theory of brain evolution must explain. Explaining the evolution of the human intellect in terms of humans' ability to co-opt spandrels is circular.

Second, Gould casually slides from saying that natural selection made the brain "big" to saying that the brain was built with "structural complexity," as if bigness and complexity were the same thing. As Gould himself has argued, bigger brains aren't necessarily more complex or smarter brains. Worse, the suggestion that humans were selected for bigger brains is a perfect example of the sin Gould attributes to others, the confusion of a byproduct with an adaptation. If *anything* is a byproduct, it is the size of the human brain, which guzzles nutrients, makes us vulnerable to blows and falls, compromises the biomechanical

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design of the woman's pelvis, and makes childbirth dangerous. Bigness of brain is surely a byproduct of selection for more complex (and hence hardware-demanding) computational abilities, ones that allowed our ancestors to deal with tools, the natural world, and one another.

A rejection of Gould's theory does *not* put nonadaptive features "outside the compass of evolutionary psychology"; nor was Gould the first to call attention to them. The original arguments for recognizing nonadaptive features came from the founding document of evolutionary psychology, George Williams's *Adaptation and Natural Selection*, long before Gould and Lewontin reiterated them (without attribution) in their "Spandrels" paper. Nonadaptive explanations have been commonplace in the field ever since, as Gould must be well aware, for in one column he touted a nonadaptive explanation of the female orgasm taken from another founder of evolutionary psychology, Donald Symons. According to the most popular view in the field, many other important human activities are spandrels, including art, music, religion, science, and dreams. Gould's accusation is not even close to being accurate.

Evolutionary psychology is "even more fatuous," according to Gould, for thinking seriously about the environment in which our ancestors evolved. That is "outside the primary definition of science," he says, because claims about that environment "usually cannot be tested in principle but only subjected to speculation." Really? Then what makes Gould so certain that our ancestors' environment lacked written language—the basis for his argument that reading is a spandrel? Obviously it is the archeological record, which shows that writing is a recent invention, and the ethnographic record, which shows that writing is absent from cultures not in contact with any of the inventors. It is precisely such evidence that leads evolutionary psychologists to infer that the ancestral environment lacked agriculture, contraception, high-tech medicine, mass media, mass-produced goods, money, police, armies, communities of strangers, and other modern features—absences with profound implications for the minds that evolved in such an environment.

Gould is uninformed when he repeats the cliché that evolutionary reasoning is just cocktail-party speculation. The standards of the field require a good empirical fit between the engineering demands of an adaptive problem and the facts of human psychology. The former is grounded in game-theoretic and other optimality analyses, in artificial intelligence and artificial life simulations, and in relevant sciences such as genetics, physiology, optics, or ecology. The latter is based on converging evidence from experiments with children, adults, and neurological patients and from survey, historical, ethnographic, paleoanthropological, archeological, and economic data. Far from being "barren," the adaptationist approach has, for over a century, driven the most rigorous, elegant, and empirically rich branch of psychology, perception. Today it is spawning new insights and intensive modeling and data-gathering on every other aspect of the mind, including reasoning, mental imagery, memory, language, beauty, sexual desire, autism, emotions such as fear and disgust, violence, the numerical abilities of children and animals, and the shaping of personality.* Gould's hostility to this exciting field is a missed opportunity for both.

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*For recent reviews, see Jerome Barkow, Leda Cosmides, and John Tooby, editors, *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (Oxford University Press, 1995); Robert Wright, *The Moral Animal: Evolutionary Psychology and Everyday Life* (Pantheon, 1994); and Steven Pinker, *How the Mind Works* (Norton, 1997).

To the Editors:

In his recent two-part article on "Darwinian Fundamentalism" Stephen Jay Gould makes the important point that natural selection is not the only element in evolution, though it is undoubtedly an important one. He quotes Darwin himself in support of this argument, and coins the memorable dictum "Variation proposes and selection disposes." Professor Gould also makes the extremely important argument that many variants are carried forward in the progeny despite conferring no survival advantage, and applies to these neutral variants the amusing term "spandrels." This term, borrowed from architecture, is appropriately used in Professor Gould's field of paleobiology, which for obvious reasons rests heavily on the architecture of fossil remains.

