The Evolutionary Biology of Constraint

Limits: The Biological Reasons

For an evolutionary biologist, the primary theme of nature is its boundless diversity. More than a million species have been described, ranging from bacteria to toads to sequoias; among mites and nematodes alone many more than a million may remain to be discovered. As Robert L. Stevenson wrote:

The world is so full of a number of things,
I'm sure we should all be as happy as kings.

My use of boundless, however, is figurative. Diversity is stunning, but it is by no means literally boundless. In fact, the strong bounds that nature places on diversity provide our best starting point for a study of limits.

The history of evolutionary thought has been dominated by two major traditions for the explanation of such limited occupancy. In one, the adaptationist program\(^1\) that has prevailed under the "modern synthetic"\(^2\) theory of evolution, constraints are imposed primarily by working solutions: all parts of the cube can be reached, and unoccupied regions represent ill-adapted forms. In the second
tradition, long popular in continental Europe but virtually unknown in America today, constraints of architecture and history prevent the colonization of regions that might house designs of perfectly adequate function. I shall refer to this second tradition as structural integration.

In the two extreme formulations of these traditions, the direction of evolution is channeled either by adaptive requirements of local environments or by the nature of variation and the morphology of the system in which it arises. No one, of course, would embrace either extreme position in its entirety. The fundamentally adaptive nature of most major changes in evolution can scarcely be doubted. Similarly, even the most ardent selectionist does not view all directions of adaptive change as equally likely or even possible. Inherited morphology plays its role: no elephant will ever fly. The issue is a more subtle one of general attitude and first line of approach toward the solution of individual problems in research. The modern synthesist will ask, “What is this for?” or “Why is this the best form for such a function?” The “classical morphologist,” working within the tradition of structural integration, will ask, “How is this
Figure 2. The "cube of life" for coiled forms. Only the shaded areas (snails and clams) and two small unshaded areas on the right face (ammonites and brachiopods) contain abundant actual animals. Most of the potential cube is unoccupied by actual forms.

particular solution constrained by the architecture and inherited morphology of ancestors? What are the nonadaptive components arising from such constraint?"

If these were merely first lines of attack in a flexible system of alternatives, a preference for one or the other position might impose no great restraint on final conclusions. But the evolutionary biology of "why" is a frustrating area, full of speculation and uncertainty. Given the inventiveness of the human mind and a preference for adaptive stories, the failure of one specific proposal merely calls forth a substitute in the same mold. And the failure of all proposals usually elicits the response that there is as yet not enough known about the functional morphology or behavior of a specified organism to say why this particular structure is right for it. Thus, the adaptationist program contains no exit in most individual cases, even though any of its exponents would admit, in theory, that alternative styles of explanation exist.

The basic Neo-Darwinian buttress for the adaptationist program is the nature of genetic variability, the raw material of evolutionary change. For this program to work, the constraints of development, architecture, and inherited morphology must be erased, thus freeing organisms to travel an evolutionary
path to optimal form in an engineer’s sense. An approach to such effacement can arise if genetic variation is copious in extent, small (step by individual step) in magnitude, and occurs, without preferred orientation, in all directions (the meaning of random as it is used by evolutionists). If natural selection can choose from a large supply of raw material, packaged as tiny steps and available in all directions, the path of evolutionary change can be determined by selection leading to optimal adaptation. The direction of selection is not seriously constrained by the nature of variation.

Many of the central beliefs of modern Neo-Darwinism—such as the gradual nature of evolutionary change and the designation of evolution as a two-stage process of chance (random raw material) and necessity (natural selection)—flow from this view of variation as copious and ubiquitous raw material, and selection as a sole directing force. As Ernst Mayr, a major architect of the modern synthesis, put it, “The proponents of the synthetic theory maintain that all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transspecific evolution [across species] is nothing but an extrapolation and magnification of the events that take place within populations and species.”

