HBES Newsletter

View from the President's Window - Fall 1999

The most testable concept in biology, Part 1

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My two pieces of bed-time reading late last night, each selected for its promise to deliver me from the burden of an unnecessary excess of consciousness, were a history of twentieth century physics, and the lead article from this month's *Linguafranca*, entitled "**OH MY DARWIN!** Who's the Fittest Evolutionary Thinker of Them All?" What I found striking in the history of modern physics was the fact that, repeatedly, the new theories that observation and logic had forced physicists to construct were far better - far more true - than even their most committed proponents believed. Time and time again, the theories were telling physicists things that they were unwilling to accept. Planck could take the first few logical steps toward quantum mechanics, but his allegiance to the norms of reasonability forged in classical physics prevented him from going further. Einstein tweaked with general relativity to eliminate the expanding universe that subsequently Hubble showed was actually there. Although in his paper on the photoelectric effect, Einstein was able to open the door so that quantum mechanics could move ahead into the territory that Planck had been unwilling to enter, Einstein himself could not subsequently accept fundamental features of quantum mechanics as it developed, and so was unable to participate in or contribute to the decades of rapid theoretical advances in physics that followed. "God does not play dice with the universe" said Einstein. His *reductio ad absurdum*, a thought experiment called the EPR paradox, was designed to show the incompleteness of quantum mechanics. Instead, recent tests bear out the bizarre predictions of the theory, rather than validating the premise that the principles that struck Einstein (and virtually everyone else) as paradoxical could not be built into the structure of nature. Similarly, despite the fact that accepted theory predicted them, most physicists once thought that black holes were preposterous theoretical entities lacking physical reality, whereas now most astronomers consider them key explanations for their observations. On issue after issue, logic operating on observation led the way ahead, dragging the few researchers able to dispossess themselves of their common sense grudgingly behind. As Bohr replied to Einstein, "Stop telling God what to do", a remark that implicitly recognizes that reality is truly strange, and not always likely to tailor itself to suit our intuitions.

One conclusion to be drawn is that successful sciences work in a way that is almost a mirror reversal of what social constructionists maintain: The cutting edge of scientific advance is not primarily the rubber stamp expression of what the dominant culture already thinks. Reality is consistently strange, and to discover that strangeness requires one to jettison much of one's culture. Successful science is not the projection of cultural prejudices, but the repudiation of them, and so science since the Copernican revolution has been one of the major forces for cultural change. Victorian belief was turned on its head, not ratified, by where physics led.

Another conclusion to take to heart is that scientists have been successful in proportion to the extent that they unburdened themselves of the pressures of cultural forces, accepted ideas, the normal bounds of what is considered reasonable, and their own emotional responses to theoretical possibilities, and instead paid attention to where logic and evidence led. Neither physics nor biology has been helped by our impulse to be "reasonable." Intuitive processes of social negotiation tempt us to believe that the truth about something must lie between "extremes", but the history of science does not bear this out. Far more often, the truth lies immensely far beyond what the most intoxicated and delirious of the radicals contemplates.

The world that Darwin and Wallace led us into is every bit as strange as quantum mechanics: a world of chemical replicators, billion year old cellular symbiosis, intrauterine siblicide, intragenomic conflict, kin-selected self-sacrifice, chemical computers, fish that change sex in response to social status, parasite-driven sexual recombination, brood parasites mimicking host offspring appearance, retroviral insertions breaking down species barriers - not to mention the direct causal linkage leading from trillions of individual selective events distributed over immense numbers of hominids in (for example) ancient east Africa, to an informational distillation reflected in nucleotides chained together into 23 immense molecules, to a neural structure that patterns the forms of our emotions and concepts to the replicative demands of the vanished past. No novel, no film, no philosophy, no deliberate dissident attempt to rebel against everything orthodox is remotely as outlandish as these discoveries. Despite repeated (and hilariously, hopelessly, inaccurate) claims that the Darwinian turn in the behavioral sciences is simply the projection of what our culture demands and rewards, the strange Darwinism that is transforming the scientific world is simply beyond the conceptual horizon of any existing lay culture, nonbiological scientific community, and even of most biologists.