As pharmacologists, we would suggest that this argument can derive even stronger support from the genetic studies of variation in drug response among present-day living organisms. Pharmacogenetics is a specialized area of genetics, more familiar to many physicians and chemical companies than to most geneticists. In medicine, pharmacogenetic variation accounts for many differences between people with respect to their responses to a given drug, even to the point that some individuals have been fatally poisoned by a drug that was curative to most of those who received it. Such dramatic variations can be due to genetically determined differences either in the metabolism of a drug or in the cellular mechanisms on which the drug acts. Pharmacogenetic variability is also manifested in the responses of insects to chemical insecticides, and of bacteria to many different antibiotics.

Many (though not all) of these variations in response to drugs or toxins arise from random gene mutations. Some of these mutations are clearly disadvantageous, decreasing the reproductive fitness of the mutant individuals or decreasing the survival of the progeny, and are therefore eliminated by the forces of natural selection. Others are advantageous in these respects, conferring a survival advantage, and therefore lead to gradual evolution of the species in accord with the classical Darwinian concept. Professor Gould's argument is strongly supported, however, by the fact that most of the mutations that survive in the offspring are more or less neutral with respect to reproductive advantage,[1] or perhaps cause slightly *reduced* fitness.[2] Why, then, do they survive? The answer appears to be that they constitute a sort of biological insurance policy for the species, rather than for the individual. Like Professor Gould's "spandrels," they have no particular use when they arise, but may acquire a use later on.

For example, a particular pharmacogenetic variation in an insect species may make certain individuals in a given insect population extremely resistant to a new insecticide. However, such variations arise long before the insecticide appears on the scene, and in many instances are somewhat maladaptive in the absence of a poison, so that the frequency of the variant gene remains low in the population. When the new chemical appears, however, the variant individuals have a much better chance of surviving, and thus enable the species as a whole to survive. Once the chemical assault has passed, the variant individuals are again at a reproductive disadvantage with respect to the typical population in the normal environment, and their numbers again decrease to the previous low "insurance" level.[3] Only if the chemical stress is maintained over generations does the mutant type eventually become the most prevalent one, through the death of the previously dominant type that was not resistant to the new insecticide. In that case, the otherwise disadvantageous mutation then becomes the basis of an evolutionary change.

In short, pharmacogenetic variation operates for the benefit of a population, but not necessarily for the overall benefit of the variant individual. Whether or not a given pharmacogenetic variant will ever be used cannot be known in advance. The "ultra-orthodox" Darwinian view, as Professor Gould has argued, is therefore a marked oversimplification, and ignores the importance of temporary or localized environmental factors in determining whether a given mutation is or is not a survival advantage, independently of its effect on general reproductive fitness.

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[1]M. Kimura, "Evolutionary rate at the molecular level," *Nature* 217, pp. 624–626, 1968.

[2]M. Gell-Mann, *The Quark and the Jaguar* (W. H. Freeman, 1994), p. 68; D. N. Cooper, M. Krawczak, and S. E. Antonarakis, "The nature and mechanisms of human gene mutation," in C. R. Scriver et al., editors, *The Metabolism and Molecular Bases of Inherited Disease* (McGraw-Hill, 1995), pp. 259–291.

[3]Dr. Neil W. Forrester, New South Wales (Australia) Agricultural Research Station, unpublished data; W. Kalow, "Pharmacogenetics in biological perspective," *Pharmacological Reviews*, in press, 1997.

Stephen Jay Gould *replies*:

If we define poetic justice as defeat by one's own favored devices—Robespierre before the guillotine or Midas in golden starvation—then we might be intrigued to find Steven Pinker, a linguist by training, upended by his own use of words.