But the adaptationist program may well be the most important consequence of this Neo-Darwinian vision—what August Weismann called the Allmacht of selection. In the adaptationist program, organisms are atomized into parts (called characters or traits), and these parts achieve their best configuration for local environments through the agency of selection. (No one denies correlation among parts by developmental and genetic linkage, but strict selectionists maintain that these correlations are weak relative to the power of selection to break them down.) The only major departures from part-by-part optimization reside in the concept of “trade-off.” The demands of an optimized whole may require some concessions among parts. The enormous antlers of the Irish elk, though useful in competition for mates, eventually drain too much energy from the whole organism or are too much of an encumbrance in moving and feeding. Thus antlers stabilize below an optimum size based on their utility alone. Yet such trade-offs are only among parts for the greater benefit to the whole; the entire organism still evolves to the best form it could possibly maintain.

To return to the subject of limits, the adaptationist program views all parts as existing “for” some function and as best designed to perform it (subject to the proviso that selection works upon entire phenotypes and that parts may adjust to optimize the whole). Evolutionary limits are imposed by engineering. Anything consistent with the architecture of inherited material can be built, but very few possibilities are realized because so few potential forms work well. Occupancy on the molluscan cube reflects the relatively few areas of efficient function. No bivalve, for example, can have too low a rate of increase in the generating curve, because the umbones of a symmetrical bivalved shell would then touch (or even interpenetrate) and the valves could not open (Fig. 3).

As for human intellect, the primary concern of this symposium, the adaptationist program leads us to the position that our basic mental capacities are direct adaptations “for” something of survival value in our evolution. An individual’s mental attributes are to be atomized and analyzed in terms of utility—in the Darwinian sense of maximizing copies of one’s genes in future generations. This tradition supports a growing and speculative literature—some of it down-
right silly and self-serving in an age of high royalties, some quite serious—on
the adaptive value of such reified traits as aggression, male dominance, and
xenophobia. The capacities that cannot be traced to pressures of selection in our
primal state—the ability to write operas, for example—are regarded as a hyper-
trophy of the genetic program (the role of music in social cohesion, for ex-
ample). The independent adaptive value of individual traits and the status of
these traits as best possible solutions (at least in our primal environments) are
the two keystones of the adaptationist program for its analysis of human
intellect.

Under this vision, limits arise for two major reasons. They are imposed
primarily by what the environment selected, not by what the organism's struc-
ture could produce. And, since our environments have changed so radically and
evolution is so slow a process, we may be stuck for the moment with traits (like
xenophobia) now injurious to global survival in a nuclear age.

Structural integration regards organisms as constrained and integrated
wholes. It does not deny the fundamental role of natural selection as an agent of

Figure 3. Why clams must maintain very high rates of increase of the generating circle. If
the generating circle increases slowly (as at the top, where its rate is 3.5—low values
imply slow increase), the shell coils several times before reaching its final size. If the rate
is very high (bottom, where its value is 10.0), the circle expands so rapidly that very little
coiling occurs before the shell reaches its final size. Since clams have two articulating
valves, they cannot be built with low rates of increase because the umbones (the beaks, or
tips, of the coil) would interpenetrate, and the shell could not open. You could not, for
example, place a second symmetrical valve under the form in the top figure.
evolutionary change, but it emphasizes two themes that the adaptationist program tends to neglect. One is that the possible routes of selection are channeled by inherited morphology, building material, and the amount and nature of variation itself. Though selection moves organisms down the channels, the channels themselves—rather than the paucity of well-designed outcomes—impose primary constraints on the direction of change. The second is that selection on one part of a structure may impose a set of correlated and nonadaptive modifications on other parts of an integrated body. Many features, even fundamental ones, may be nonadaptive (though not, to be sure, strongly inadaptive) either as developmental correlates of primary adaptations or as “unanticipated” structural consequences of primary adaptations themselves.

Let me cite an example that contrasts the reasons for limits under the adaptationist program with the view of structural integration. Recently a colleague, a noted follower of the adaptationist program, assured me that land vertebrates had four legs because this number represented optimal design for locomotion of a bilaterally symmetrical, elongate body under gravitational conditions. Scarcely believing my ears, I reminded him that ancestral fish had four fins, the homologues of our arms and legs, for reasons quite unrelated to their later invasion of the land. We had inherited this configuration; fortunately (for we would not be here otherwise) it worked well. Four legs may be optimal, but we have them by conservative inheritance, not selected design. Other options are simply not available among the variations spontaneously occurring within the vertebrate body plan. (Reduction to two might not have discombobulated the developmental plan—since evolutionary losses are accommodated more easily than gains—but Orwell’s pigs were wrong, or at least making a social rather than a biological statement.)