The audience for public intellectuals, on the other hand, is this broader social world, and one way public intellectuals can become popular is precisely through exploiting this gap - that is, through pandering to the entrenched cultural biases, appetites, vested interests, and misunderstandings that are inevitable in those who have not had the opportunity to consider the scientific issues as carefully. From the vantage point of normality, the scientific forefront will often appear far-fetched, absurd, contrary to common sense, disturbing, hard to understand, and subversive of morality -- a sitting duck for exploitive misportrayal. Even worse, owing to the natural course of cultural epidemiology, those public intellectuals who succumb to this temptation will tend to be mistaken by the intellectual community at large to be leaders and theoretical powerhouses in their disciplines: Isn't it natural to anoint someone as the authority because he reassures you about what you already want to believe? Williams, Hamilton, and Maynard Smith, for example, remain relatively unknown outside of the evolutionary community, despite their transformation of our understanding of the world. In contrast, Steve Gould correctly and appealingly paints the biological world as full of marvels, but safe marvels, distant marvels - in his telling, strange realities do not wander among us or within us, nor influence our thoughts and our choices. Nothing too new or threatening here. The evolutionary community is fortunate to have such supremely gifted people as Richard Dawkins, Steve Pinker, and Dan Dennett, who can brilliantly synthesize their own contributions while at the same time performing the hard and subtle work of finding ways to bring nonspecialist readers into the eerie universe that professionals understand. But we also remain burdened with public intellectuals whose success is based on playing to and hence disinforming readers, thanks to the ongoing social demand for such figures.

This brings us to the article in *Linguafranca ("The Review of Academic Life")*, which unsurprisingly reflects the dominant prejudices endemic to the culture of academics. It is not without its high points, as when Steve Gould rebukes audience members who were leaving before his talk was over, by echoing Jesus to his disciples: "but most of these folks you have all the time. Me you only got for a little while." Still, the article is organized around the traditional and familiar criticisms that Gould and Lewontin have made of modern selectionist and adaptationist thinking. What is important to recognize is that these arguments have won the hearts and minds of large numbers of neuroscientists, biomedical researchers, anthropologists, psychologists, linguists, and even a substantial number of nonevolutionary biologists. Many in the intellectual world at large now have come to believe that the core biological idea of adaptation is a weak, nonempirical concept whose application involves unfalsifiable claims and subjective criteria, and whose use is therefore inherently scientifically suspect. Explanatory accounts of how the world acquired its present organization, such as are common in geology, astronomy, and physics, are now viewed with a knowing condescension when they appear in biology and the behavioral sciences.

It is easy to see that Gould and Lewontin have earned their reputation for sophistication, rigor, and intellectual depth through their own stringent refusal to make claims that are unsubstantiated, unfalsifiable, or just so stories. For example, many have heard of their argument that language and most other human cognitive abilities are side effects of the fact that our brain grew big for reasons that had nothing to do with the fitness consequences of those cognitive abilities. Inconveniently for anyone who might want to subject these claims to empirical test, Lewontin and Gould have left these reasons unspecified, but they have made clear why: They assert they simply cannot be reconstructed. In his recent article "The Evolution of Cognition: Questions We Will Never Answer," Lewontin shares his findings that "It might be interesting to know how cognition (whatever that is) arose and spread and changed, but we cannot know. Tough luck." Displaying his easy mastery of the technical details of modern neuroscience, Lewontin explains that our cognitive abilities are epiphenomena of "all those loose connections with nothing to do."

One can see advanced intellects from all over the world, pouring over the *Linguafranca* article, nodding slowly, sagely rubbing their chins, the corrugator muscles on their foreheads working as they struggle to absorb these profound ideas from the intellectual leaders of evolutionary biology. There are all those loose connections in the brain! They have nothing to do! Unlike in my stereo, loose connections in computational systems reliably produce highly organized information-processing, rather than noise as those feeble engineers, computer scientists, and probability theorists think! Recursion is a nonadaptive trait! Lewontin says so! And Lewontin also knows we cannot know! "I'm a man, and I don't go around screwing young girls," Lewontin says. "I'm human, and so I have to be explained." Ah, of course - if only those benighted adaptationists were aware of and addressed the question of behavioral variation, rather than foolishly claiming that every member of the species expresses identical behavior. With Lewontin pointing the way, perhaps they might even eventually hit on the idea that cognitive programs might have contingent procedures built into them that respond differently to different circumstances. In the far distant future, perhaps they might even test hypotheses about such conditional decision systems! Intellectuals, contemptuous of the abysmally low standards for testable claims prevailing among selectionist biologists must be impressed at how these ideas stack up in comparison. One can see that Popper himself would be heartened at this introduction of such scientific rigor into biology, and of the tight fit between cautious inference and careful observation.