He begins by unjustly characterizing my two recent articles on "Darwinian Fundamentalism" as a misguided attack on the nascent field of evolutionary psychology. I can't imagine, first of all, what thesaurus could cast such a broad net for synonyms of "fanatic." More importantly, I cite evolutionary psychology as just one illustration within a much wider critique—and I devote only the last part of my second article to the subject. My objections, however forceful, are clearly offered with constructive intent, for I praise the field's goal, while arguing that a truly evolutionary psychology cannot arise when leading practitioners so strongly exaggerate an adaptationist style of explanation that represents but one mode of evolutionary causation among many legitimate alternatives. I wrote:

> Humans are animals and the mind evolved; therefore, all curious people must support the quest for an evolutionary psychology.

I also stated my central critique:

> Evolutionary psychology could, in my view, become a fruitful science by replacing its current penchant for narrow, and often barren, speculation with respect for the pluralistic range of available alternatives that are just as evolutionary in status, more probable in actual occurrence, and not limited to the blinkered view that evolutionary explanations must identify adaptation produced by natural selection.

Pinker then follows his false opening charge with a three-part argument overturned by its own illogic and verbal inconsistency. The first third denies that evolutionary psychologists rely exclusively on adaptation. The second third (as I shall document below) shows how Pinker's restrictive focus upon adaptationist thinking leads him to misunderstand the concept of spandrels. The closing third then extols the power and range of adaptationist explanation, but gives the game away by equating this limited mode with "evolutionary reasoning" in general.

But the first and third parts contradict each other. Which claim does Pinker want to make: that pluralism reigns in evolutionary psychology (and I characterized the field unfairly), or that adaptationism reigns as a synonym for "evolutionary reasoning" (and my warnings are sterile)? He can't have them both. (My true position, of course, holds that adaptationism rules wrongly and too restrictively.)

Pinker then centers the second part, the guts of his critique, upon another verbal error that exposes the depth of his commitment to adaptationist logic, and his consequent inability to conceptualize the alternatives properly, if at all. (Words and taxonomies often exert a tyranny over thoughts. If you have neither a term nor a category for something, you may not be able to see it—no matter how largely or evidently it looms.)

Pinker quotes me correctly in noting that I accept natural selection as the only known cause of "eminently workable design"—and he then writes, again correctly (although I would add the restrictive adjective "complex" to the beginning of the phrase), that "adaptive design must be the product of natural selection." But, two paragraphs later, and now in the sarcastic mode, he ridicules me with a very different claim that he regards as equivalent:

> Those blinkered, narrow, rigid, miserly, uncompromising ultra-panselectionists whom Gould attacks are simply explaining complex design in terms of its only known cause.

I'm astonished that Pinker doesn't see the key fallacy here (and he states the point several times, so he has not just made a careless slip): "complex design" does not equate with "complex adaptive design" (or what I preferred to call "eminently workable design"). Complex design forms a much broader category than adaptive design—and has many other potential evolutionary causes. Which brings us to the subject of "spandrels"—just one of the *nonadaptive* ways to build crucial parts of complex designs (but incomprehensible as a concept to Pinker because he conflates complexity with adaptation).

Spandrels are architectural byproducts, or automatic consequences, of building something in a certain way (and I am happy to allow that natural selection usually sets the mode of building in biology—not at all the same thing as saying that "every part of the building is an adaptation!)[1] Pinker then makes a truly strange move to deny the importance of spandrels—one that lays bare his adaptationist bias. He argues that when an ancestral spandrel becomes modified for an adaptive purpose in a descendant species, then natural selection is the agent of modification. Sure—and I have said so, prominently, in all my papers on the subject.[2] But so what? The *origin* of the spandrel remains nonadaptive as an automatic architectural byproduct. The secondary modification for utility is, well, secondary—and therefore not a criticism of the claim for nonadaptive origin of the original feature.