The adaptationist program relies on the belief that genetic variation is copious, small in extent, and available in all directions. Structural integration must therefore hold a different view about genetic variability. Nearly one hundred years ago Francis Galton used a striking metaphor to describe this alternative view by arguing that evolving objects are not spheres (as in the adaptationist program) but many-sided polyhedrons. The sphere evolves by rolling and can go in any direction through all gradual intermediate stages. The polyhedron rests on one face and can move only in directions represented by adjacent stable faces; its motion, moreover, must be per saltum rather than by insensibly graded steps. Constrained direction and discontinuous evolution arise as limits imposed by the inherited structure itself—the form of the polyhedron—not as a restriction of natural selection. Selection determines whether or not the polyhedron shall (metaphorically) topple over, and in which of a few possible directions it shall move, but the primary constraints are prior and structural.

Of the many reasons for structural constraint in complex organisms, the delicate orchestration of embryonic development must rank first. For 300 million years, embryos of land vertebrates have continued to form, and then to lose or to convert into other structures, the gill slits (and their complex pattern of circulatory tubes) that persist, for obvious functional reasons, into the adult stage of ancestral and modern fishes. This complex and circuitous pathway works well enough in building a human baby, but no engineer starting from scratch would have ordained such a design. It is not an adaptation but a reflec-
tion of how difficult it is to alter the early stages of development when complex embryonic structures are differentiating in a hundred directions, all dependent on prior configurations. Radically new and improved designs can be conceived, but nature provides no way to get there. The adaptationist program is an unwarranted extrapolation from minor adaptations (responses to small changes in local environments) to major overhauls in design. These minor adaptations are "easy" changes in late stages of ontogenetic development. You can repaint your car any color you wish, but this exuberance of choice is no model for its potential conversion to solar propulsion.

Minor adaptations are multifarious, but major reorganizations are rare and strongly constrained by inherited structure. Moreover, major alterations in external form are often based on small underlying genetic changes. These changes can have substantial impact on adult phenotypes because they operate by altering rates of development early in ontogeny, with cascading effects throughout later growth. The stability of integrated systems may be so high that even major changes of form imply little alteration of the underlying developmental program. Evolution is, as François Jacob perceptively stated, a tinkerer, not a noble architect. Many of her most impressive products use only slightly reconstituted genomes, not fundamentally new blueprints.

We ourselves represent a striking example of this conservative principle. King and Wilson have reported remarkably small overall genetic differences between humans and chimpanzees. We share more genes than any measured pair of species within the same genus (though we are conventionally classified in different genera) and are even more alike than most pairs of so-called sibling species (those that are virtually indistinguishable in morphology). Our substantial overt differences in form and behavior are probably for the most part results of relatively minor genetic changes that have slowed down developmental rates in humans, leaving us, as adults, strikingly similar in many ways to the juvenile stages of other primates.

Under the adaptationist program, limits to human intellect are imposed by the paucity of good designs and by the environments that established selective pressures for specific traits. In the view of structural integration, the limits reside primarily in the fact that we are, fundamentally, only slightly rebuilt apes. Most of the traits that we like to regard as quintessentially human (and tend to view as direct acquisitions "for" their current function) are inherited structures whose basic adaptation may have been set in distant ancestors. We may reconstitute these structures for different functions, but their basic design must constrain us in ways we scarcely understand.

Much of our hubristic intellectual history has involved a search for signs of our adaptive uniqueness. T. H. Huxley impaled Owen for his claim that only human brains contained a hippocampus minor, and that the secret to our godliness must lie there, for Huxley had found this structure in all the great apes as well. More recently, we have located (perhaps properly) human uniqueness in language and abstract conceptualization, and have regarded cerebral asymmetry and some aspects of cerebral localization as its physical sign—and, presumably, as a direct adaptation in humans "for" these traits. But apes display a similar asymmetry, and some even have a lump where Broca's area is found in humans. These features may be fundamental in human evolution, but they are
reconstitutions of something that existed for other reasons (if for any direct reasons) in apes, not novel atomized and optimized attributes of *Homo sapiens*.