Enough. That such comically crank ideas appear competitive to fair-minded third parties signals a problem that evolutionary biologists must analyze, face, and solve for the further development of our discipline. And leaving aside the separate problem of disinformation, at a fundamental level the fault is ours, for not making the theory underlying key scientific practices fully explicit, so that its objectivity can be appreciated. Adaptation is a conceptual keystone of Darwinism. After Darwin, George Williams, in particular, set us on the theoretical road toward the careful development of this idea, and many others, from Dawkins to Thornhill have made major contributions to our understanding of it. But if many still have difficulty appreciating the objective nature of the concept, then this is a sign that we need to go further toward developing formal measures that can be skeptically and consensually applied across the evolutionary sciences, producing potentially quantitative measures of adaptation for hypothesis-testing purposes. To practicing evolutionary scientists, this may seem tedious, cumbersome, and altogether unnecessary for their own understanding, but controversies end and sciences advance when the implicit is made explicit so that even those who are not central participants can follow the demonstrations being made. So, to maintain and broaden the scope of Darwinism, a set of measures needs to be developed that are so self-evidently and empirically unassailable that fair-minded individuals will be able to recognize the crankish positions without the enormous waste of time and resources that it takes today.

What is genuinely at issue? Although Lewontin, with his usual care, defines an adaptationist as someone who "assumes without further proof that all aspects of the morphology, physiology and behavior of organisms are adaptive optimal solutions to problems," he knows that all parties are agreed that the features of organisms are there because of some combination of selection, engineering byproducts of selection, and chance. So what is the debate actually about? For all of their wambling rhetoric about testability, falsifiability, and empiricism, Gould and Lewontin not only display no actual interest in such things, but manifest an active and desperate antipathy toward the development, acceptance, or recognition of methods that could reliably decide whether, in a specific case, something was the product of selection, an incidental byproduct, or a random outcome. The actual identity of their opponents, who they call adaptationists, are those who maintain that there are methodological and theoretical tools, and standards of evidence, that allow the investigation and reliable determination, in specific cases, of which category a trait falls into (and not the nonexistent set of people who believe that all traits are optimal adaptations). Against this, Gould and Lewontin adopt the position that "we cannot know."

So, what are the objective criteria that can be used to determine whether something is an adaptation? An adaptation is a set of features, in an organism, whose genetic basis was maintained and organized in the past because it reliably caused outcomes, in ancestral environments (continuing up until the parental generation), that led to the propagation of its genetic basis. How do you test whether something is an adaptation? George Williams' answer is that you determine whether there is a nonrandom coordination between an ancestrally recurrent adaptive problem (which includes the adaptation's environment) and the properties of the hypothesized adaptation, such that the adaptation solves the problem in a better than random way. The causal process that generates engineering byproducts is random with respect to function, as are the stochastic components of evolution that lead to random gene substitution. Accordingly, selection is the only force that modifies organismic design nonrandomly with respect to function, and it can be recognized by its nonrandom effects. Consequently, the only two explanations for a functional coordination are coincidence (which standard statistical tools are perfectly capable of calculating the probability of) and selection. To establish something as an adaptation, all one needs to do is to collect evidence that justifies the rejection of the hypothesis that the structure arose by chance (with respect to function). The "subjectivity" in the concept of adaptation - when made explicit - rests in the entirely standard question of where a scientific community wishes to set its statistical criterion for hypothesis rejection. If the concept of adaptation is to be considered subjective, then so is every other instance of hypothesis testing in every science. Just as in any other science, hypothesis-testing is based on statistical inference, and the probability of obtaining the observations that support the hypothesis if the hypothesis were true, as compared to the probability of obtaining the same observations if the hypothesis were not true.

This method involves comparing the problem-solving quality of a hypothesized adaptation with the problem-solving properties of other possible alternatives, sampled at random from an appropriate formal space of possibilities. If, like a key in a lock, the properties of the hypothesized adaptation are sufficiently better than random at solving the adaptive problem (in a way that can be computed in some fashion, given a consensually agreed on statistical criterion) then one is justified in concluding it is an adaptation. Hence, one can evaluate the likelihood that something is an adaptation (or evaluate the quality of an adaptation) by comparing it to members of the set of possible alternative configurations of phenotypic properties. Improbable outcomes are defined as belonging to a target set that is small relative to the set of possible outcomes, and specified independently of the observations - in this case, by an independent physical analysis of function. When the adaptation is too improbably functional to have arisen by chance, the chance hypothesis is rejected. Frequentist approaches to probability give an objective and quantitative character to computations of probability that can be useful in constructing formal approaches to the analysis of adaptations. Entropic processes are always acting to disorder ordered systems, so the tools in information theory can also be used to measure the information content or improbability of adaptations.

Why should we get so pretentiously and annoyingly formal about something so straightforward? Because the alien nature of Darwinism creates a wide market for claims that the basic theories and results in biology are weaker than those of other sciences, whereas in fact they are often far stronger.