In fact, Lewontin and I coined the term "spandrel" precisely to make this crucial distinction between nonadaptive *origin* and possible later utility.[3] We did this in order to expose one of the great fallacies so commonly made in evolutionary argument: the misuse of a *current utility* to infer an adaptive *origin*.

Reasons for origins must not be confused with alterations for later use. Since evolutionary biologists are primarily interested in the origins of features, such an error becomes crucial. The snail umbilicus is, I admit, a fairly trivial example—but it illustrates the point and fallacy particularly well. The umbilicus arises nonadaptively as a spandrel—a necessary geometric consequence of growth by winding a tube around an axis. The fact that a *very few* species later adapt this space secondarily as a brood chamber doesn't challenge the claim for a nonadaptive origin of the space itself. After all, *thousands* of snail species have umbilici and do not brood their young (or do much of anything) in the necessary space.

Similarly, many universal features of human cognition—the primary data of evolutionary psychology—probably arise as spandrels of a general consciousness evolved for other reasons (almost surely adaptive). Freud argued that our fear of death acts as a key inspiration for the universal human institution of religion (for which many adaptationist explanations have been proposed, largely in the speculative mode). But I don't see how a biologist could argue that the human brain evolved consciousness in order to teach us that we must die. Knowledge of death is therefore probably a spandrel—an ineluctable consequence of consciousness evolved for other reasons. But this spandrel may then have inspired one of our defining institutions.

Pinker then appends two specific errors to this general fallacy—both further illustrating his failure to conceptualize the centrality of spandrels and other forms of nonadaptation. First, in trying to argue further that spandrels are adaptations (or intrinsically bound with adaptations), Pinker errs in writing that "we evolved from organisms without eyes, feet, and other complex organs. The organs must have originated in precursors that were spandrels for some ancestral organism." Here Pinker confuses spandrels with the fascinating and well-known notion—so important for understanding the quirky and unpredictable nature of evolutionary pathways—of "functional shift," a concept stressed by Darwin himself, and often identified with the unfortunate and confusing name of "preadaptation."

Structures evolved as adaptations for one function often get co-opted for a different role in a descendant lineage. (In the classic case, feathers evolved for thermoregulation in small running dinosaurs get co-opted later for flight in birds.) I don't think that eyes or legs originated as spandrels, but they did arise for one function and get co-opted for another (proto-eyes for light sensitivity, later co-opted for image forming; legs (as fins) for balancing in fishes, later co-opted for locomotion in terrestrial vertebrates)—whereas spandrels arise nonadaptively, and may then be co-opted for later utility.

The distinction between spandrels and preadaptations couldn't be more crucial—

[1]The concept of spandrels has been much debated in the biological literature. I have tried to analyze and rebut these criticisms in a technical article to be published this month in the *Proceedings of the National Academy of Sciences*, and entitled: "The exaptive excellence of spandrels as a term and prototype."

[2]See S.J. Gould and E.S. Vrba, "Exaptation: a missing term in the science of form," *Paleobiology*, 1984.

[3]See S.J. Gould and R.C. Lewontin, "The spandrels of San Marco and the Panglossian paradigm," *Proceedings of the Royal Society of London*, 1979.

CORRECTION

We regret that, owing to a printer's error, the final three lines were dropped from Timothy Ferris's review on page 20 of the September 25 issue. The last sentence of the review should read as follows:

> It would be the ultimate irony if it turned out that the human species had forestalled inquiry into the still-mysterious essentials of planet management just when such ignorance had come to pose an immediate threat to our future. □

—*August 28, 1997*

for preadaptation is an important and subtle concept within the adaptationist program (the co-optation of one adaptive design for another and quite different function), while a spandrel is a nonadaptive architectural byproduct that might (but also might not, as in most snail umbilici) be co-opted later for an adaptive use.

Pinker, I assume, doesn't grasp the distinction because his viewpoint only admits arguments about adaptation into the domain of "evolutionary reasoning" (his words)—so he cannot see beyond the single common feature of secondary co-optation in spandrels and preadaptations, while he misses the key distinction that spandrels *originate* as nonadaptive side consequences, and therefore differ fundamentally from preadaptations.