**Constraints and Consequences**

This revised notion of limits may seem more discouraging and inexorable than the constraints based on good design advocated by the adaptationist program. Are we really slightly reconstituted apes, constrained by structures built for roles only loosely related to our needs, and so tightly integrated in development that major pathways of potentially fruitful change are foreclosed? Would we not rather view ourselves as bodies composed of numerous parts, each directly designed for its immediate role?

Paradoxically perhaps, I regard the view of structural integration as not only closer to our current understanding of evolution, but also freer of a truly depressing notion of limitation. Under the adaptationist program, each major mental attribute is either a direct adaptation for something related to (or at least once related to) survival or a hypertrophy of the adaptation and, therefore, still based on and constrained by it. At its worst, the adaptationist program represents a kind of vulgar Panglossianism that relates everything we do to a material notion of utility. But the alternative view that I advocate here, with its focus on nonadaptation, frees us from the need to interpret all our basic skills as definite adaptations for an explicit purpose. We inherited, under great constraint to be sure, an ancient structure with minor modifications. Those modifications may have been adaptations for specific functions, but they also engendered a host of nonadaptive consequences. Our large brains, for example, may be minor reconstructions, based on a prolongation of rapid fetal growth rates to later stages of ontogeny. But the magnitude of structural change may bear little relationship to functional impact, while under the adaptationist program we have to view each impact itself as separately selected. A much bigger brain may be able to do all manner of wondrous things bearing no relationship to the initial adaptive reasons for increase, just as a computer designed only to issue the company's paychecks might stalemate me perpetually in tic-tac-toe. We need not view *Don Giovanni* as the hypertrophy of some primal instinct but as an important, nonadaptive byproduct based on a general level of complexity attained for other reasons.

Constraints and consequences. Under the adaptationist program, structures are expressly and optimally designed for their functions. What else can they do? Under structural integration, every constraint entails a suite of nonadaptive consequences that might be commandeered later for some (perhaps novel) function. The stricter version of constraint also implies a greatly extended flexibility in evolution. Constraints and consequences.

We may illustrate this paradox with a famous story from the history of evolutionary thought, usually told backwards because raconteurs do not identify it correctly as a debate about adaptation. Alfred Russel Wallace distressed Darwin greatly because he balked at the threshold itself: he applied natural selection consistently to all nature but refused to ascribe the human mind to its operation, opting instead for divine intervention in this case alone. Darwin, aghast, wrote: "I hope you have not murdered too completely your own and my child."
This story is usually told as an example of Wallace's cowardice and wishy-washy support for natural selection compared with Darwin's courageous consistency. In fact, this interpretation must be inverted. Wallace was the rigid selectionist of Darwin's era; Darwin himself was a pluralist (who believed, to be sure, in the primacy of selection, but who understood and emphasized the theme of nonadaptive consequences). Wallace applied his rigid adaptationist program to the human mind and came up short because the program itself is flawed, not because he felt at all unsure about the power of selection.

Wallace was one of the few nonracists of nineteenth century science. He believed that "primitive" humans possessed a brain every bit as good as his own. Yet, as a cultural chauvinist he did not doubt the superiority of British ways. If selection can only build for immediate use (the adaptationist program), how could it construct a brain capable of Victorian refinement in a savage who neither needed nor developed such haute culture. Wallace wrote:

A brain one-half larger than that of the gorilla would . . . fully have sufficed for the limited mental development of the savage; and we must therefore admit that the large brain he actually possesses could never have been solely developed by any of those laws of evolution, whose essence is, that they lead to a degree of organization exactly proportionate to the wants of each species, never beyond those wants. . . . Natural selection could only have endowed savage man with a brain a few degrees superior to that of an ape, whereas he actually possesses one very little inferior to that of a philosopher.12

Thus, the Lord himself must have stepped in to award the savage his remarkable capacity.

Darwin, of course, did not deny that the brain had evolved "for" some set of functions; in that sense, he attributed its size in humans to natural selection. But he also understood that original function does not determine potential use. The brain is, after all, a complex machine. Evolved "for" one function, it can perform so many others as nonadaptive consequences of its architecture. God may be glorified in the B-Minor Mass, but the majesty of its opening Kyrie does not prove His existence.