How do you go about generating an appropriate space of possible alternatives, and objectively quantifying the process of sampling and comparing? There are many ways this can be done, depending on the exact nature of phenomenon being studied. For example, one might take a structural gene and compare it to the set of all alternative nucleotide combinations of the same length. (To limit the alternatives to the same number of base pairs is an arbitrary choice made to be conservative - that is, to cut against the hypothesis of adaptation - and for mathematical convenience. The actual space of alternatives is much larger.) If the gene's structure is simply the output of processes that are random with respect to function - that is, in which selection played no role -- then there is no reason to expect that substitution with a randomly generated stretch of nucleotides will degrade the organism's fitness any more often than it will increase it. But for virtually anything that is not junk DNA, we know from many converging sources the true situation: genes are, in design space, astronomically far from random with respect to function, and nearly all randomly generated substitutions would impair if not kill the organism. For those for whom this is not evident, it is quite possible to conduct such experiments in the laboratory with modern genetic techniques. Naturally occurring mutations are far more benign in comparison. As bad as many mutations are, they are far better than randomly generated nucleotide sequences would be, since mutations are created by starting with a functional gene, and introducing only some random changes into it. (It is also clear from such reasoning that neutral genes are not really neutral at all with respect to functionality when the true comparison set is introduced: neutral alleles are in fact highly fit alleles, representing only a tiny fraction of the set of possible nucleotide sequences - those that happen to be approximately equivalent in their high levels of fitness to other alleles present at the same locus.) Similar comparison sets can be computed for proteins by generating the set of all possible amino acid sequences of a specified length. Comparing random sequences with existing proteins, where this has been done, once again highlights that amazing degree of functionality present in biological systems: Rhodopsin, or hemoglobin, or the active elements of rattlesnake venom, or chlorophyll, or the proteins that allow the lens to be transparent - all occupy extremely narrow regions of protein space, and only a tiny subset of all possible substitutions would produce molecules that are remotely comparable in function. One doesn't need to create all possible proteins to do this. All you need to do generate random samples large enough for purposes of meaningful statistical comparison, and researchers in molecular biology have already, in effect, done this. Random features are recognizable by, among other things, the tolerance of the organism's propagation to their substitution, and functional features are recognizable by the organism's intolerance to their being modified.

Once one ventures outside the realm of individual genes or proteins, other property sets can be evaluated using other comparison sets, to explore adaptations involving larger anatomical structures, physiological processes, enzymatic pathways, the physical distribution of proteins in tissues, the timing of events in development, the logical organization of computational circuitry, or the patterns in behavior. One yardstick is the set of physically possible arrangements of chemical elements of equal mass to the adaptation in question, in proportion to the frequency of those elements in the organism's environment, or in the rest of the body of the organism - a vast and bleak set of inert alternatives. Skeptics might argue that this is an improper comparison, because we don't know the subset of these arrangements that could be realized within a biological system. But one cannot make such an argument about any arrangement already present in some organism on earth, and so the set of features present in the totality of organisms constitutes is a possible comparison set. Although arguments about phylogenetic constraints might be made against using this set, one can fall back to an even more restricted set: It is hard to deny that structures present in some other location of the organism's body are possible in some causal sense for the organism. So, another comparison set is supplied by randomly swapping around features of the human body (e.g., gastric acid for glial cells; eyes facing inward rather than out; tibia in the mitral valve) at whatever scale and according to whatever descriptive grid is consensually persuasive. Similarly, one can remove items, since the nonproduction of complex entities is always more likely than their production, and is easily attainable by knocking out their genetic basis. For example, if you turned all the hemoglobin in the body into water, or cytochrome c, or cortisol, or glucose, or any other chemical found in the body, you would die: a notable impairment, demonstrating that hemoglobin, out of the very conservative comparison set provided by the tens of thousands of chemicals produced in the body, is the product of selection. Going through the list of structural proteins, and doing such a thought experiment, one is forced to conclude that the constituents of the body are, by immense margins, improbably well-organized by selection. In almost all cases, their removal or their substitution by random alternatives would be harmful or catastrophic. Natural selection causes organisms to levitate at dizzying heights over the random disorder generated by entropic processes in the physical world. I suspect that, just as in physics, our theories are far more powerful than we think they are. And rather than being unfalsifiable, hypotheses about adaptation are exceptionally easy to falsify: It is easy to demonstrate that something is not well-organized for performing a specified function, and for the products of selection, it is equally easy to falsify the claim, using objective measures, that something is the product of chance.

In the next installment, I'll discuss the objective description of adaptive problems, optimality, appropriate comparison sets for behavior, neural circuitry, and other phenomena, as well as why it might be worth the bother of developing such seemingly sterile formal demonstrations. In the meantime, we are stuck with all those loose connections with nothing to do.