Second, Pinker makes a serious, and false, charge about our integrity by claiming that Lewontin and I failed to credit George Williams for formulating "the original arguments for recognizing nonadaptive features" in "the founding document of evolutionary psychology." I love Williams's book and cite it frequently—but not in our spandrels paper because neither he, nor I, nor anyone else in our century invented the idea. The concept has always been part of evolutionary theory. It was stressed most prominently by William Bateson, the inventor of the term "genetics," in his 1894 book, *Materials for the Study of Variation*. Darwin also discussed the concept (under the phrase "correlations of growth")—as Lewontin and I explored at length in our original paper, in a section entitled "The master's voice re-examined." The problem does not lie in full ignorance, but in the tendency of strict adaptationists to treat this inconvenient exception as a trivial oddity at best—one that is then swept under the rug of their favored and exclusive mechanism. Moreover, while I greatly value (and quote) Symons's support for the nonadaptive status of clitoral orgasm, I derived the argument from Alfred Kinsey's physiological studies. Interestingly, before Kinsey switched his life's work to the source of his iconic notoriety, he spent twenty years working on the taxonomy of the gall wasp *Cynips*, writing two famous monographs well known for their iconoclastic doubts about adaptationist explanations for the origin of new species.

The interesting letter from Kalow and Kalant illustrates (without so intending) the importance of maintaining pluralistic alternatives in evolutionary explanation. Strict Darwinians would explain this phenomenon—maintenance of neutral (or even slightly deleterious) variation that may later prove of great value in offering fortuitous resistance to a new insecticide—as a classical case of ordinary selection at the conventional organismic (or even genic) level, rather than, as Kalow and Kalant maintain, "a sort of biological insurance policy for the species, rather than for the individual." Strict Darwinians argue that mutations arise fortuitously, and at a low but dependable rate, due to the chemistry of nucleic acids. If slightly deleterious, these mutations get eliminated from the population, but only slowly. So populations naturally maintain mutational variation of this kind, not because selection acts at the unconventional level of groups, or even species (as Kalow and Kalant argue), but because mutations constantly arise, and only get removed slowly. If one such mutation turns out to confer a lucky advantage in a new situation (a blast of DDT, for example), then the population survives by good fortune—and again, strictly by ordinary Darwinian selection on organisms now fortuitously "blessed" with a suddenly crucial mutation.

Ironically perhaps, I suspect that this standard Darwinian explanation is probably correct and adequate in most cases of this sort. But Kalow and Kalant's alternative explanation—positive selection at the species level, based on enhanced variability as the feature subject to selection—does represent a possible and testable alternative. Genetic variability is a trait of populations, not of organisms—so if selection works by conferring greater geological longevity or higher speciation rates upon more variable species, then Darwin's process also operates at the species level, a form of "supra-organismic" selection much disfavored (and formerly strongly anathematized, but no longer as evidence and renewed respect accumulates) by strict Darwinians. It is surely preferable, and more within the spirit of science, to work with such interesting and testable[4] alternatives, rather than simply to assert by fiat, speculation, and a priori satisfaction, that natural selection on genes and organisms builds all complex form and pattern in the richly varied history of life.

[4]See E. Lloyd and S.J. Gould, "Species selection on variability," *Proceedings of the National Academy of Sciences*, 1993.

THE RIGHT SLOGGER

To the Editors:

In writing from memory about nineteenth-century cricket and the man once widely known as "The Champion" ["Making the Wrong Joyce," *NYR*, September 25], I conflated the cricketer W.G. Grace with the international conglomerate W.R. Grace & Company. Neither appears in *Ulysses* or its standard commentaries. Like James Joyce when writing of Dublin sportsmen and merchants, I relied unfortunately on memory instead of checking a print source. It was my intention to write parenthetically that "(Other rumors say W.G. Grace was the champion slogger.)" I trust that fans of the game will emend my slip.

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