As a methodology the adaptationist program has been most detrimental in the subtle way it discourages any emphasis on structure and its consequences. If every overt action is an adaptation, we ask "why" and focus on the construction of scenarios to explain utility. We do not pay much attention to structure, since optimal forms can always be made; the key question becomes, Why this form rather than another, not, What range of things can this form do? But if we switch our principal concern to the nonadaptive consequences of inherited structure in systems of change that affect all parts in integrated and unanticipated ways, then we must analyze the structures themselves. We must solve some basic riddles of neurology if we wish to understand why operas can be written, not only talk about the adaptive value of music. (We must also remember that basic answers to why they are written have little if anything to do with such reductionistic styles of science.) We may illustrate this important theme about structure and its consequences with an amusing contretemps about fingerprints between Francis Galton (no fan of the adaptationist program) and Herbert Spencer (a devoted zealot): Galton writes:
Much has been written, but the last word has not been said, on the rationale of these curious papillary ridges; why in one man and in one finger they form whorls and in another loops. I may mention a characteristic anecdote of Herbert Spencer in connection with this. He asked me to show him my Laboratory and to take his prints, which I did. Then I spoke of the failure to discover the origin of these patterns, and how the fingers of unborn children had been dissected to ascertain their earliest stages, and so forth. Spencer remarked that this was beginning in the wrong way; that I ought to consider the purpose the ridges had to fulfill, and to work backwards. Here, he said, it was obvious that the delicate mouths of the sudorific glands required the protection given to them by the ridges on either side of them, and therefrom he elaborated a consistent and ingenious hypothesis at great length. I replied that his arguments were beautiful and deserved to be true, but it happened that the mouths of the ducts did not run in the valleys between the crest, but along the crests of the ridges themselves.\footnote{13}

A Brief Note on External Limits

Thus far, I have only discussed limits imposed by the structure and development of organisms themselves. I have tried to emphasize a paradoxical theme that I call constraints and consequences: a view of structural constraint far stronger than that permitted under the conventional adaptationist program actually implies in its concept of prevalent nonadaptation, a freedom and potential for design far surpassing that implied by the Panglossian view that each separate structure is designed explicity (and best) for its function.

Other structural limits must be imposed externally by the nature of environments and ecological space. I refer not only to the obvious adaptive restrictions of specific habitats (air is not dense enough to support heavy creatures in flight). Rather, I wish to emphasize the more general principle of potential limitation upon the number of coexisting species in a region—what ecologists call the principle of “limiting similarity.”

Environments cannot house an unlimited number of species. Although “the world is so full of a number of things,” that number is not infinite. Limits based on organic design (as discussed in the previous sections) are central to our consideration, but the nature of external space imposes its constraints as well. The ecological barrel can hold just so many apples.

An old principle of ecology called “competitive exclusion” holds that no two species can occupy exactly the same niche in an ecosystem, for if two species shared all resources and used them in the same way, one would almost surely hold an edge in efficiency, however slight. Even the tiniest advantage would, in time, lead to domination and eventual elimination of the less efficient species.

Stated in this way, competitive exclusion is an unsurprising truism. But it does lead, by implication, to a more interesting question. How many species may be packed into a single ecosystem? How similar can two species be before shared resources overlap sufficiently to guarantee the elimination of one. This degree of closeness is called limiting similarity.

Among ecological concepts that are easy to conceptualize and extraordinarily difficult to use, limiting similarity stands out. How can we measure the tightness of packing among species in an ecosystem? The general problem is far from resolution, but we have obtained some interesting empirical hints in very simplified circumstances. We can search for regularity in packing among species known to share single, measurable resources (particle sizes of food among seed-
eating birds, for example). When resources can be quantified in such a linear way, we may establish "resource axes" and plot the ranges of utilizing species on them.

In a famous article, G. Evelyn Hutchinson noticed that coexisting species, competing along at least one resource axis at the same level in a food web, often differed from each other in average body length by a factor surprisingly close to 1.26—the cube root of 2. (Since volume is length cubed, the 1.26 length ratio implies a doubling of weight between each pair of coexisting species.) The study of limiting similarity is still in its infancy, and numerology is always a dangerous game, but I can't help wondering whether this difference by doubling—a regularity that has shown up again and again since Hutchinson published his article—represents some fundamental aspect of limits to the closeness of spacing among objects of similar function.

Indeed, ecologists Henry Horn and Robert May have found the 1.26 ratio in an impressive series of sets designed to function either together or for similar purposes—a consort of recorders, graded wheel sizes in a manufacturer's series of tricycles and bicycles, and in a set of skillets. The one apparent exception they found may be interpreted as further confirmation. The four stringed instruments of a modern orchestra increase too rapidly in length (1.8 for cello to viola and 1.7 for bass fiddle to cello). But they were not designed to be played together as a consort. A newly designed violin consort, a set of eight matched instruments built to be played together by a musician with no knowledge of Hutchinson's ratio, average 1.267.

A Longer Note on Cultural Limits

I stood in the Cathedral of Pisa last year, trying to read the inscription under Christ's feet in the large mosaic of the apse. I stared at it for half an hour and could make no sense of it, because one phrase talked of a lion and a dragon, while the other seemed to refer, quite reasonably, to an apse (where the mosaic stood) and a basilica (a style of church, if not, technically, the form of Pisa's Duomo). Finally I saw the small serpent squashed under Christ's foot, and I remembered the 91st Psalm: super aspidem et basiliscum ambulabis et conculcabis leonem et draconem (you shall walk upon the asp and basilisk and shall trample under foot the lion and dragon). During what I had regarded as a half hour of raw, objective empiricism, I had at least twenty times reversed the p and s of aspidem and had failed to notice the second s in basiliscum.

Anyone could tell similar stories of the channeling of perception by expectation. And if the effect of a momentary fixation can be so strong, what of the powerful and pervasive influences of culture and class? I was assigned the task of outlining some basic approaches to biological limits and have therefore devoted most space to this subject. Yet I believe that the social and cultural limits on thought and perception are so strong, prior, and pervasive, that the deeper and more purely biological limits rarely display themselves in any definite way.

The cultural conditioning of thought plays a particularly important role within science, largely because our positivistic traditions deny its impact. Scientists (even after reading T. S. Kuhn or even P. K. Feyerabend) tend to view the
expunging of cultural prejudice and strict adherence to an objective scientific
method as the marks of success or at least of rectitude. And he who denies the
existence of a potent influence is least free from its effects. Scientists should be
required to study the history of science not only for general humanistic reasons,
but primarily because cultural influence is so hard to detect in medias res, yet
easier to identify when the culture itself has been superseded. (Of course, the
historians would also have to combat the positivistic prejudice that science
marches to truth by shucking superstition and the notion that clear cultural
influences in the past do not imply the continuing influence of such shackles.)

The history of many entire subjects reflects virtually nothing about the em-
pirical world, and records instead a changing set of social influences (consider
such fields as the study of group differences in intelligence, where the ratio of
data to social importance is so low). The identification of prior prejudice in the
“scientific” study of race is scarcely news, but I have approached the subject in a
somewhat different way. I have reanalyzed the quantitative procedures and
data—not just the interpretations—used by nineteenth century craniometri-
cians and twentieth century mental testers, and I have consistently uncovered
extensive cases of unconscious finagling and manipulation of data.16 (Conscious
fraud exists as well, but limits imposed by cultural presupposition reside in the
extensive massaging of data that people perform without realizing what they are
doing.)

Such overt and specific prejudice is relatively easy to identify and even to
expunge. Far more subtle, deeper, and pervasive are the general attitudes that
any age regards as obvious, logical truth. My own field of paleontology has been
constrained to the point of direction by deep beliefs in ideas of linear progress,
gradual change, and causal determinism—all cultural prejudices rather than evi-
dent truth, and all incapable of encompassing the entire fossil record. I have
been particularly struck by how ideas of progress, hierarchy, and linear-ranking
surface again and again, in field after field, to constrain the arrangement of
messy data into a unilinear, ascending hierarchy, with strong remaining
“disorder” regarded as an epiphenomenal disturbance of the primary rank, a re-
sidual, or the mark of a second and less important process causing lateral
ramification. Thus, Charles Spearman identified clear evidence for cohesion
among groups of mental tests (arithmetic and verbal clusters, for example) as
mere “disturbers of g,” his favored concept of general intelligence. And
Lamarck a century earlier forced the ramifying tree of life into a primary com-
ponent of rising complexity, and ranked everything that didn’t fit as a secondary
and tangential adaptation branching from the main ladder.

But even these prejudices, however deep and subtle, can be identified. What
about constraints and limits that arise because solutions require metaphors or
modes of thought that have not yet been conceptualized at all? Here history
must aid us, for we cannot analyze the present. In the great eighteenth century
embryological debates, for example, preformationists argued that a homunculus
must exist in the egg or sperm, and that development must represent an unfold-
ing of this preexisting structure. Epigeneticists argued that complexity arises de
novo as a result of some unknown external directing force. Charles Bonnet, ad-
mitting that no one had seen a homunculus with the poor optics then available,
declared that preformation represented “one of the most beautiful victories of
pure reason over the senses.”17 It just had to be true. Order and complexity
cannot arise from nothing. The structure must exist from the start. He was right, of course: information for the final result must somehow be contained in the egg. But he was wrong in conceiving this necessary information as the preformed parts themselves. We now know that it exists in the form of coded instructions within the fertilized egg. But the eighteenth century had no common metaphor for coded instruction. The pattern-weaving machine had been invented, and the music box might have served imperfectly, but an age without computers (not to mention player pianos) must be excused for not conceptualizing this happy resolution that rendered both sides right—epigenesis for its observation of increasing complexity, preformation for its insistence that information for the final structure must "be there."

Scientists are such a miserable lot of unreconstructed positivists! The original version of this article ended here, with the clear implication that culture acts only to constrain science and that scientists must study it in order to recognize the impediment. Then, at the Emory Symposium, Meredith Skura gently pointed out to me that I had made a surpassingly strange argument. I had spoken bravely of constraints and consequences when discussing the limits imposed by organic architecture and development. As my major claim I had argued that structural limits also display a flip-side of liberation: nonadaptive consequences pregnant with flexibility for responding to unanticipated environmental changes (while the adaptationist program views every structure as directly optimized and endowed with little "play"). Then, forgetting my own claim, I came to culture and discussed it only as an impediment. In a way, I have proved my point at my own expense. I was so caught in the ethos of science (even though I have tried, consciously, to combat this particular aspect of it), that I could only discuss culture as a veil before external truth. I failed to apply to culture my own argument of constraints and consequences. Dr. Skura reminded me, in short, that culture facilitates as well as constrains. Darwin, a century earlier, would have been regarded as a fool or madman (except that he would never have developed a theory that depended so heavily on Adam Smith's economics and Malthus's demography, to mention just a few facilitating sources from his general intellectual culture; and, like the unanticipated consequences of organic architecture, the facilitating aspects of Darwin's culture did not exist in order to call forth the truth about organic history!).

The pervasive influence of culture upon science is depressing only to those who still advance the discredited myth that knowledge so constrained is tainted and impure. I am no relativist. I share the metaphysical faith of all my colleagues that an external reality exists, and that it teems with definite answers if only we could know them. But cultural constraint, though it forces us to peer through a glass darkly, does assert the unity of science with all creative human activity. And as a practical matter it encourages greater humility and self-scrutiny. The identification of cultural limitation should be a primary activity of any scientist's searching. We might begin by suspecting that the conjunction of a conference on limits with the late 1970s is, unhappily, no accident.

References

Julian Huxley coined this name in 1942 for the modern version of Neo-Darwinism, still a reigning orthodoxy among evolutionists, yet (in my opinion) on the verge of crumbling. It synthesized Mendelian genetics with the classical subjects of natural history by identifying small-scale Darwinian random variation with particulate micromutations of Mendelian character.


Such reductions have, of course, occurred in the evolution of vertebrates, but no lineage has gained appendages. Many vertebrates move on two legs, but use their forelimbs for other functions. A few, like *Tyranosaurus* and the kiwi, have reduced their forelimbs so much that they may not be (or have been) functional at all. Snakes, for obvious reasons, have no limbs at all.


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This general process, a slowdown in rates of somatic development, is called neoteny. In addition to its probable role in human evolution, it may be responsible for the origin of many major animal groups. See Gould, *Ontogeny and Phylogeny*.


